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Created in 1849, the United States Department of the Interior—a department of conservation—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

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Created in 1849, the Department of the Interior—America's Department of Natural Resources—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

IDENTIFICATION OF NEW ENGLAND YELLOWTAIL FLOUNDER GROUPS

By FRED E. LUX, *Fishery Biologist*, BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

Data from yellowtail flounder marking experiments, fin ray counts, and the incidence of infestation by trematode parasites are reported. A distinguishable, although not completely discrete, group of yellowtail

was recognized on each of three adjoining New England grounds: a southern New England group, a Cape Cod group, and a Georges Bank group.

A study of the subpopulations of the commercially important yellowtail flounder, *Limanda ferruginea*, was undertaken to identify clearly the exploited yellowtail groups found off New England. Data from marking experiments, fin ray counts, and the incidence of infestation by trematode parasites were used for the purpose. Results of this study are reported here.

Fisheries workers have sometimes applied different meanings to terms that are commonly used to identify fractions of fish populations. To avoid misunderstanding, the terms used in this paper are therefore defined here. Definitions for "population" and "group" given by Marr (1957) are:

Population.—A population of fish includes all individuals of a given species when there are no subspecies or, if there are subspecies when their distributions are not discrete.

Group.—A group is a fraction of a population with distinctive characteristics, the nature of which (phenotypic or genotypic) has not been determined.

Under these definitions, yellowtail found off New England are members of the same population since there are no recognized subspecies. Yellowtail groups are the presently distinguishable parts of this population.

NOTE.—Approved for publication September 29, 1961.

YELLOWTAIL FLOUNDER FISHERY

Large-scale exploitation of yellowtail began in the 1930's. Annual United States landings rose to a peak of 70 million pounds in 1942 and then declined to a low of 12 million pounds in 1954. In more recent years landings have averaged about 30 million pounds. About 70 percent of the catch is landed at New Bedford, Mass., with other southern New England ports accounting for a large part of the remainder.

Royce, et al. (1959) defined three principal yellowtail fishing grounds fished by United States vessels (fig. 1). The southern New England ground covers the area from off eastern Long Island to south of Nantucket Island (statistical subareas XXII O, Q, R, S, and area XXIII). The Georges Bank ground is the large shoal ground east of the southern New England ground (subareas XXII H, J, M, and N). The Cape Cod ground, the least important of the major grounds in terms of catch, is found off the tip of Cape Cod and extends northward along the Massachusetts coast (subareas XXII E, and G).

MARKING EXPERIMENTS

In the years 1942-49 Royce, et al. (1959) marked 2,597 fish in 14 different lots on the three principal fishing grounds. They obtained 377 recoveries. Movements were generally found to be within the grounds, but there was also some

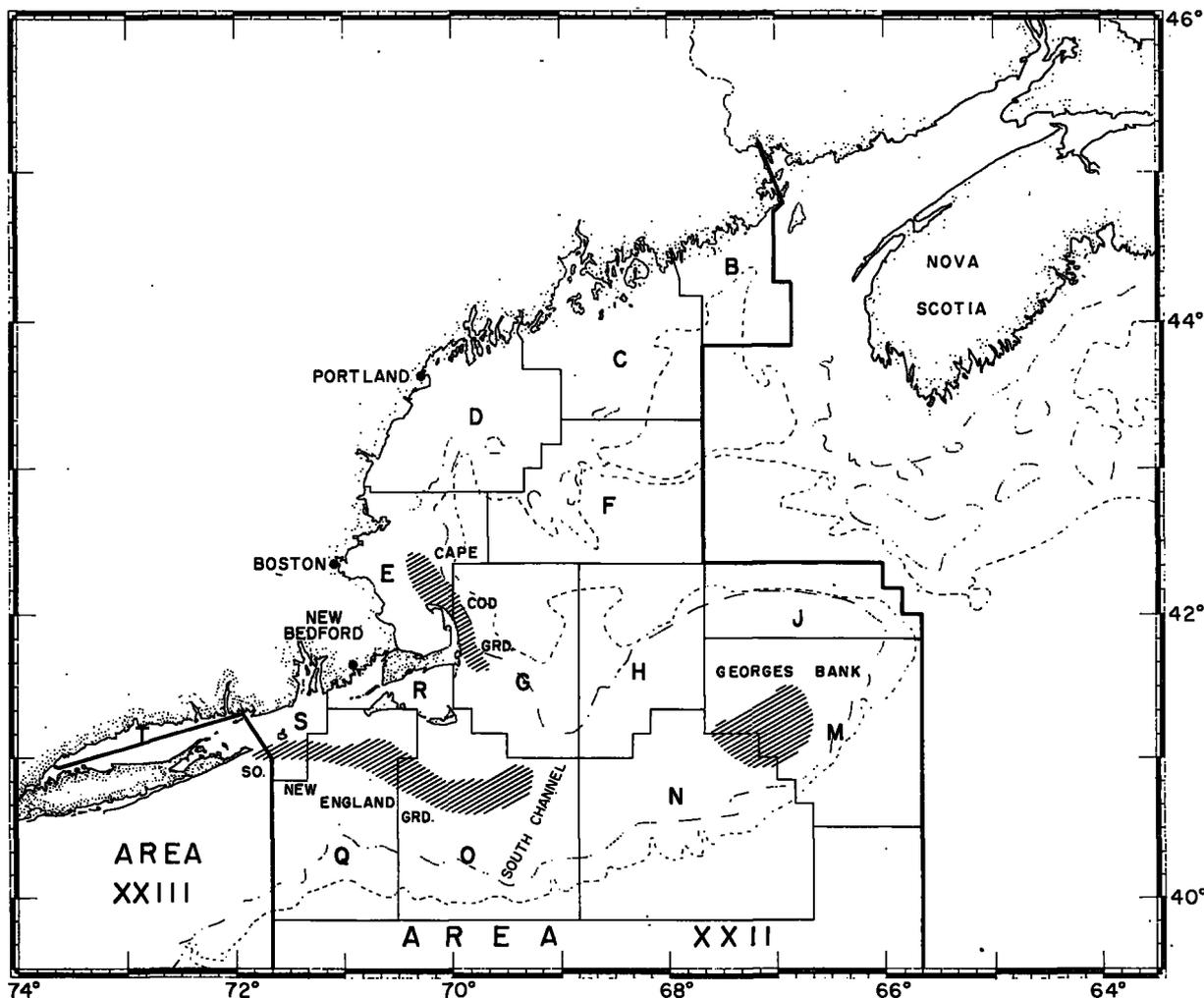


FIGURE 1.—Chart of the New England fishing areas showing the three principal grounds where yellowtail flounder are caught. Depth contours are for 50 and 100 fathoms. Statistical areas are those adopted by the North American Council on Fishery Investigations (Rounsefell, 1948).

interchange of fish between the grounds. From these results and the distribution of fishing effort, they concluded that yellowtail flounder on each of the fishing grounds were relatively separate, but that there was some intermingling between groups.

In this study 1,800 yellowtail in 12 lots were tagged and released on the three principal grounds to obtain further information on yellowtail movements and the degree of separation of fish on these grounds (table 1). There were 431 recoveries from these lots.

Recapture locations obtained from the fishermen usually were given in the form of Loran bearings for the general area of fishing operations. These

locations and areas where tagged fish were released are reported in table 1 by subarea, using statistical subareas (fig. 1).

METHODS

The fish, aside from lots 7 and 8, were tagged from catches of commercial otter trawlers. Lots 7 and 8 were tagged from research vessel catches. A plastic Petersen disk, $\frac{1}{16}$ inch in diameter, was attached to each side of the nape of the fish with a stainless steel pin pushed through the nape. One disk carried a serial number; the other, instructions to the finder. Sex of each fish and its total length in millimeters were recorded at time of tagging. Sex was determined by holding the

fish before a light. The ovaries extend posteriorly from the intestinal cavity along the ventral interhaemal spines and appear as a dark area. Since

there is only a very slight posterior extension of the testes, no dark area is apparent in this region of males.

TABLE 1.—Areas of tagging, dates of tagging, numbers tagged, and numbers recaptured, by area and calendar quarter following tagging, for 1955 and 1957 yellowtail flounder marking experiments

[Capital letters indicate statistical subareas]

Period of recovery	Number of fish recaptured in area											Unknown	Total		
	XXII														
	E	G	H	J	M	N	O	Q	R	S	XXIII				
Lot No. 1: 1 fish tagged April 8, 1955, XXII Q															
July-September 1956.....						1									1
Total.....						1									1
Lot No. 2: 93 fish tagged April 21, 1955, XXII S															
April-June 1955.....										3			4	7	
July-September 1955.....					1								1	1	
October-December 1955.....							1	2					1	4	
January-March 1956.....										2				2	
April-June 1956.....							1							1	
October-December 1956.....								1			1		1	3	
January-March 1957.....													1	1	
April-June 1957.....							1							1	
October-December 1957.....													1	1	
April-June 1959.....								1					1	1	
October-December 1959.....									1					1	
Total.....					1		3	4		6			8	22	
Lot No. 3: 25 fish tagged April 28, 1955, XXII Q															
April-June 1956.....													1	1	
July-September 1956.....	1													1	
January-March 1957.....								1						1	
Total.....	1							1					1	3	
Lot No. 4: 27 fish tagged May 9, 1955, XXII S															
May-June 1955.....											3			3	
October-December 1955.....								1						1	
July-September 1956.....		1												1	
October-December 1956.....													1	1	
Total.....		1						1			3		1	6	
Lot No. 5: 126 fish tagged June 22-24, 1955, XXII O															
June 1955.....							1							1	
July-September 1955.....							1							1	
October-December 1955.....					2		3	4					3	12	
January-March 1956.....								2					2	6	
April-June 1956.....							1			1	2		2	4	
October-December 1956.....							2						1	3	
January-March 1957.....							1	1						2	
July-September 1957.....													1	1	
October-December 1957.....							2	1						3	
January-March 1958.....													1	1	
October-December 1958.....							1							1	
Total.....					2		12	8		1	2		10	36	
Lot No. 6: 24 fish tagged July 23-26, 1955, XXII S. (No recaptures reported.)															
Lot No. 7: 7 fish tagged February 14, 1957, XXII Q															
July-September 1957.....								1					1	2	
October-December 1957.....													1	1	
July-September 1958.....					1									1	
April-June 1959.....													1	1	
January-March 1960.....								1						1	
Total.....					1			1	1				3	6	

TABLE 1.—Areas of tagging, dates of tagging, numbers tagged, and numbers recaptured, by area and calendar quarter following tagging, for 1955 and 1957 yellowtail flounder marking experiments—Continued

[Capital letters indicate statistical subareas]

Period of recovery	Number of fish recaptured in area												Unknown	Total	
	XXII														
	E	G	H	J	M	N	O	Q	R	S	XXIII				
Lot No. 8: 45 fish tagged February 26, 1957, XXII S															
July-September 1957					2			1	1						4
October-December 1957								3	1						4
January-March 1958									3						3
April-June 1958								1							1
July-September 1958					2										2
October-December 1958								1							1
January-March 1959								1							1
April-June 1959								1							1
July-September 1959								1							1
January-March 1960								1							1
Total					4			9	5						18
Lot No. 9: 447 fish tagged April 4 and April 12, 1957, XXII S															
April-June 1957		1							6			13			20
July-September 1957								7	5					1	13
October-December 1957		1						10	2						13
January-March 1958		1							1			4	8		18
April-June 1958									6	1		3		1	11
July-September 1958								2							2
October-December 1958					1			4	1			1			7
January-March 1959								4	2					1	3
April-June 1959									2						2
July-September 1959		1							2						2
October-December 1959									2						2
April-June 1960												1			1
Total		3			1			25	25	1		22	8	3	88
Lot No. 10: 547 fish tagged May 1-4, 1957, XXII G															
May-June 1957	3	79												4	86
July-September 1957	11	4													15
October-December 1957	4	5												3	12
January-March 1958	6														6
January-March 1960		1													1
Total	24	89												7	120
Lot No. 11: 28 fish tagged May 5, 1957, XXII G															
May-June 1957		6												1	1
July-September 1957		1													1
October-December 1957		1													1
July-September 1958														1	1
Total		8												2	10
Lot No. 12: 430 fish tagged August 21-23, 1957, XXII M															
August-September 1957				1	31									3	35
October-December 1957				1	12									2	15
January-March 1958					2					2			1		5
April-June 1958					7										8
July-September 1958				1	37	1								1	40
October-December 1958				1	5	1			1						8
January-March 1959					1										1
April-June 1959				1											1
July-September 1959					3	3								2	8
Total			2	4	98	5	1	2			1			8	121

Nearly all fish marked on the southern New England and Cape Cod grounds were tagged during the spawning season in the spring. It is therefore probable that relatively pure groups were tagged on those grounds. On Georges Bank, the fish were tagged during August, considerably after

the spawning season, so these fish may not have been of a pure Georges Bank group.

A reward of one dollar was paid for each returned tag, and after May 1958 an additional dollar was paid if the fish was returned with the tag. Most of the recovered tags were recaptured during the

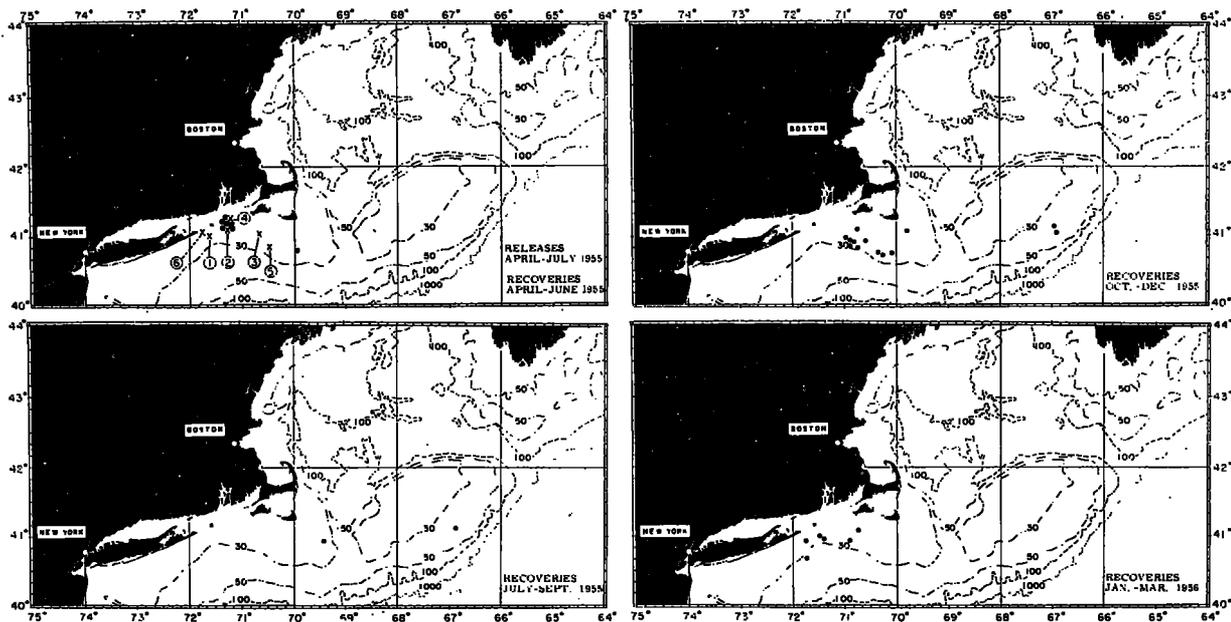


FIGURE 2.—Tagging on the southern New England ground, April–July 1955, lots 1 to 6. (Locations of releases indicated by X's; recoveries, by calendar quarters, indicated by dots.)

first 3 years following the release. All were taken by otter trawlers.

Tags and tagged fish were recovered mostly by fishermen or workers unloading catches, who gave them to Bureau of Commercial Fisheries personnel stationed at ports of landing. Reliable recovery information usually accompanied these returns. Other tags were not found until the fish had reached fillet plants or fish markets. Recovery information for these tags frequently was lacking or was unreliable.

RESULTS

Southern New England Ground, 1955

In 1955, 296 yellowtail in 6 lots were tagged and released at the locations shown by X's in the first chart of figure 2. Through August 1960, 68 of the fish, 23 percent of the total tagged, were recaptured (table 1).

Recaptures by calendar quarters for the first year following tagging show the seasonal movement patterns (fig. 2). Spring recoveries (April–June 1955) were mostly from areas of tagging. The two recoveries during the summer months (July–September 1955) showed that some movement to the eastward had occurred. One August recapture had crossed Great South Channel, which separates the southern New England ground from

Georges Bank, and was caught on southeastern Georges Bank, a distance of about 200 miles from release point. Fall recoveries (October–December 1955) were mostly from the middle and eastern parts of the southern New England ground, but two recaptures in October also were from subarea M of Georges Bank. Winter recoveries (January–March 1956) were caught near release points or somewhat to the westward of them.

Where tagged fish were caught depended largely upon the distribution of fishing effort. Effort was low on the southern New England ground in the summer months, and only one recapture was obtained there. In the fall, effort increased greatly, and the number of recoveries went up as well. Fishing effort on Georges Bank was highest during summer and fall months. Fish tagged on the southern New England ground were recaptured on Georges Bank only in these seasons.

The pattern of recoveries for the first year after release indicated that yellowtail moved to the eastward in summer, with three tagged fish being recaptured as far east as Georges Bank, and to the westward in winter months. Recaptures in subsequent years (table 1) suggest that this pattern was repeated. One fish, however, (table 1, lot 3), moved far to the northward to the Cape Cod ground, subarea E. This return was the only indication from these releases of intermingling

between yellowtail from the southern New England and Cape Cod grounds.

Southern New England Ground, 1957

In February and April 1957, 499 yellowtail in 3 lots were tagged on the southern New England ground and released at the locations shown by X's in the first chart of figure 3. Through August 1960, 112 of the fish, 22 percent of the total tagged, were recaptured (table 1).

The seasonal distribution of recoveries is shown by calendar quarters during the year following tagging (fig. 3). There were no recaptures in February and March of 1957. Spring recaptures (April-June 1957) were mostly from the release areas, although a number of fish were caught well to the eastward of these points. One recapture was from the Cape Cod ground, subarea G, again indicating that some movement to this ground from southern New England waters takes place. Summer recaptures (July-September 1957) were mostly from the eastern part of the southern New England ground. However, two fish had crossed Great South channel and were caught on Georges Bank, subarea M. Fall recaptures (October-December 1957) were spread over the middle and eastern parts of the southern New England ground. In addition, one fish was recaptured on the southern part of the Cape Cod

ground, subarea G. Winter recaptures (January-March 1958) all were from the western part of the southern New England ground. Several of them were from area XXIII, well to the westward of points where they had been released the preceding spring. Recaptures after the first year at liberty (table 1) showed that the general seasonal pattern of returns described above was repeated.

Here again the locations of recovery were related to the distribution of fishing effort. Effort expended during the summer and fall was mostly on the eastern part of the southern New England ground, where most recaptures were obtained. In the winter and spring, effort was primarily on the western part of the ground, and most tagged fish were caught there in those seasons.

The seasonal distribution of recoveries from lots 7, 8, and 9 indicated that annual migrations occurred which were similar to those shown by the 1955 experiments. The movement patterns were as follows: (1) There was a general movement of fish from the western to the eastern part of the southern New England ground in spring and summer. A few fish had moved as far to the eastward as Georges Bank by late summer and early fall. (2) There was a general movement of fish from the eastern to the western part of the southern New England ground in fall and winter. (3) There was a small amount of movement of southern

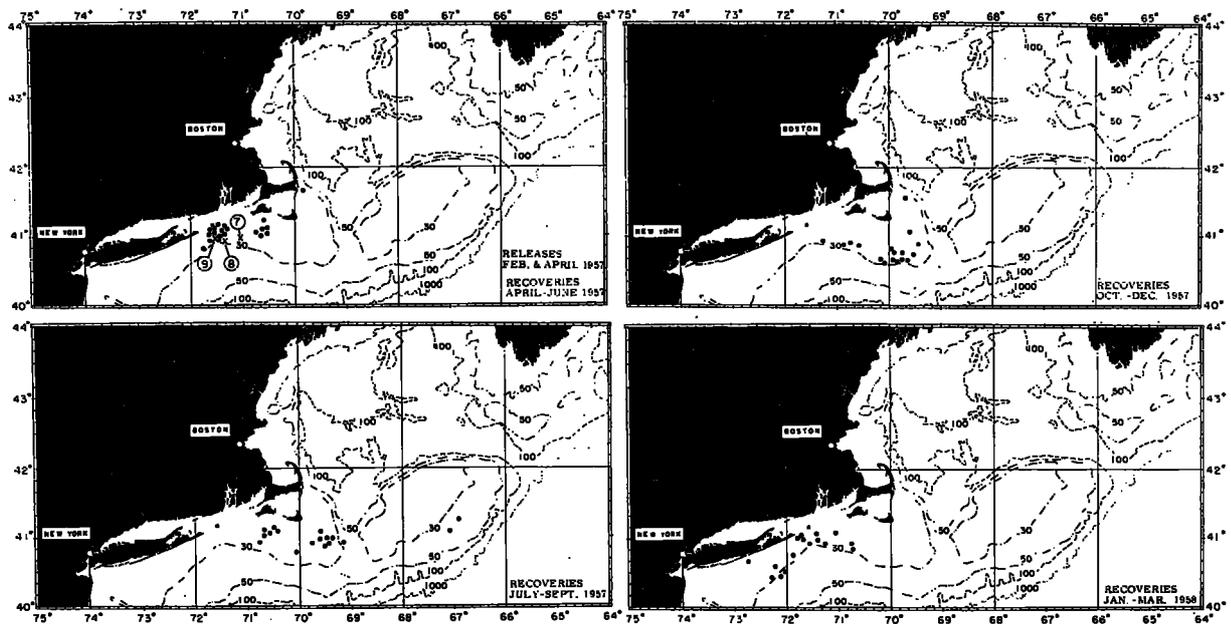


FIGURE 3.—Tagging on the southern New England ground, February and April 1957, lots 7 to 9. (Locations of releases indicated by X's; recoveries, by calendar quarters, indicated by dots.)

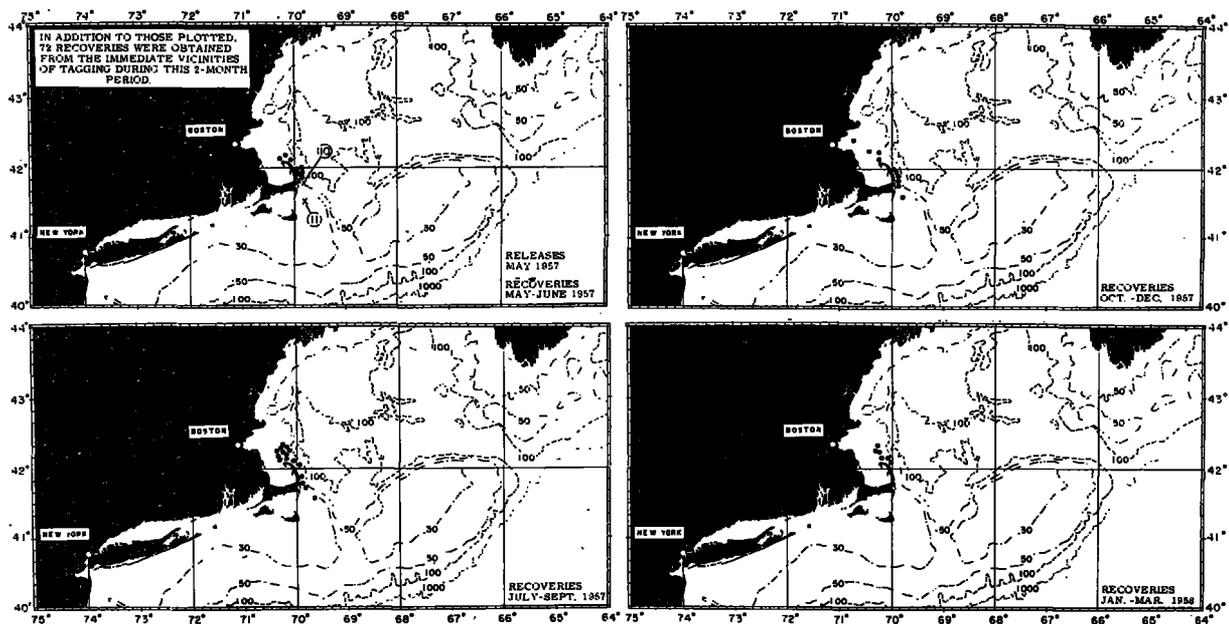


FIGURE 4.—Tagging on the Cape Cod ground, May 1957, lots 10 and 11. (Locations of releases indicated by X's; recoveries, by calendar quarters, indicated by dots.)

New England yellowtail to the southern part of the Cape Cod ground, but the seasonal nature of this movement was not clear.

Cape Cod ground, 1957

In May 1957, 575 yellowtail in 2 lots were marked on the Cape Cod ground and released at the locations shown by X's on the first chart of figure 4. Through August 1960, 130 of the fish, 23 percent of the total tagged, were recaptured (table 1).

Recaptures by calendar quarters during the year following tagging show the movement patterns (fig. 4). The numerous spring recaptures (May–June 1957) were mostly from the immediate vicinity of tagging, although some northward movement was indicated. Summer (July–September), fall (October–December), and winter (January–March 1958) recaptures showed further evidence of a northward movement from the release point. Almost no recaptures were obtained from these releases after the first year following tagging (table 1).

The recovery patterns on the Cape Cod ground suggest that a northward dispersal of yellowtail occurred rather than an annual migration. No movement from the Cape Cod ground to either of the other two major grounds was indicated.

Georges Bank, 1957

In August 1957, 430 yellowtail were marked on Georges Bank and released at the location indicated by the X on the first chart of figure 5. Through August 1960, 121 of the fish, 28 percent of the total tagged, were recaptured (table 1).

Recapture positions for each calendar quarter in the 16 months following tagging (fig. 5) show the seasonal movements. Summer recaptures (August–September 1957) were mostly from the vicinity of marking, although one fish had moved about 40 miles to the eastward. Fall recaptures (October–December 1957) all were from Georges Bank, with two of the recoveries showing a northward movement on the Bank. Winter recaptures (January–March 1958) showed that some westward movement had occurred. Three of the five fish recaptured in this quarter had moved west across South Channel and were caught on the southern New England ground, about 200 miles west of the point of release. Spring recaptures (April–June 1958) were widely scattered about the vicinity of tagging. Summer recaptures (July–September 1958) were tightly clustered around this area. The pattern of fall recaptures (October–December 1958) was similar to that of the preceding fall, with scattered returns from over the Bank. One fall recapture, however, was from the eastern part of the southern New England

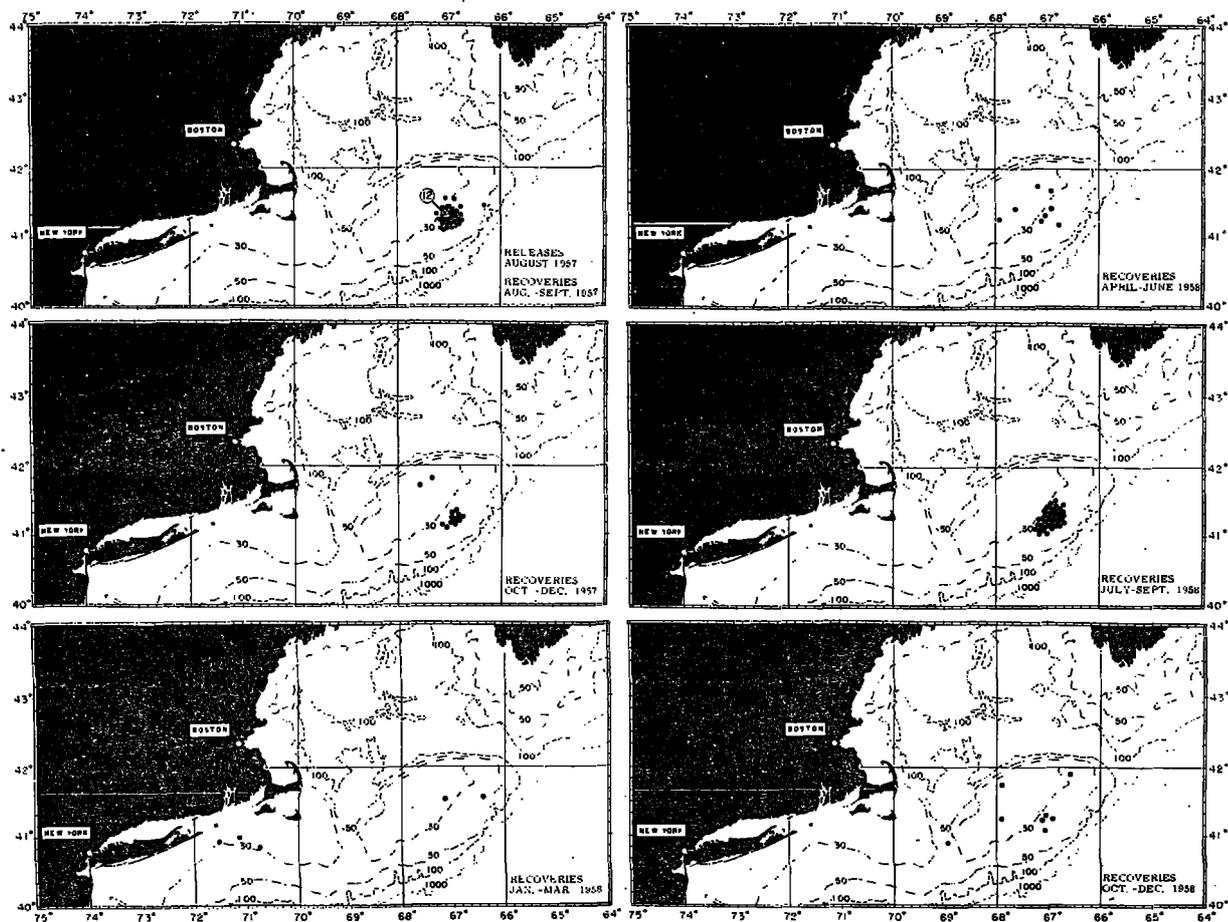


FIGURE 5.—Tagging on Georges Bank, August 1957, lot 12. (Location of releases indicated by the X; recoveries, by calendar quarters, indicated by dots.)

ground, subarea O, and one was from the northwestern part of Georges Bank, subarea H. Recaptures during 1959, while few in number, showed that the patterns described above were repeated (table 1).

Recovery positions of Georges Bank releases were principally determined by the distribution of fishing effort. Effort on the Bank was greatest during the summer, and it was concentrated in the vicinity where tagged fish were released. Most Georges Bank recoveries were obtained during the summer months, and they were from the area where fishing activity was greatest.

The following migration patterns were shown by yellowtail tagged on Georges Bank. (1) There was some movement to the westward during the winter months; a few of the fish were recaptured as far to the west as the southern New England ground. The fish apparently returned to the vicinity of tagging on Georges Bank in the

summer. (2) Although there was some movement to other parts of Georges Bank from the release point, there was no clear migration pattern on the Bank itself. Most Bank recaptures were from area of release. (3) No movement from Georges Bank to the Cape Cod ground was indicated.

FIN RAY COUNTS

In a comparative study of Nova Scotian and southern New England yellowtail flounder, Scott (1954) investigated meristic and morphometric variation in fish from both of these areas. He found a significantly higher number of dorsal and anal fin rays in Nova Scotia yellowtail than in those from southern New England. Dorsal and anal fin ray counts were therefore selected to compare yellowtail from the New England grounds.

Frequency distributions and means of fin ray numbers for fish from the three New England grounds are given in table 2. Analysis of variance indicated that there was no significant difference in fin ray numbers between the grounds, and it was concluded that yellowtail from the three grounds were the same with respect to these meristic characteristics.

TABLE 2.—Frequency distributions and mean values of dorsal and anal fin ray numbers of yellowtail flounder from the three principal New England grounds

Number of dorsal rays	Southern New England ground 1957	Georges Bank 1957	Cape Cod ground 1957 and 1960	Number of anal rays	Southern New England ground 1957	Georges Bank 1959	Cape Cod ground 1957 and 1960
73	1		1	55			
74		3		56	1	1	4
75	2	2	1	57	2	4	7
76	2	2	7	58	5	10	7
77	8	7	8	59	11	22	13
78	8	12	11	60	7	25	20
79	10	15	11	61	7	15	19
80	17	19	8	62	5	16	11
81	15	14	17	63	1	8	11
82	10	15	10	64	1	7	5
83	7	7	10	65	1	4	
84	2	4	6	66		1	1
85	2	4	2				
86	2	4	2				
87		1					
88		1					
89			1				
Totals	86	110	95		41	113	98
Means	80.13	80.40	80.26		59.95	60.59	60.37

INCIDENCE OF PARASITISM

Information indicating that Cape Cod ground yellowtail were geographically isolated from those of the southern New England ground and Georges Bank was obtained from the incidence of infestation by metacercariae of the trematode *Cryptocotyle lingua*. A large percentage of yellowtail from samples caught on the Cape Cod ground were infested with this parasite. In 1958, 36 percent of the fish from a sample of 370 were infested; in 1959, 38 percent of the fish from a sample of 61 were parasitized. No infested fish were observed in samples from either of the other grounds in these or in other years. This information suggests that yellowtail from the southern New England ground and Georges Bank do not inhabit the Cape Cod ground where they presumably could become infested with the parasite.

The initial larval hosts of *C. lingua* are periwinkles, *Littorina* spp., which inhabit shoreline waters in New England (Stunkard, 1930). Cercariae leave the periwinkles and penetrate and

encyst in the skin of fishes, the cysts appearing as black, pinhead-sized specks. The metacercariae apparently remain encysted throughout the life of the host fish. The cercariae are shed only in shoal water, where periwinkles are found, and they die within about 2 days if they fail to find a host. Yellowtail on the Cape Cod ground, in order to become hosts of the parasite, must therefore be found in water close to the shore at some time during their lives.

SUMMARY AND CONCLUSIONS

Yellowtail flounder are caught on three fishing grounds off New England: the southern New England ground, the Cape Cod ground, and Georges Bank. Recoveries of fish marked on the southern New England ground showed that yellowtail there followed a migratory path that was chiefly within this ground. The fish moved to the eastward in spring and summer months and to the westward during the fall and winter. Some of the tagged fish moved greater distances, however, and were caught on the other two New England grounds. Of the 180 recoveries from southern New England tagged fish, 10 were made on Georges Bank during summer and early fall months, while 5 were made on the Cape Cod ground between late spring and early fall. This movement pattern coincided closely with the one shown by Royce et al. (1959) for the southern New England ground during the 1940's.

Recoveries of yellowtail marked on the Cape Cod ground indicated that there was a gradual northward dispersal of fish there. None of these releases were recaptured on either of the other principal grounds, indicating that they were a relatively local and stationary group. The incidence of infestation with the trematode parasite *Cryptocotyle lingua* furnished additional evidence that yellowtail of the Cape Cod group were separate from those found on the other fishing grounds. About one-third of the yellowtail from samples collected on the Cape Cod ground were infested with metacercariae of this parasite, while no infested fish were found on the other two grounds.

Recoveries of yellowtail marked on Georges Bank were mostly from area of tagging, subarea M, which is the part of the Bank that supports an intensive summer yellowtail fishery. Some

of the late fall and winter recoveries were from parts of the Bank to the north and west of the tagging point, suggesting that the migratory path on Georges Bank was to the westward during winter months and to the eastward in the summer. Four of the fish moved off the Bank and were recaptured on the southern New England ground during the winter. None of the fish were recaptured on the Cape Cod ground, indicating that there was no movement between the Georges Bank and Cape Cod groups.

Number of dorsal and anal fin rays were the same for all three yellowtail groups, indicating that there is no difference in these meristic characters.

Data presented here corroborate and strengthen conclusions of Royce, et al. (1959) regarding divisions of the New England yellowtail population. Each of the three principal fishing grounds supports a group of yellowtail which is essentially separate from fish on the other grounds, although a small amount of seasonal intermingling takes place between the groups.

ACKNOWLEDGMENTS

The marking experiments of 1955 were carried out by David Miller, Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Mass. His part in the tagging program is gratefully acknowledged.

Further thanks are due to the captains and crew members of the New England draggers *Portugal*, *Jacquelyn*, *Anna Grace*, *Comber*, and *Capt. Bill II*, from whose catches most of the yellowtail were tagged.

LITERATURE CITED

- MARR, JOHN C.
1957. The problem of defining and recognizing subpopulations of fishes. In: Contributions to the study of subpopulations of fishes. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries no. 208, 129 pp.
- ROUNSEFELL, GEORGE A.
1948. Development of fishery statistics in the North Atlantic. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report no. 47, 27 pp.
- ROYCE, WILLIAM F., RAYMOND J. BULLER, and ERNEST D. PREMETS.
1959. Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin 146, vol. 59, pp. 169-267.
- SCOTT, DAVID M.
1954. A comparative study of the yellowtail flounder from three Atlantic fishing areas. Journal of the Fisheries Research Board of Canada, vol. 11, no. 3, pp. 171-197.
- STUNKARD, HORACE W.
1930. The life history of *Cryptocotyle lingua* (Creplin), with notes on the physiology of the metacercariae. Journal of Morphology and Physiology, vol. 50, no. 1, pp. 143-191.

COMPARISON OF GROWTH OF FOUR STRAINS OF OYSTERS RAISED IN TAYLORS POND, CHATHAM, MASS.

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BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

Former buyers of Wareham River, Massachusetts, seed oysters claim that these oysters are slow growing and have a high mortality rate. The purpose of this experiment was to determine whether Wareham River oysters are truly slow growing.

Seed oysters from Wareham River, Mill Creek, Massachusetts; Long Island Sound, Connecticut; and James River, Virginia, were suspended side by side from a Fiberglas raft in Taylors Pond, Chatham, Mass. from autumn 1958 to autumn 1960. The growth rates for all strains were determined and then compared.

At the end of 1958 the Mill Creek oyster strain was significantly larger than the other three strains.

During 1959 the growth rate of the Wareham River strain was significantly slower than those of the Long Island Sound and Mill Creek strains. During 1960 the growth rates of all strains were significantly similar. At the end of 1960 the oysters from Wareham River were significantly smaller than those from Mill Creek and Long Island Sound.

The study demonstrates that in a single environment the Wareham River oysters grow slower than oysters from Long Island Sound and Mill Creek. Further studies are necessary to determine the reasons for this apparent slow growth.

Spear and Glude (1957) demonstrated that soft clams, *Mya arenaria*, from different origins assume similar growth rates when transplanted to a new environment. Other investigators (Loosanoff, 1949; Butler, 1952; and Andrews and McHugh, 1957) had similar results with transplanting of the eastern oyster, *Crassostrea virginica*. In most cases the surviving oysters adapted themselves to the new environment and developed growth patterns similar to the native populations. Beaven (1952), however, observed different growth rates among four groups of oysters held in trays at Solomons, Md.. He concluded that, in general, oyster seed from local sources grow the best.

In autumn 1956 the Bureau of Commercial Fisheries Biological Laboratory at Woods Hole, Mass., received a report from a commercial fisherman stating that he could no longer find buyers

for Wareham River, Massachusetts, seed oysters. All former customers claimed that these oysters, which were removed from Wareham River and planted on growing grounds in areas such as Long Island Sound, Connecticut or Oyster Pond River, Chatham, Mass., grew very slowly and had a high mortality rate. They further commented that in no case did they ever recover their investment. From the above report it appeared that Wareham River oysters were possibly stunted.

Since Wareham River is capable of producing thousands of bushels of seed oysters and failures in setting are rare (Galtsoff, Prytherch, and McMillin, 1930), the Bureau of Commercial Fisheries felt that this important resource should be investigated. In 1956 studies of the history and growth of the Wareham River oyster were initiated. The purpose of this paper is to report the results of an experiment which demonstrates that

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Wareham River oysters are slow growers. Further studies will be necessary to determine the causes for the apparent slow growth.

PROCEDURE

The first phase of the investigation began with the mailing of questionnaires to all known buyers of young Wareham River oysters. Each buyer was asked when the oysters were bought, where they were planted, how many years passed before they reached market size, and what was the ratio of bushels harvested to bushels bought.

The second phase of the study dealt with a growth analysis of the Wareham River oysters which were collected from the 1958 year class. For a comparison of growth rates, seed oysters of the same year class were obtained from Long Island Sound, Connecticut; James River, Virginia; and Mill Creek, Massachusetts. The shells on which the young oysters had attached were punctured and then strung on either nylon rope, nylon parachute cord, or polyethylene tubing. The strings were then suspended side by side from a Fiberglas raft (Shaw, 1960) in Taylors Pond, West Chatham, Mass. The origin, approximate time of setting, and the date of suspension for each strain are shown in table 1.

Growth of all four groups was measured as an increase in shell height (greatest dorsoventral distance) and length (greatest anteroposterior distance). Initial measurements were taken on Oct. 30, 1958. Thereafter, except for the James River stock, each strain was measured monthly during the growing season.¹ The James River oysters were measured only four times during the study. Since 80 percent of these oysters died during the winter of 1958, the authors felt that handling of these oysters should be kept at a minimum in order to prevent further possible deaths.

TABLE 1.—Origin, approximate time of setting, and date of suspension for each group of experimental oysters grown from raft in Taylors Pond, West Chatham, Mass.

Origin	Approximate time of setting	Date of suspension
	1958	1958
Mill Creek, Mass.-----	July 18-23-----	Sept. 2-26.
Wareham River, Mass.-----	Aug. 1-7-----	Oct. 7.
Long Island Sound, Conn.-----	July 28 to Aug. 3-----	Oct. 15.
James River, Va.-----	Aug. 3-21-----	Oct. 30.

¹ In Cape Cod waters the growing season generally begins in May and ends in November.

To measure growth, approximately 100 oysters from each strain were selected. The oysters were first cleaned of all foreign matter, and care was taken not to damage any new shell deposition. They were then measured with vernier calipers to the nearest 1.0 mm. Immediately after the measurements were completed, the oysters were restrung and attached to the raft.

During 1960 many of the experimental oysters,² which broke away from the strings, were placed in chicken-wire bags. Since about equal numbers of oysters from each group were put in wire bags, the final growth analysis was not considered to be affected. On November 2, 1960, the last measurements were taken. The growth rates of all four groups were then determined and compared by statistical analysis.

DESCRIPTION OF AREA

The growth experiments were conducted in Taylors Pond, West Chatham, Mass. (fig. 1). The pond is about 400 yards long and 200 yards wide. Its depth ranges from 1 to 9 feet. The bottom along the shore is sand but in deeper waters changes to mud. The pond is surrounded by high cliffs which shelter the water from strong winds. From 1958 through 1960 the salinity of the pond varied from 28.22‰ to 31.46‰; the surface water temperatures fluctuated from a summer high of 26.7° C. to a winter low of -0.1° C.; the average pH was 7.9

ANALYSIS OF RESULTS

Answers to Questionnaire

Answers from the questionnaire were received from three companies, two on Long Island Sound, Conn., and the other at Oyster Pond River, Chatham, Mass. A total of 73,540 bushels of Wareham River oysters were bought by these firms during the years 1949-54. In all cases the oysters showed poor growth and high mortality.³ In one instance a company planted 16,254 bushels in Long Island Sound in 1952 and 5 years later only 2,000 bushels were large enough to be sold. Since these oysters were grown in areas where native oysters do well, it appeared that the Wareham River strain was slow growing.

² The authors wish to thank Jay D. Andrews, J. Richards Nelson, and Gilbert Covell for contributing oysters used in the experiment.

³ Possible lack of careful treatment during transportation might explain the high mortality.

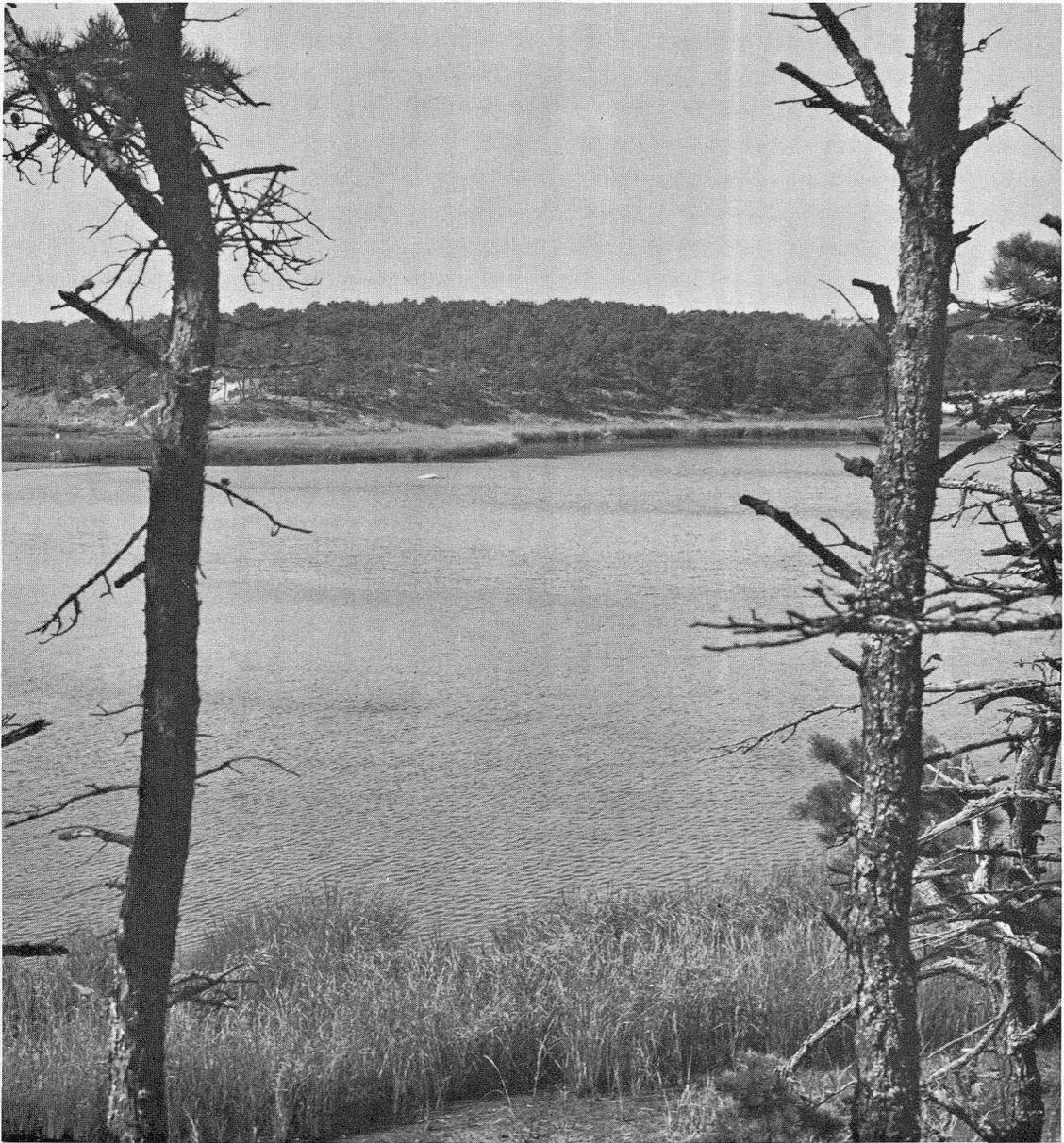


FIGURE 1.—Taylors Pond, West Chatham, Mass.

ANALYSIS OF SHELL GROWTH

As shown in table 2 and figure 2, the growth of the experimental oysters varied. An analysis of variance of the height data for November of 1958, indicated that the differences between the mean heights of the four strains were highly significant ($F=18$). Further analysis, using a modification of the Tukey Method (Snedecor, 1956), showed that a difference between the means equal to or larger than $1.99 (Q_{.05} S_n^2)$ was signifi-

cantly different. Thus the mean height of the Mill Creek oysters was significantly greater than the heights of the other three strains by the end of 1958.

These differences in mean heights at the end of 1958 were more than likely due to the fact that the initial time of setting was not the same for all four groups. Setting in Mill Creek occurred between July 18 and 23, while setting in the other three areas did not take place until 5-29 days later

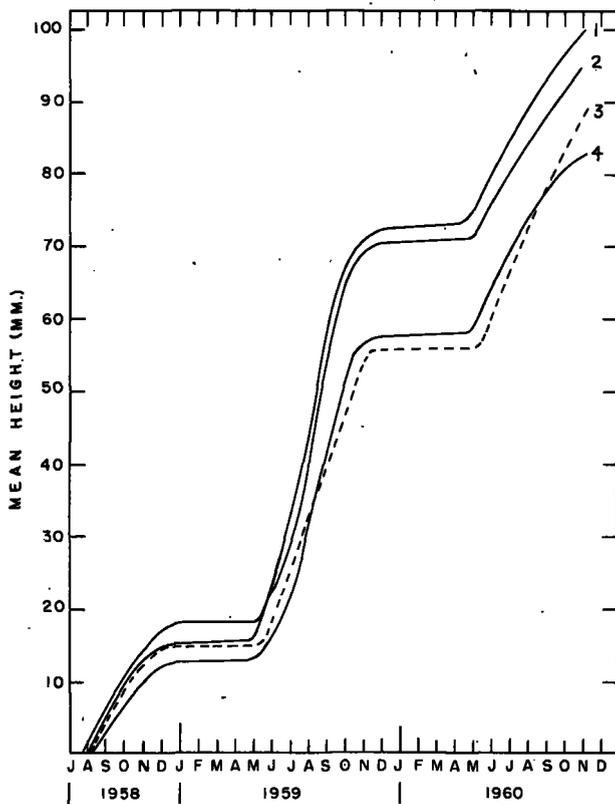


FIGURE 2.—Growth curves for strains of oysters attached to raft in Taylors Pond. Origin of oysters was as follows: 1. Long Island Sound; 2. Mill Creek; 3. James River; and 4. Wareham River.

TABLE 2.—Total yearly mean growth of experimental oysters in Taylors Pond for the years 1958, 1959, and 1960. Based on the difference between total height and initial height for each growing season

Origin	1958	1959	1960
	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
Long Island Sound.....	15.4	57.3	26.8
Mill Creek.....	18.4	52.1	24.6
Wareham River.....	13.0	45.3	24.6
James River.....	13.9	42.4	32.1

(table 1). It is, therefore, logical that oysters with the earliest start, in this case the Mill Creek stock, were the largest at the end of the setting year,⁴ while the oysters with the latest start, in this case the Wareham River and James River stocks, were the smallest.

In 1959 the Long Island Sound oysters grew 57.3 millimeters and the Mill Creek oysters grew 52.1 mm. At the same time, the Wareham River and James River oysters grew only 45.3 mm. and 42.4 mm., respectively (table 2). From these

⁴ From time of setting to January 1 is the setting year.

data it appears that the Long Island Sound and Mill Creek strains grew faster than the other two groups. When the growth curves for 1959 are examined (fig. 2), the differences in growth are apparent.

An analysis of variance of the height data at the end of the 1959 growing season indicated that the differences between the means were again highly significant. Further analysis ($Q_{.05}S_n^2=6.50$) showed that the means of the Long Island Sound and Mill Creek strains were significantly greater than the Wareham River and James River strains, but the Long Island and Wareham River strains were not significantly different from the Mill Creek and James River strains respectively.

Assuming the growth rate of each strain was linear within a single growing season, a comparison of the growth rates of the three strains⁵ was made by using covariance analysis. This comparison during the 1959 growing season indicated that the growth rates were significantly different at the 5-percent level. Further analysis using the t-test (Snedecor, 1956) showed that the growth rates of the Mill Creek and Long Island Sound strains were significantly faster than the growth rate of the Wareham River strain (fig. 3).

An analysis of variance of the data at the end of 1960 indicated that the differences between the means were significantly different. Closer examination showed the relationship of the four strains ($Q_{.05}S_n^2=5.88$) had not changed from the previous year. An analysis of covariance also indicated the growth rate for the four strains were also statistically similar (fig. 4). It is also interesting to note that on comparing the regression coefficients for both years, the growth rates for all strains in 1960 was about one-half as fast as that in 1959.

COMPARISON OF WEIGHTS AND VOLUMES

The question arose whether the selection of shell height as measurement for comparing growth differences between oyster strains gave reliable results. To check our findings, a random sample of 25 oysters was selected from each experimental strain on November 2, 1960. The total weight, weight of shell, weight of meat and liquor, wet weight of meat, and total volume of meat and liquor were determined for each sample and then compared (table 3).

⁵ Not enough data to include James River strain for 1959.

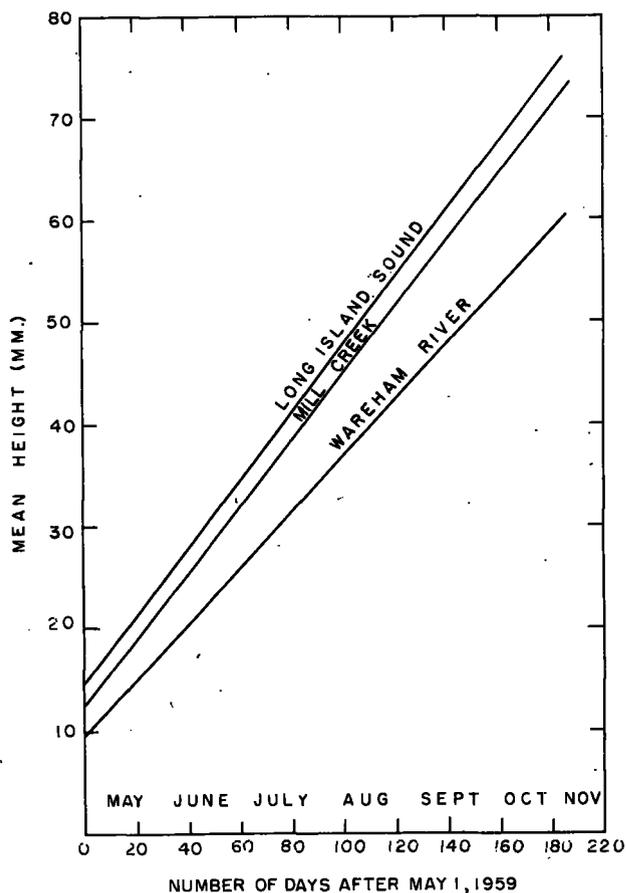


FIGURE 3.—Growth rate regressions of three strains of oysters cultured in Taylors Pond, Chatham, Mass., during the 1959 growing season.

TABLE 3.—Total weight, weight of shell, weight of meat and liquor, and weight of meat for 25 oysters selected from each strain on Nov. 2, 1960

[Measurements in grams]

Origin	Total weight	Weight of shell	Weight of meat and liquor	Weight of meat
Long Island Sound.....	2,560	1,920	637.7	370.9
Mill Creek.....	2,210	1,660	555.5	333.6
James River.....	2,010	1,560	448.1	260.8
Wareham River.....	1,880	1,370	464.4	281.3

The data clearly showed that the oysters from Long Island Sound and Mill Creek have greater weights in all categories than the corresponding weights for oysters originating in the James River and the Wareham River (table 3). Likewise, the former two strains have greater meat and liquor volumes than the latter (figure 5). The above weight and volume comparisons between strains are similar to the results obtained when the mean

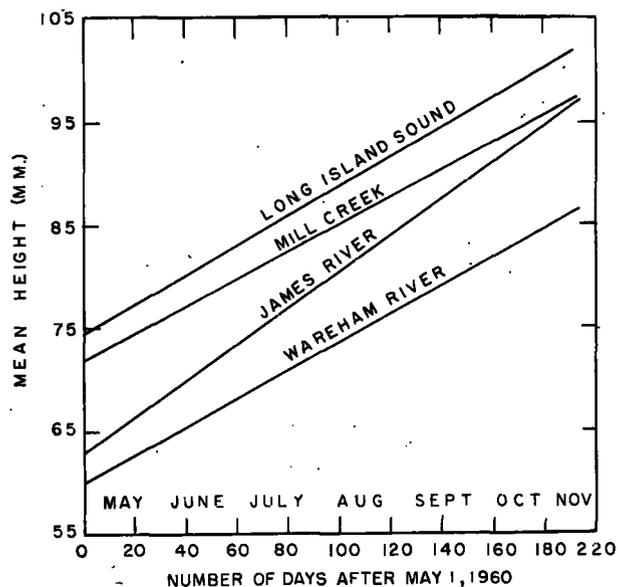


FIGURE 4.—Growth rate regressions of four strains of oysters cultured in Taylors Pond, Chatham, Mass., during the 1960 growing season.

heights for these strains were compared at the end of 1960 (fig. 2). It seems, therefore, that the use of shell height is justified in this experiment.

MORTALITY

As mentioned earlier, the James River oysters had a mortality of 80 percent during the winter of 1958. Little further mortality of these oysters was observed either in 1959 or 1960. Mortality among the other strains was less than 10 percent from the fall of 1958 until the spring of 1960. During 1960 approximately 32.5, 22.4, and 6.3 percent of the Mill Creek, Wareham River, and Long Island Sound oysters died, respectively.

The high mortality among the Mill Creek and Wareham River strains in 1960 was attributed to the fact that many of these oysters, which had originally set on bay scallop shells, broke away from the strings and fell to the bottom. The scallop shells apparently were unable to support the additional weight of the growing oysters and, consequently, fell apart. The low mortality among the Long Island Sound oysters in 1960 can probably be attributed to these oysters being originally caught on oyster shells which were able to support the additional weight.

FUTURE RESEARCH

Our study shows clearly that the Wareham River oysters grow slower than oysters originating

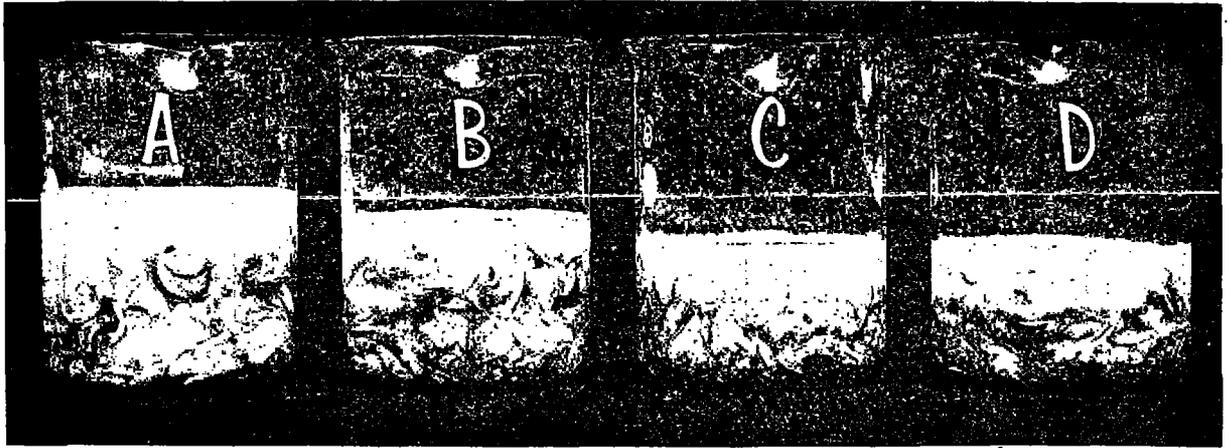


FIGURE 5.—Total meat and liquor volumes for 25 oysters selected from each strain on Nov. 2, 1960. Origin of oysters was as follows: A. Long Island Sound; B. Mill Creek; C. Wareham River; and D. James River.

from Long Island Sound and Mill Creek. The evidence suggests that the slow growth may be caused by hereditary characteristics. One should not overlook the possibility that the growth of this strain might be the results of environmental conditions which occurred during either embryonic or larval stages. The true answer must await further laboratory and field experiment.

SUMMARY

1. Former buyers of Wareham River seed oysters claim that these oysters are slow-growing and have a high mortality rate.

2. The purpose of the experiment was to determine whether the Wareham River oysters are slow-growing. The determination was made by comparing the rate of growth of this strain with the rates of growth of oysters from other areas.

3. Seed oysters from Wareham River, Mill Creek, Long Island Sound, and James River were suspended side by side from a raft in Taylors Pond, Chatham, Mass.

4. Growth for each strain was measured by monthly samples taken during the growing season.

5. At the end of 1958, the mean heights of the Long Island Sound, Wareham River, and James River strains were significantly smaller than the mean height of the Mill Creek strain.

6. During 1959, the growth rate of the Wareham River strain was significantly slower than the

growth rates of the Long Island Sound and Mill Creek strains. The average height of the Wareham River strain at the end of 1959 was significantly smaller than the average heights of the Long Island Sound and Mill Creek strains.

7. During 1960, the growth rates of all strains were significantly similar. The average height of the Wareham River strain at end of 1960 was still significantly smaller than the average heights of the Long Island Sound and Mill Creek strains.

8. A comparison of total weight, weight of shell, weight of meat and liquor, wet weight of meat, and total volume of meat and liquor showed that the oysters from Long Island Sound and Mill Creek had greater weights and volumes in all categories than the corresponding weights and volumes for oysters from Wareham River and James River.

9. Mortality among the Wareham River, Long Island Sound, and Mill Creek strains was less than 10 percent from autumn 1958 until spring 1960. Approximately 32.5, 22.4, and 6.3 percent of the Mill Creek, Wareham River, and Long Island Sound strains died, respectively, during the remainder of 1960. About 80 percent of the James River oysters died during the winter of 1958.

10. The results of the experiment indicates that the Wareham River oysters grow slower than oysters originating from Long Island Sound and Mill Creek. Further research is necessary to determine the causes for the apparent slow growth.

LITERATURE CITED

- ANDREWS, JAY D., and J. L. McHUGH.
1957. The survival and growth of South Carolina seed oysters in Virginia waters. Proceedings of the National Shellfisheries Association, vol. 47, (1956), pp. 3-17.
- BEAVEN, G. FRANCIS.
1952. Some observations on rate of growth of oysters in the Maryland area. Proceedings of the National Shellfisheries Association, vol. 43, (1952), pp. 90-98.
- BUTLER, PHILIP A.
1952. Seasonal growth of oysters (*C. virginica*) in Florida. Proceedings of the National Shellfisheries Association, vol. 43, (1952), pp. 188-191.
- GALTSOFF, PAUL S., H. F. PRYTHERCH, and H. C. McMILLIN.
1930. An experimental study in production and collecting of seed oysters. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 46, pp. 197-263; (also as Document No. 1038.)
- LOOSANOFF, VICTOR L.
1949. Connecticut experiments with Maryland seed oysters. Atlantic Fisherman, vol. 30, no. 1, pp. 18, 35.
- SHAW, WILLIAM N.
1960. A fiberglas raft for growing oysters off the bottom. The Progressive Fish-Culturist, vol. 22, no. 4, p. 15±.
- SNEDECOR, GEORGE W.
1956. Statistical methods. 5th ed. Iowa State College Press, Ames, Iowa, 485 pp.
- SPEAR, HARLAN S., and JOHN B. GLUDE.
1957. Effects of environment and heredity on growth of the soft clam (*Mya arenaria*). U.S. Fish and Wildlife Service, Fishery Bulletin 114, vol. 57, pp. 279-292.

HERRING TAGGING EXPERIMENTS IN SOUTHEASTERN ALASKA

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BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

Results of herring tagging experiments in southeastern Alaska during 1934-37 were studied to provide background information for more recent taggings. Recovered tags evidenced extensive movement and intermingling between Sitka and Craig stocks, which were previously considered discrete. Tagging was concentrated on a single year class during these 4 years, and the extent of the migrations apparently increased with age of the herring.

Results of tagging experiments and racial studies on herring (*Clupea harengus pallasii*) in southeastern Alaska have influenced existing management practices in the commercial fishery. Rounsefell and Dahlgren (1933) and Dahlgren (1936), reported on tagging experiments conducted to 1935, but results of subsequent tagging in 1936 and 1937 have not been published. In recent years the need for additional tagging studies has been emphasized by three factors:

1. The recent changes in fishing areas.
2. The contention of salmon trollers that local herring populations have been seriously depleted by the commercial reduction fishery.
3. The exclusion of herring in the North Pacific Treaty rights of abstention.

Detailed information on mortality, migratory patterns, and degree of intermingling among races of herring is needed to answer questions which arise from these problems. Before undertaking additional tagging studies, it is both logical and expedient to gather as much background information as possible. The purposes of this paper are

Total mortality increased with each year of recovery in each experiment, and successively later experiments indicated higher mortality rates. The fishing effort exhibited a general decline during this period. These results coupled with the concentration of tagging on a single year class support the conclusion that natural mortality increases with age.

Recommendations for future tagging in southeastern Alaska are included in the discussion.

to provide a summary and analysis of results from previous experiments that may serve as a guide and basis for subsequent tagging.

TAGGING AND RECOVERIES

As pointed out by Rounsefell and Dahlgren (1933), conventional external tagging and marking experiments on herring before 1930 had not been successful. To test the feasibility of tagging herring, they began a study at Holmes Harbor in Puget Sound, Washington, during 1932. The study was designed to provide information on the following points:

1. The relative merits of different tagging methods.
2. The mortality of tagged or marked herring.
3. The development of a field technique for tagging.
4. A method of recovery suitable for a reduction fishery.

The results of this study and the initial experiments in southeastern Alaska showed that tagging on an extensive scale was practical. Rounsefell and Dahlgren (1933) and Dahlgren (1936) pre-

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sented detailed information on the methods and procedures used in tagging and recovery. Internal metal tags were found to be superior to external tags, both from the standpoint of low mortality caused by tagging and adaptability of the technique to field conditions. An electromagnet was designed to provide a mechanical means of recovering metal tags from fish meal, and later an electronic detector was developed to recover tags before the fish were processed. Detectors were not installed in all of the reduction plants, and the majority of recoveries were from electromagnets. Dahlgren (1936) emphasized the limitations of the magnet recoveries.

The allocation of tags to specific areas of catch was, at times, impractical or uncertain, and such recoveries were designated "area unknown" or "doubtful." On the other hand, when fishing was concentrated within a restricted area for an extended period, recoveries could be reliably assigned to a specific area. Further, the recapture area of tags recovered by the magnet was in many cases substantiated by tags recovered from the electronic detector. Also, though isolated recoveries were classified as "doubtful," multiple recoveries from a given area reduced the error of assigning such an area as a possible point of recovery.

From 1930 to 1940, the southeastern Alaska herring reduction fishery was concentrated on two stocks. The spawning beaches of these stocks centered about Sitka on the west coast of Baranof Island, and in the vicinity of Craig on the west coast of Prince of Wales Island. Other stocks in southeastern Alaska contributed relatively minor catches to the reduction fishery, and tagging was concentrated in the Sitka and Craig areas.

In each year, fish were tagged in the spring, and recoveries were made during the summer fishing period, June through September. For management purposes, the fishery had been divided into two general areas which were utilized for a breakdown of tag recoveries:

1. The Cape area encompassing the entire west and southeast coasts of Baranof Island. Sitka is located in this area (fig. 1).

2. The non-Cape area, including the west coasts of Kuiu and Prince of Wales Islands and the lesser islands in the vicinity. Craig is located in this area (fig. 1).

In summarizing the results of published tagging experiments, a listing of the original data is not warranted in this report, and only a gross examination of these data and unpublished data from tagging studies in 1936 and 1937 will be considered.

TABLE 1.—Recoveries from Sitka tagging experiments

Year of tagging	Number tagged	Year of recovery	Number and locality of recovered tags							Total	
			Non-Cape area			Non-Cape or Cape		Cape area			Un-known
			Warren Island	Kulu Island	Other	Warren or Ormaney	Kulu or Ormaney	Cape Ormaney	Other		
1934	11,964	1934	14	7	0	5	0	463	1	6	496
1935		11	0	0	14	0	71	2	110	208	
1936		4	3	3	3	0	10	5	10	38	
1937		0	7	0	0	0	3	4	0	14	
1938		0	1	0	1	0	1	1	0	4	
Total			29	18	3	23	0	548	13	126	760
1935	27,911	1935	86	0	0	113	0	929	68	878	2,074
1936		87	35	21	20	130	233	34	97	647	
1937		0	130	0	4	111	97	22	21	385	
1938		0	7	0	1	5	26	2	2	43	
1939		0	0	0	0	0	1	0	1	2	
Total			173	172	21	138	236	1,286	126	999	3,151
1936	10,784	1936	26	16	7	6	80	184	29	53	401
1937		1	58	1	3	69	70	8	7	217	
1938		0	2	0	0	3	11	1	0	17	
1939		0	0	0	0	0	0	0	1	1	
Total				27	76	8	9	152	265	38	61
1937	14,021	1937	0	50	1	3	94	122	20	12	302
1938		0	3	0	0	1	22	2	5	33	
1939		0	0	0	0	0	1	1	0	1	
Total				0	53	1	3	95	145	22	17
Grand total			229	319	33	173	483	2,244	199	1,203	4,883

From 1934 through 1937, 100,911 tags were inserted in herring from the Cape and non-Cape areas. The number of insertions at Sitka totaled 64,680 from which there were 4,883 recoveries (table 1). At Craig the number of insertions was

36,231, from which there were 1,114 recoveries (table 2).

Most recoveries from the Sitka experiments were taken in the Cape area, whereas most recoveries from the Craig experiments were taken

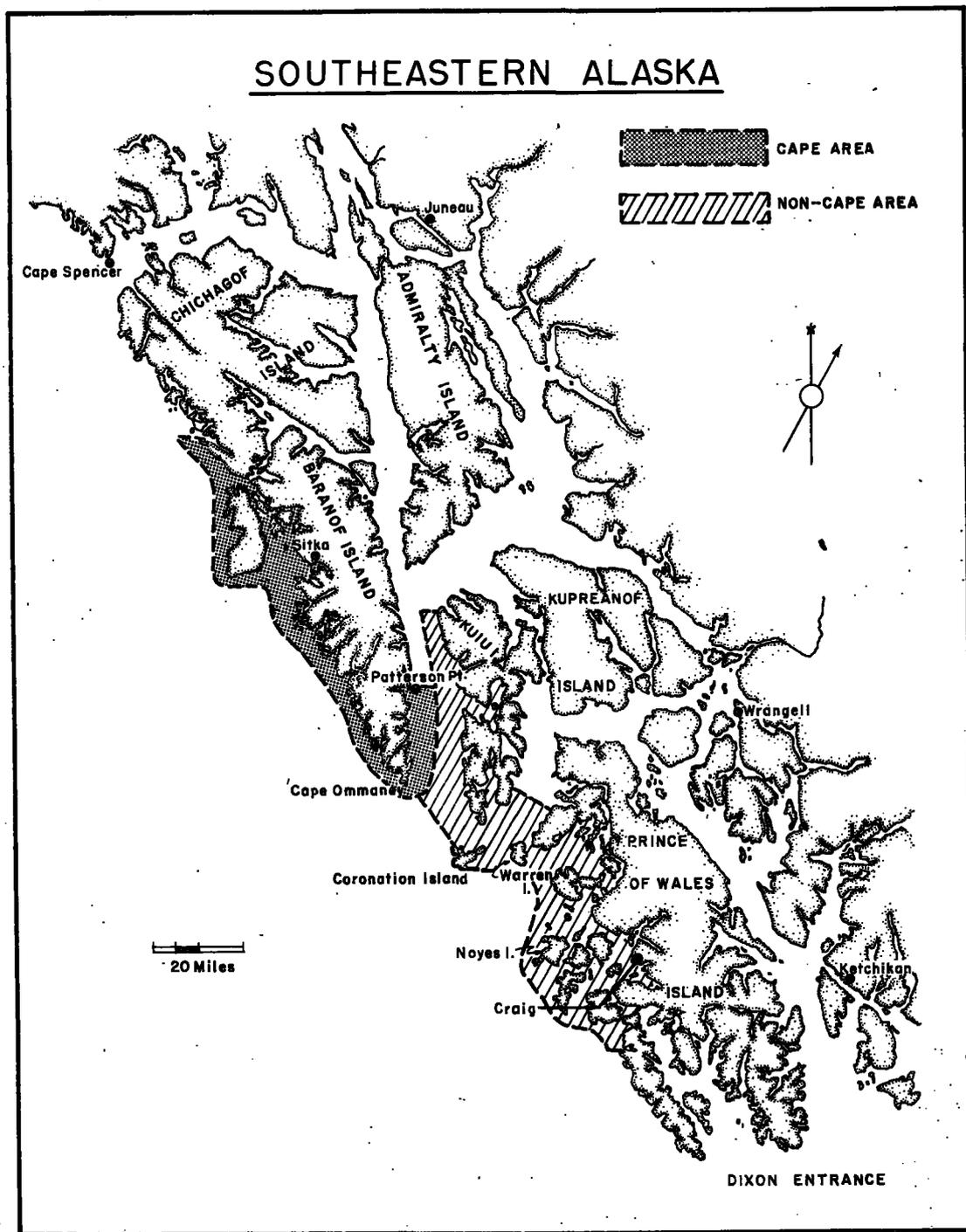


FIGURE 1.—Southeastern Alaska showing Cape and non-Cape areas of the herring fisheries.

TABLE 2.—Recoveries from Craig tagging experiments.

Year of tagging	Number tagged	Year of recovery	Number and locality of recovered tags							Total	
			Non-Cape area			Non-Cape or Cape		Cape area			Un-known
			Warren Island	Kulu Island	Other	Kulu or Om-maney	Cape Om-maney	Om-maney	Other		
1934.....	7,439	1934	78	1	0	5	3	62	0	0	149
1935		24	0	0	13	0	18	1	27	83	
1936		10	3	2	2	4	5	1	3	30	
1937		0	9	0	1	4	1	1	1	17	
1938		0	1	0	0	0	2	0	0	3	
Total.....			112	14	2	21	11	88	3	31	282
1935.....	13,008	1935	74	0	0	61	0	31	0	117	288
1936		34	14	26	10	13	25	4	49	175	
1937		0	42	1	3	28	12	5	6	97	
1938		0	0	0	0	2	4	1	1	8	
Total.....			108	56	27	74	43	72	10	178	563
1936.....	4,880	1936	20	3	15	0	10	7	0	18	73
1937		0	34	2	0	20	8	1	3	68	
1938		0	6	0	0	2	1	0	0	9	
Total.....			20	43	17	0	32	16	1	21	150
1937.....	10,904	1937	0	49	6	1	27	7	4	4	98
1938		0	0	7	0	5	6	0	0	18	
1939		0	0	0	0	0	0	0	0	3	
Total.....			0	49	13	1	32	13	4	7	119
Grand total.....			240	162	59	96	118	189	18	232	1,114

in the non-Cape area. Although recoveries were initially designated by exact location of the catch, the low number of recoveries in certain localities discourages analyses that are based on such specific assignment. Rather, possible discrepancies are considered minimized by designating recoveries to more general areas. Unknown and uncertain recoveries have been assigned to the two areas in the same proportion as known recoveries.

MIGRATIONS

Though the distribution of recoveries in the Cape and non-Cape areas from each experiment follows a general pattern of fluctuation, the annual variations in locality distribution of recovered tags shown in tables 1 and 2 merit attention. Variations of fishing effort expended in the areas will, of course, influence the number of tag recoveries and must be considered in the analyses. The practice in the herring fishery has been to measure effort in ton-days. This unit represents the net tonnage of vessels utilized and the number of vessel-days fished and provides an index comparable with the early years of the fishery when vessels were smaller than in recent years. Large vessels were found to be more efficient than small ones. Rounsefell (1930) discussed the signifi-

cance of change in vessel size to 1929 and the accompanying graph (fig. 2) extends Rounsefell's data to the 1955 fishery. The average vessel size during the period of tagging experiments (1934-39) was relatively stable.

The effort expended in the Cape and non-Cape areas was obtained from records maintained by vessel and plant operators. The ratio of recoveries to effort in each recovery year from successive tagging experiments at Sitka and Craig are compared in tables 3 and 4 and figures 3 and 4.

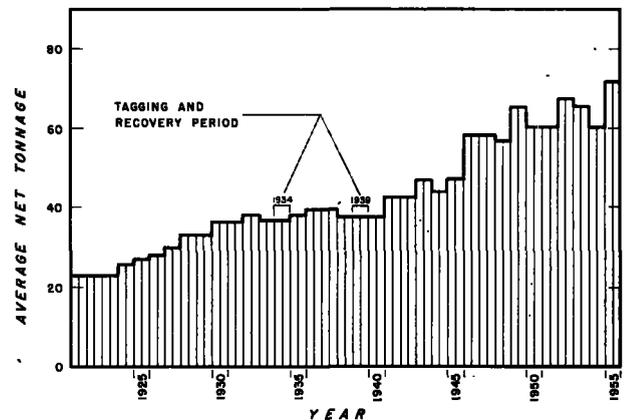


FIGURE 2.—Average net tonnage of herring vessels in southeastern Alaska, 1921-55.

TABLE 3.—Fishing effort and recoveries of Sitka tagging experiments

Year of tagging	Year of recovery	Cape area			Non-Cape area		
		Effort in ton-days <i>f</i>	Recoveries <i>R</i>	$\frac{R}{f}$	Effort in ton-days <i>f</i>	Recoveries <i>R</i>	$\frac{R}{f}$
1934	1934	3,278	474	0.1448	693	22	0.0317
	1935	3,065	181	.0591	1,200	27	.0225
	1936	1,604	23	.0143	1,005	15	.0149
	1937	2,147	7	.0033	1,743	7	.0040
	1938	1,294	3	.0023	1,136	1	.0009
1935	1935	3,065	1,909	.6228	1,200	165	.1375
	1936	1,604	421	.2625	1,005	226	.2249
	1937	2,147	184	.0857	1,743	201	.1153
	1938	1,294	34	.0263	1,136	9	.0079
	1939	898	2	.0022	1,806	0	0
1936	1936	1,604	326	.2032	1,005	75	.0748
	1937	2,147	123	.0573	1,743	94	.0539
	1938	1,294	14	.0108	1,136	3	.0026
	1939	898	0	0	1,806	0	0
	1937	2,147	215	.1001	1,743	77	.0442
1937	1938	1,294	29	.0224	1,136	4	.0035
	1939	898	1	.0011	1,806	0	0

The results show that the vulnerability of tagged fish from each Sitka experiment is greater in the Cape area than the non-Cape area during the first years of recovery; but that vulnerability in subsequent years is about equal in the two areas.

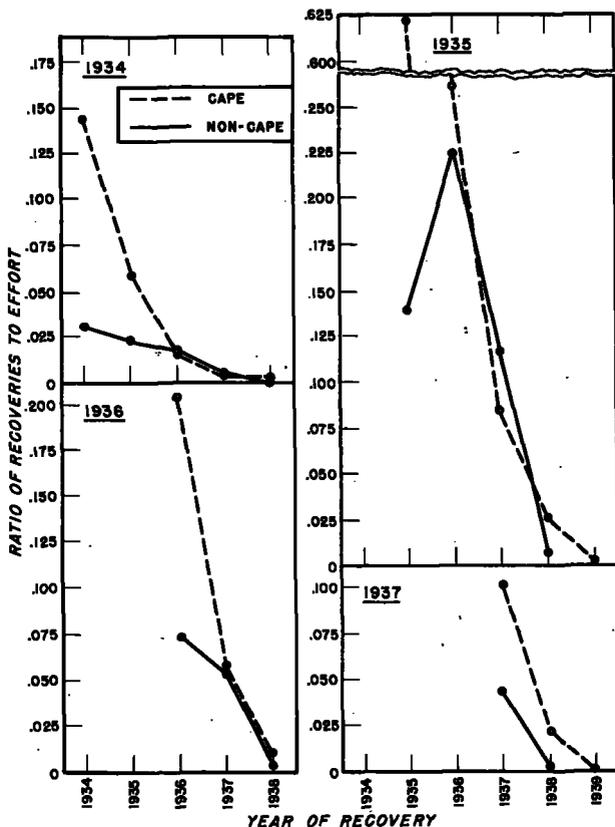


FIGURE 3.—Sitka tagging experiments: the ratio of tag recoveries to effort in the Cape and non-Cape areas.

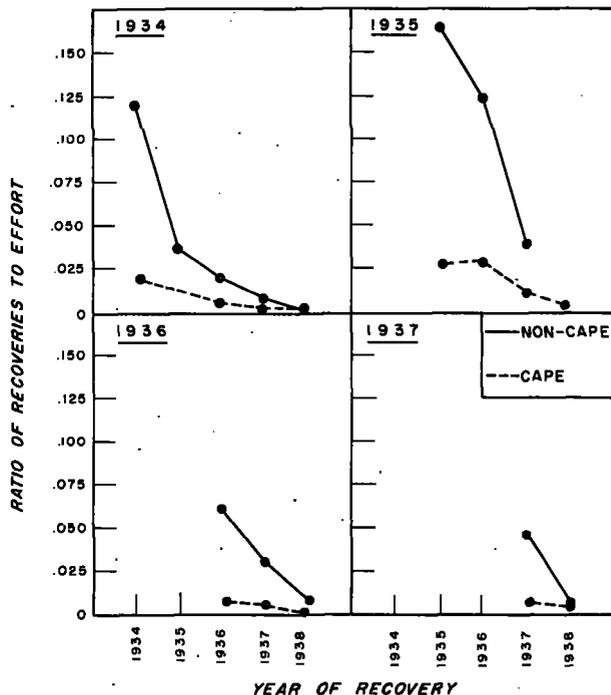


FIGURE 4.—Craig tagging experiments: the ratio of tag recoveries to effort in the Cape and non-Cape areas.

Similarly, results of each Craig experiment show a higher vulnerability in the non-Cape area than the Cape area during the earlier years of recovery, but the difference decreases in the later recovery years of each tagging. The ratio of recoveries to the catch in each area exhibits the same phenomenon.

Individual examination of either Sitka or Craig experiments would perhaps suggest that the change of vulnerability was due to a differential mortality rate in the two recovery areas. The change, how-

TABLE 4.—Fishing effort and recoveries of Craig tagging experiments

Year of tagging	Year of recovery	Cape area			Non-Cape area		
		Effort in ton-days <i>f</i>	Recoveries <i>R</i>	$\frac{R}{f}$	Effort in ton-days <i>f</i>	Recoveries <i>R</i>	$\frac{R}{f}$
1934	1934	3,278	66	0.0201 ¹	693	83	0.1196
	1935	3,065	37	.0121	1,200	46	.0383
	1936	1,604	9	.0056	1,005	21	.0209
	1937	2,147	3	.0014	1,743	14	.0080
	1938	1,294	2	.0015	1,136	1	.0009
1935	1935	3,065	84	.0274	1,200	199	.1658
	1936	1,604	49	.0305	1,005	126	.1254
	1937	2,147	27	.0126	1,743	70	.0402
	1938	1,294	8	.0062	1,136	0	0
	1939	898	13	.0075	1,806	61	.0607
1936	1936	1,604	14	.0087	1,005	61	.0607
	1937	2,147	2	.0009	1,743	54	.0310
	1938	1,294	2	.0015	1,136	8	.0070
1937	1937	2,147	16	.0075	1,743	82	.0470
	1938	1,294	8	.0062	1,136	10	.0088

ever, follows the same pattern in each series of experiments from both areas and rather indicates a movement and progressive mixing of fish between the Cape and non-Cape areas. This conclusion is based on the apparent rapid decrease of the vulnerability ratio in the area where tags were inserted as compared to the relatively slow change in the other recovery area.

After the 1934 and 1935 tagging, Dahlgren (1936) concluded that only "occasional migrants" from Sitka experiments mingled with fish in the non-Cape area and that there was "no counter migration" of the Craig stock to the Cape area. The vulnerability of tagged individuals during these 2 years indicates partial agreement with Dahlgren's findings. Subsequent recovery years (1936-39), however, indicate a more extensive and progressive mixing of the two stocks. This mixing may be the result of random dispersion or may be associated with definite migration patterns. To further examine the mixing phenomenon, the expected recoveries from equal effort in the two areas are compared.

SITKA EXPERIMENTS

Assuming that the proportion of recoveries to effort in the non-Cape area would not be significantly altered by a change in effort, the expected number of non-Cape recoveries can be calculated from effort equal to that of the Cape area. With this adjustment, a comparison of the vulnerability of tagged fish in the two areas can be made—that is, the ratio of the non-Cape recoveries to the total recoveries, Cape and non-Cape (fig. 5). The ratio increases with each year of tagging until 1938 when a decrease is recorded. The increase indicates a greater proportion of tags available in the non-Cape area from one year to the next. The phenomenon points again to migration from the Cape area. The successively higher ratio of non-Cape recoveries to total recoveries is also noted in the initial recovery year of the four experiments. The 1938 decrease suggests a reversal of the 1934-37 trend.

CRAIG EXPERIMENTS

Again adjusting to equal effort, the ratios of Cape recoveries to the total recoveries from Craig experiments do not show as concise a trend as the Sitka experiments (fig. 6). The ratios from 1934 through 1937 fall within the same general range

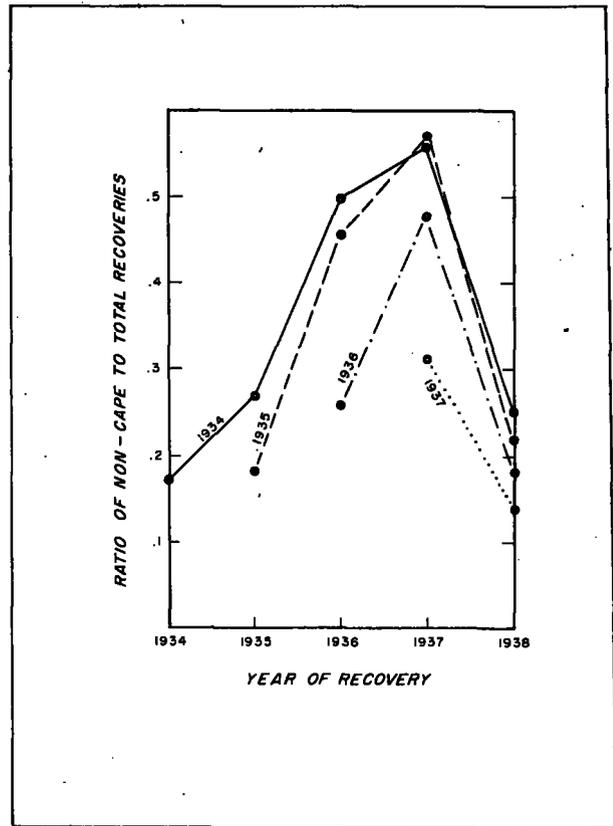


FIGURE 5.—Sitka tagging experiments: ratio of non-Cape to total recoveries.

of 0.10 to 0.25. Apparently, the migration of Craig stocks to the Cape area during this period is considerably less and more consistent than the migration of Sitka stocks to the non-Cape areas. The 1938 data indicate that individuals tagged in the Cape and which had migrated to the non-Cape area, apparently returned en masse to the Cape area. An explanation is not apparent, but the phenomenon may indicate that migration patterns are indeed flexible.

In view of the intermingling between the two stocks, there is some question as to the validity of the Cape and non-Cape divisions for purposes of managing the fishery. Verification of the extent of intermingling is essential to the proper management of the fishery. Management practices have been based on the existence of independent populations and regulatory measures were instituted accordingly. If the mixing of the two stocks, Sitka and Craig, is extensive and consistent, the management concepts should be altered accordingly. For example, the recovery data

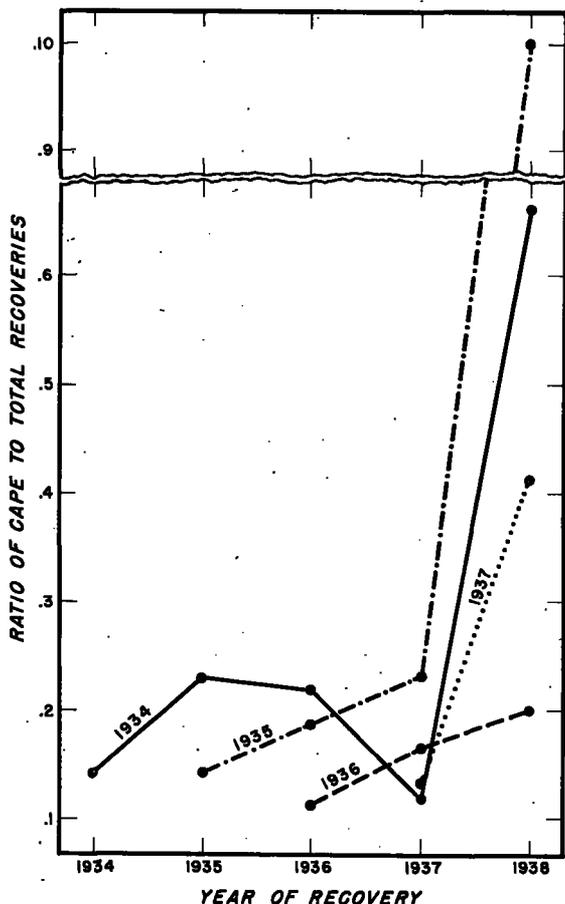


FIGURE 6.—Craig tagging experiments: ratio of Cape to total recoveries.

(tables 1 and 2) show considerable mixing of the two stocks in the vicinity of Kuiu and Warren Islands, and the allocation of these islands to the non-Cape area is not justified.

The conclusions of racial studies by Rounsefell and Dahlgren (1935) do not support the hypothesis of mixing derived from the tagging data. The authors, however, make this statement in their summary (page 140)—

... It must be borne in mind that where morphological differences have not been shown we can only assume that the populations are the same, until such time as we obtain evidence to the contrary. Such evidence may come from tagging experiments.

Ideally, comparisons of the two hypotheses should utilize data from the same year classes but meristic counts and morphological measurements were not recorded during the years of tagging. Re-examination of racial data for other year classes (Rounsefell and Dahlgren, 1935)

does provide some evidence in support of intermingling between the Cape and non-Cape areas. The information presented cannot be conclusively credited to mixing, as there is a geographic progression of meristic characters and length of fish which may occur in response to environmental differences. This progression, however, does agree with expected results from mixing and should be noted. Mean vertebral counts from Cape Ommaney samples were higher than those from Craig, and mean counts from Warren and Noyes Islands (located between the Cape and Craig) were intermediate in value (see figure 1 for locations). The mean vertebral counts for the 1926 year class were: Cape, 52.423; Warren, 52.357; Noyes, 52.342; and Craig, 52.254. That the status of Warren Island samples was questioned is apparent in the statement of Rounsefell and Dahlgren (1935):

Therefore the Warren Island samples must be regarded with some suspicion, especially as the proportion of the observed z forms of the calculated z is larger in the Warren Island samples than in those from other localities.

Length-frequency data listed by these authors for the 1926 and 1927 year classes show a comparable progression, the size of fish from Warren Island being intermediate to those from Noyes Island and Cape Ommaney (fig. 7). Rounsefell and Dahlgren (1935) made the following statement (page 133) about fish size which also can be explained on the basis of mixing.

To gain an insight into the growth increments during the summer months the data have been grouped by 10-day periods. (See table 8). For Larch Bay 5-year-olds (herring in their fifth summer) taken during 1930, a consecutive series of eight periods shows no consistent changes in length during the first five periods (from June 21 up to and including August 10). There is an abrupt increase in length, however, between the fifth and sixth periods, the fish of the last three periods averaging about a half centimeter greater in body length. Such a sudden increase in length can scarcely be ascribed to growth but is probably due to an influx of new schools of herring onto the fishing grounds.

That such a sudden change in body length is not due to growth is supported by the Noyes Island data, in which both the 4- and 5-year-olds taken during the last of June, the largest difference, that between the 5-year-olds, being 6 millimeters.

The tagging results coupled with the morphometric inconsistencies, which can be explained by mixing, favor the acceptance of stock intermingling

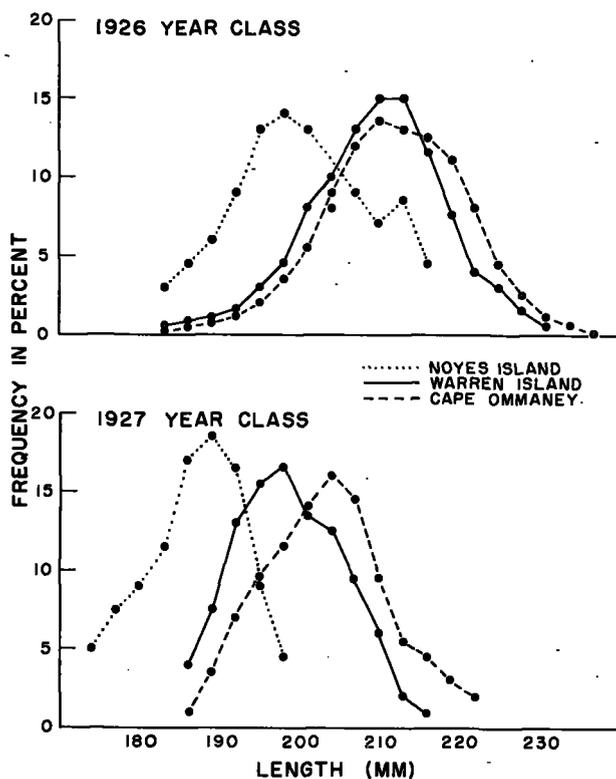


FIGURE 7.—Length-frequency distribution of two year classes taken in 1930. (Data from Rounsefell and Dahlgren, 1935.)

rather than a theory of discrete populations within the Cape and non-Cape areas.

MORTALITY ESTIMATES

Delineation of the migration patterns and mixing areas can be determined generally by examining recovery data. Estimates of population parameters, however, necessitate the assurance that the data fulfill certain requirements and that the limitations be known. Other than the previously mentioned limitations regarding tag recovery, the following items are not accounted for in the data:

1. Proportion of each year's catch which was searched by the magnets.
2. Efficiency of the various magnet installations.
3. Efficiency of tag collection by reduction plant personnel.

The assumption is that the proportion of catch examined and efficiency of recovery varied slightly among the years of study.

To determine whether tagged individuals were distributed as untagged members of the popu-

lation, the recoveries from each experiment can be compared to the catch of the year classes which were in the postrecruit stage at the time of tagging. Dahlgren and Kolloen (1944) estimated the numbers of herring taken from each year class from 1929 through 1938. These estimates were obtained on an annual basis from the total catch, percentage age contribution, and average weight at each age. To utilize these data, the first consideration is to determine the age at which the majority of fish are recruited to the fishery. After the method described by Tester (1955), the estimates of Dahlgren and Kolloen have been weighted to 10,000 fish per year and averaged to establish the age of recruitment (table 5). It is evident that recruitment continues during the 5th year of life in some years, but the major portion of recruitment is completed by the 4th year of life.

TABLE 5.—Estimated numbers of herring by year of life, weighted to 10,000 fish per year

Year of capture	Year of life								
	2	3	4	5	6	7	8	9	10+
1929									
1930		151	8,913	461	220	119	99	9	29
1931		39	1,797	7,689	209	140	72	30	24
1932		1,250	1,020	2,247	5,125	258	20	60	20
1933		410	3,817	1,179	1,217	2,967	410		
1934		319	960	2,768	1,279	1,488	3,185		
1935		9	7,684	439	859	399	479	131	
1936		121	379	9,070	309	70	51		
1937	40	871	1,403	839	6,492	218	113	16	8
1938	210	4,600	1,832	679	462	2,139	70	8	
1938		2,090	6,125	466	289	257	740	16	16
Total	250	9,860	33,930	25,837	16,461	8,055	5,289	270	97
Average	25	986	3,393	2,584	1,646	805	524	27	10

The catch estimates by Dahlgren and Kolloen (1944) for the tagging and recovery period are based on Cape catches, but from the evidence in the previous section on intermingling, their data are considered representative of both Cape and non-Cape for this analysis (table 6). Further, the age composition of the catch is considered representative of the population at time of tagging. In each year of capture, the number of fish taken during the 4th year of life is underscored in table 6 with a solid line and the year classes below this line are not considered members of the population at time of tagging. (Unpublished data of several workers indicate that although some southeastern Alaska herring enter the summer fishery during their 3d year of life, relatively few of them are

TABLE 6.—Estimated catch of herring from each year class in millions of fish¹

Year class	Year of capture					Total by year class
	1934	1935	1936	1937	1938	
1926	5.5					6
1927	20.2		0.1			20
1928	16.8	1.3	0.2			18
1929	36.2	1.8	1.4	0.2	0.1	40
1930	18.5	7.9	2.7	1.8	0.1	31
1931	323.8	232.2	80.5	55.1	4.6	696
1932	.04	9.7	10.4	11.9	1.6	34
1933		3.1	17.4	17.5	1.8	40
1934			10.8	47.2	2.9	61
1935			0.5	118.5	38.1	157
1936				5.4	13.0	18

¹ The number of fish taken from the original population during the tagging year is determined by adding the number of individuals in the 4th year of life and older.

mature the previous spring.) The total number of fish taken from the original population during the tagging year is determined by adding the number of individuals in the 4th year of life and older. The number of fish taken from the same population the following year is obtained by adding the number of individuals in the 5th year and older. Thus, the figures above the dotted lines in table 6 are added to determine the numbers captured from the initial population of each tagging experiment in a given year of fishing.

The number of fish removed each year from

each tagging population is compared with recoveries of tagged individuals from the same population (table 7). The recoveries are the total for each year of tagging and recovery as shown in table 1. The recoveries from each tagging experiment can now be compared with the catch in the several recovery years from each experiment. To analyze the results of each tagging year and of subsequent recoveries, the ratio of each year's recovery to the previous year's recovery and the ratio of each year's catch to the previous year's catch are determined (fig. 8). As shown in the scatter diagram, an increase in the catch ratio, C_i/C_{i-1} , is generally reflected by an increase in the recovery ratio, R_i/R_{i-1} . A *t*-test,

TABLE 7.—Comparison of tagged individuals recovered and catch (in millions of fish) from initial tagging population

Year of capture	Tagging year							
	1934		1935		1936		1937	
	Recov-eries	Catch	Recov-eries	Catch	Recov-eries	Catch	Recov-eries	Catch
1934	645	421						
1935	291	243	2,357	253				
1936	68	85	822	95	474	113		
1937	31	57	482	69	285	87	400	134
1938	7	5	51	6	26	8	51	11

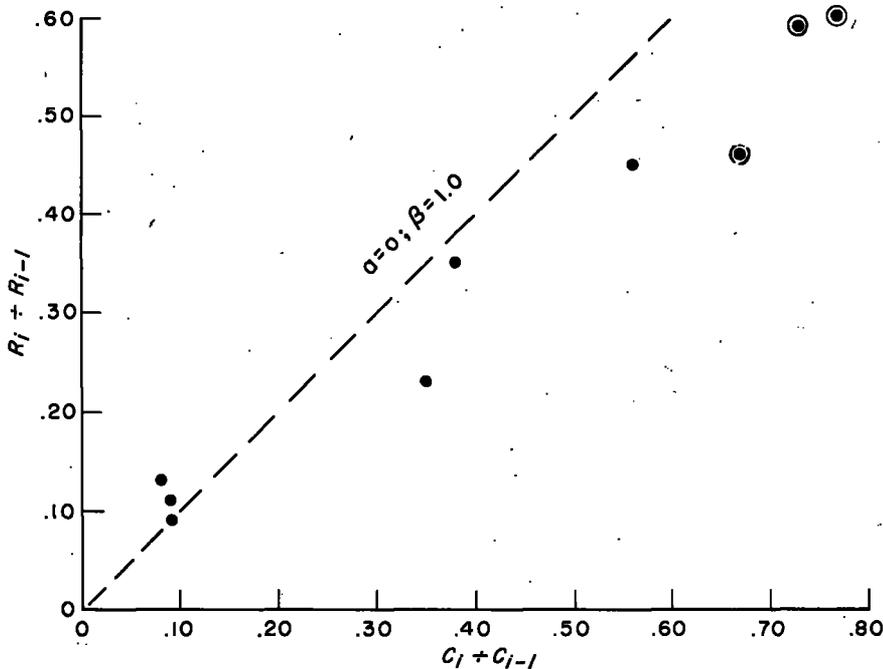


FIGURE 8.—Comparison of tag recoveries ratios (R_i/R_{i-1}) and commercial catch ratios (C_i/C_{i-1}), 1934-38. Circled dots represent data from the years 1936 and 1937.

however, indicates rejection of the hypothesis that the regression of the recovery ratios on catch ratios is 1.0. These results lead to the conclusion that the population of tagged fish is not distributed as the population(s) of untagged fish in the catch; however, further examination of the data reveals features which suggest that this conclusion should be qualified.

The catch ratios generally exceed the recovery ratio, and, presumably, this difference might account for losses caused by tagging mortality, lost tags, inadequacies of the recovery method, or immigration of fishes from other than the original tagging population. That immigration is an important consideration is evidenced by the following exercise. By subtracting the recoveries of non-Cape experiments from the total recoveries (table 7), the regression of catch ratio and recovery ratio deviates further from the hypothetical 1:1. This indicates that fish of non-Cape origin emigrate and contribute to catches in the Cape area and that non-Cape tagging experiments must be included to validate the comparison. Immigration from populations of unknown origin is also considered plausible, and the 1936-37 catch data may reflect such a phenomenon. This ratio, C_{37}/C_{36} , is suspiciously higher than any of the other catch ratios in the three tagging experiments in which it is represented. When these three ratios (circled in figure 8) are omitted from the calculation of the regression, the "t-test" indicates that a regression of 0.95 is not rejected. Considering the limitations of the recovery data, coupled with the limitations of the catch estimates, it is perhaps surprising that the regression is as close to 1.0 as shown. With this evidence, the assumption is made that differences in the distribution of tagged and untagged fish are not sufficiently great to negate a comparison of recovery and catch data.

Estimates of mortality rates from the tagging data are influenced by the limitations listed in the previous section. Because of these limitations, specific values of population parameters are open to question. Nevertheless, the estimates are considered useful in determining the comparative success of the several experiments and the differences in mortality of the Sitka and Craig stocks.

The following equation was selected as most suitable for the data, and calculations of mor-

tality for each year of the Sitka and Craig experiments are derived by this method.¹ The symbols utilized are essentially those of Ricker (1948 and 1958).

The reader will note that fishing effort is assumed proportional to the rate of exploitation. Justification of this assumption is discussed in the appendix which includes excerpts from a letter (dated March 18, 1958) from R. A. Fredin.

The equation:

$$\frac{R_t}{R_{t-1}} = \frac{Nk[1-(u_{t-1}+v_{t-1})] \frac{f_t}{f_{t-1}} u_{t-1}}{Nk u_{t-1}}$$

$$\frac{R_t}{R_{t-1}} = [1-(u_{t-1}+v_{t-1})] \frac{f_t}{f_{t-1}}$$

where:

- $(u_{t-1}+v_{t-1}) = a$ = Annual rate of mortality²
- N = Number of fish tagged
- k = Tagging mortality
- R = Recoveries
- u = Exploitation rate
- v = Natural death rate²
- f = Effort

The results of these analyses provide the calculated "a" for successive tagging experiments at both Sitka and Craig (fig. 9). A point located on a given year expresses the rate of mortality from the previous year to the given year. The two rates circled on the graphs are presumed aberrant but do not materially influence the trend established by the remaining points. The comparison is concerned with the trend of a given experiment as well as the results between successive experiments. The results show:

1. In a given experiment, the mortality increases with each year of recovery. The two exceptions are circled on the graphs.
2. Between experiments, the later tagging exhibits a progressively higher rate of mortality in the initial and subsequent recovery years. An exception to this progression occurs in the Sitka

¹ The selection of an equation suitable for providing estimates of mortality rates created a number of problems, and in seeking advice, the author seldom found agreement among the critics as to the appropriate choice. Most individuals agreed, however, that mortality estimates should be presented and were necessary as comparative indexes for studying the tagging results. Of the different approaches tested, each either had characteristics which were not applicable or necessitated assumptions which the data could not meet. Comments from the reader regarding the treatment of the data will be welcomed.

² See Discussion section for comments on the definition of terms a and v .

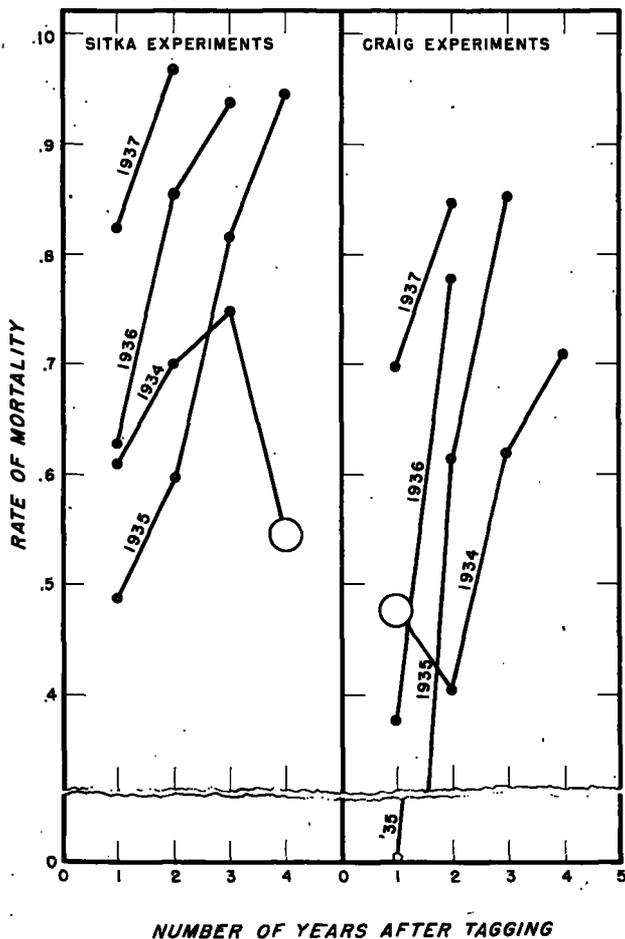


FIGURE 9.—Annual total mortality rates by year of recovery as determined from Sitka and Craig tagging experiments.

and Craig experiments of 1934. In some instances the mortality rates in the first and second recovery years of this experiment exceed the mortalities indicated in later experiments.

As effort did not increase, evidence of the mortality increase in the tagging experiments coupled with the fact that the trend parallels the decline of the fishery suggests that the mortality increase was not spurious and represents an actual biological change in the population.³ Examination of both fishing and natural mortality is necessary to determine the causal factors of this trend.

³ Catches in 1934 and 1935 averaged 120 million pounds per year, whereas catches in 1936 and 1937 averaged 85 million pounds, and in 1938 and 1939, less than 50 million pounds per year (Skud, Sakuda, and Reid, 1930).

Tester (1955) discusses a mortality increase with age in herring of British Columbia and the possibility of such an increase in the Alaska data should be considered. Ages of southeastern Alaska tagged herring were not determined, and the only means of checking the age composition of the tagged fish recovered would have been from the catches of the commercial fishery. However, this assumes that age groups in the commercial fishery are comparable to age groups on the spawning grounds where the fish were tagged. Field work undertaken by the author in 1956 provides a comparison of age groups from the summer fishery and the bait fishery—the latter being conducted on the Sitka spawning grounds (fig. 10). The age composition of the two groups, as determined from scales, does compare favorably and suggests the assumption is not unreasonable.

The data of Dahlgren and Kolloen (1944) in table 6 are utilized to calculate the percentage age composition during the years of tagging (fig. 11). As mentioned earlier in this section, fish in their 3d year of life in the summer fishery are not considered members of the previous spring's spawning population, and the percentage age composition presented includes only fish in their 4th year and older. The age composition during

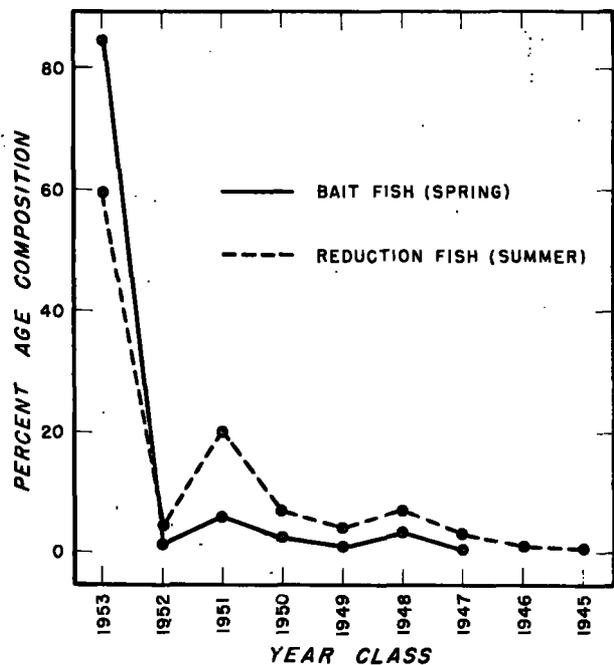


FIGURE 10.—Age composition of herring in the spring and summer fishery in southeastern Alaska.

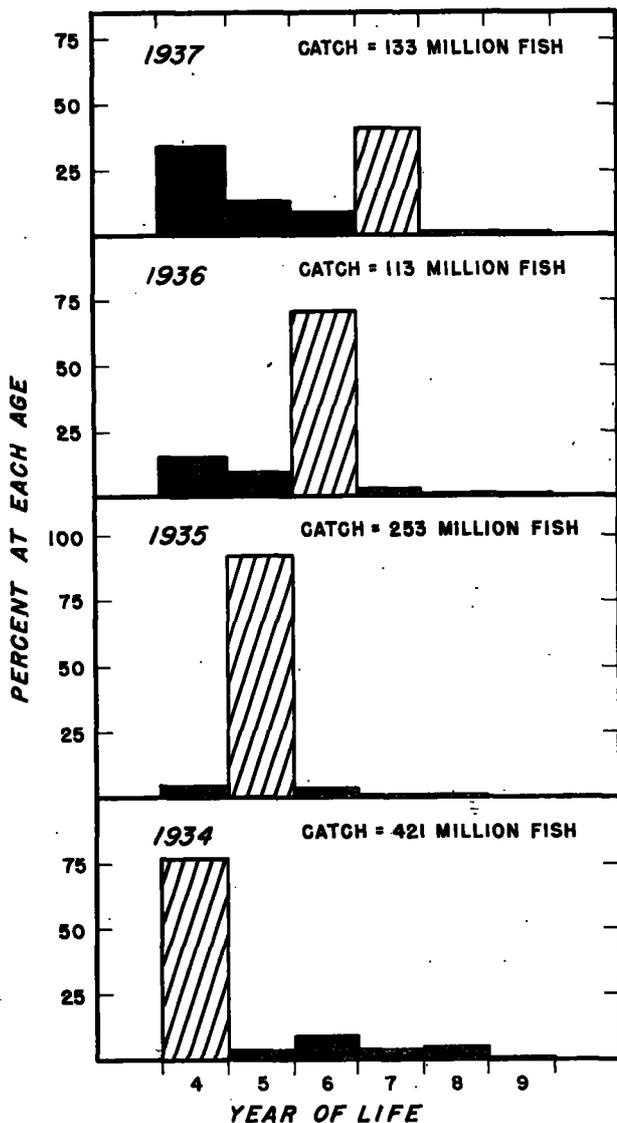


FIGURE 11.—Age composition of the catch in the summer fishery, 1934-37.

this period is dominated by the 1931 year class. In 1934, 1935, and 1936, this year class, represented by fish in their 4th, 5th, and 6th year of life, respectively, annually accounted for more than 70 percent of the total age composition. As fish in their 7th year, the contribution of the 1931 year class approximated 40 percent and was still dominant. In essence, the tagging experiments must have been concentrated on a single year class, 1931, and analyses of recovery data should reflect this phenomenon.

If we consider that the major portion of the tagging was carried out on a single year class and

that the catch generally declined during this period, reexamination of figure 9 indicates an apparent mortality increase with age. That is, the earlier experiments carried out with younger fish exhibited a lower mortality than later experiments with older fish. From Sitka recoveries, calculations of mortality rates assigned to year of capture represent mortality between successive ages of the year class (fig. 12). Again, as in figure 9, the trend depicted by the 1935, 1936, and 1937 experiments is disrupted by the 1934 tagging experiment. Other than the 1934 experiment, an increased mortality with age is indicated. One difference in the 1934 experiment which may have influenced returns of tags is the heavy recruitment of the 1931 year class that occurred after the 1934 tagging.

Figure 5, which shows that the availability of Sitka tags in the non-Cape area generally increases with time, suggests that the movement of herring also may be associated with age.

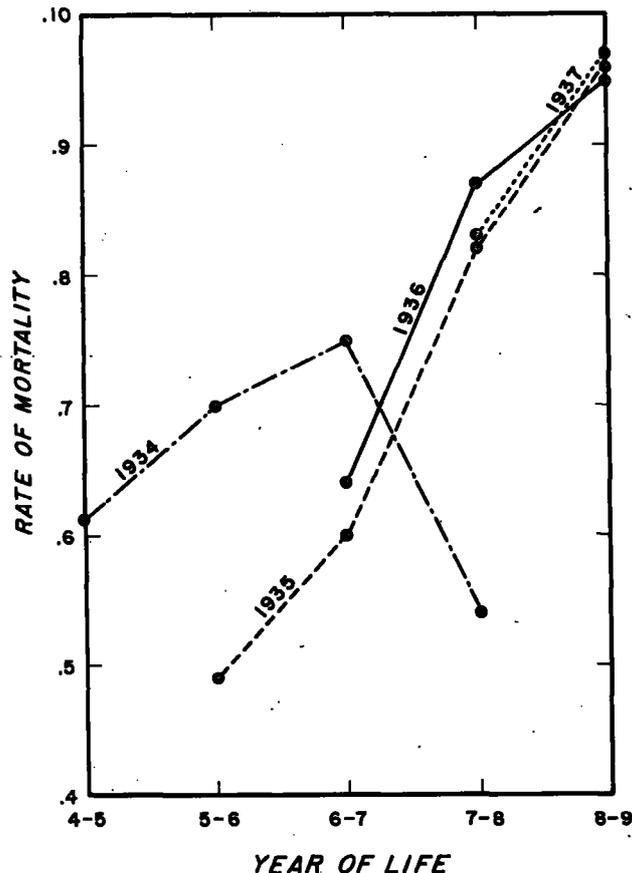


FIGURE 12.—Annual total mortality between ages as determined from Sitka experiments.

DISCUSSION AND CONCLUSIONS

Results of these tagging experiments indicate that the definition of a , total mortality, should include those losses which result from the emigration of individuals from the fishing area. The definition of v , natural mortality, lacks the connotation of losses other than natural deaths. Beverton and Holt (1957) using terms F and X present the necessary refinements for a tagging study. That is, F is the coefficient of reduction of marks due to fishing and X the sum of all other causes which reduce marks—natural deaths, tagging mortality, emigration, etc.

Estimates of population parameters based on the recovery of tagged individuals require that certain established criteria be fulfilled. The possibility of realizing such fulfillment in natural populations is slight. In this study, various assumptions regarding recoveries were necessary when precise data were lacking. Some of these assumptions have little factual support but have only a minor consequence in the analyses. The distribution of tagged fish and the efficiency of recovery, however, are factors of major consequence. A comparison of recovery data and catch data supported the assumption that tagged and untagged individuals were equally vulnerable to capture and that efficiency of recovery varied but little from year to year.

The conclusions from this report are:

1. Intermingling between Sitka and Craig stocks was more extensive than previously indicated and was centered in the vicinity of Kuiu Island and Warren Island.
2. Because of this intermingling, Cape and non-Cape divisions of the fishing grounds cannot be considered distinct in regard to management of the commercial fishery.
3. The 1931 year class dominated the age composition in the summer fishery during each tagging year, 1934-37.
4. An increase in natural mortality with age was indicated.

Whether or not these conclusions are valid in the present day fishery is not known, but they most certainly should be investigated, and the following suggestions should be considered in any future tagging experiments:

1. Design the experiment to further test the degree of intermingling between Sitka and Craig stocks.

2. Conduct summer as well as spring tagging to determine if fish return to the same spawning beaches after mixing on the fishery grounds.

3. Age tagged individuals to: (a) relate intermingling with age, (b) determine variations in recovery of age groups, (c) provide more precise estimates of mortality.

4. Assess recovery methods to: (a) determine portion of catch examined, (b) test efficiency of recovery at each plant.

5. Conduct tagging experiments in other areas to determine the degree of emigration and immigration of fish in this fishery.

ACKNOWLEDGMENTS

I did not participate in either the original field work or in compiling the original data presented in this report and I wish to acknowledge the thorough work of former investigators. The initial tagging experiments reported by Rounsefell and Dahlgren (1933 and 1935) and Dahlgren, (1936) included a comprehensive review of tagging results through 1935. Subsequent experiments were supervised by Dahlgren and the late L. N. Kolloen. The success of their early work is evidenced by the rather wide acceptance of the tagging procedures in both Canadian and European herring investigations. The author is indebted to each of these men, particularly George A. Rounsefell who suggested preparing this report and commented on the original manuscript. The author also wishes to acknowledge the comments of Reynold A. Fredin, Basil B. Parrish, William E. Ricker, and the late Clyde C. Taylor.

LITERATURE CITED

- BEVERTON, RAYMOND J. H., and SIDNEY J. HOLT.
1957. On the dynamics of exploited fish populations. Great Britain Ministry of Agriculture, Fisheries and Food, Fishery Investigations, series 2, vol. 19, 533 pp.
- DAHLGREN, EDWIN H.
1936. Further developments in the tagging of the Pacific herring, *Clupea pallasii*. Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer, vol. 11, no. 2, pp. 229-247.
- DAHLGREN, EDWIN H., and L. N. KOLLOEN.
1944. Outlook for the Alaska herring fishery in 1944. U.S. Fish and Wildlife Service, Special Scientific Report No. 25, 18 pp.
- RICKER, WILLIAM E.
1948. Methods of estimating vital statistics of fish populations. Science Series, No. 15, Indiana University Publications, 101 pp.

RICKER, WILLIAM E.

1958. Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin No. 119, 300 pp.

ROUNSEFELL, GEORGE A.

1930. Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska. Bulletin of the U.S. Bureau of Fisheries, vol. 45, pp. 227-320.

ROUNSEFELL, GEORGE A., and EDWIN H. DAHLGREN.

1933. Tagging experiments on the Pacific herring, *Clupea pallasii*. Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer, vol. 8, no. 3, pp. 371-384.

1935. Races of herring, *Clupea pallasii*, in southeastern Alaska. Bulletin of the U.S. Bureau of Fisheries, vol. 48, pp. 119-141.

SKUD, BERNARD E., HENRY M. SAKUDA, and GERALD M. REID.

1960. Statistics of the Alaska herring fishery, 1878-1956. U.S. Fish and Wildlife Service, Statistical Digest 48, 21 pp.

TESTER, ALBERT L.

1955. Estimation of recruitment and natural mortality rate from age-composition and catch data in British Columbia herring populations. Journal of the Fisheries Research Board of Canada, vol. 12, no. 5, pp. 649-681.

APPENDIX

Excerpts from letter by R. A. Fredin (March 18, 1958):

Fishing effort is assumed to be proportional to rate of exploitation in the model (see appendix). The following indicates the amount of error introduced by this assumption when fishing effort is proportional to the instantaneous rate of fishing. The rate of exploitation is given by the equation

$$u = \frac{pa}{i}$$

when

$$a = 1 - e^{-(p+q)}$$

$$p + q = i$$

$$p = kf$$

k being a constant of catchability and f being the units of fishing effort.

The rate of change of u with respect to p (or f , since p is proportional to effort) is as follows:

$$\frac{\Delta u}{\Delta p} = \frac{i \frac{\Delta pa}{\Delta p} - pa \frac{\Delta i}{\Delta p}}{i^2}$$

$$\frac{\Delta pa}{\Delta p} = p \frac{\Delta a}{\Delta p} + a \frac{\Delta p}{\Delta p}$$

$$\frac{\Delta a}{\Delta p} = \frac{\Delta[1 - e^{-(p+q)}]}{\Delta p} = e^{-(p+q)}$$

$$\frac{\Delta p}{\Delta p} = 1$$

$$\frac{\Delta pa}{\Delta p} = pe^{-(p+q)} + a$$

$$\frac{\Delta i}{\Delta p} = \frac{\Delta(p+q)}{\Delta p} = 1$$

$$\begin{aligned} \frac{\Delta u}{\Delta p} &= \frac{i[pe^{-(p+q)} + a] - pa}{i^2} \\ &= \frac{ipe^{-(p+q)} + (i-p)a}{i^2} \end{aligned}$$

Two tables were constructed, one using p -values ranging from 0.05 to 1.90 with a q -value (natural mortality rate) of 0.1, the other using p -values ranging from 0.05 to 1.70 with a q -value of 0.3. When values for $\Delta u/\Delta p$ are plotted against p , the slope of the curve is found to be changing and not constant, which it would be if u was proportional to f . However, within a limited range of p , the error caused by a changing slope is not too great.

Using effort data from your manuscript and assigning values of k (catchability) ranging from 0.0001 to 0.0004 to the effort data and selecting q -values of 0.1 and 0.3, "true" u and estimated u -values were calculated and compared. The results show that at low fishing mortality rates (where $k=0.0001$) the difference between the "true" and estimated u -values is insignificant, less than 0.01. As the fishing rate increases (i.e., at higher k -values) the error increases up to about 0.10 in some years.

MODEL OF THE MIGRATION OF ALBACORE IN THE NORTH PACIFIC OCEAN

By TAMIO OTSU and RICHARD N. UCHIDA, *Fishery Biologists*

BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

On the basis of tag recovery data, age and growth information, and distribution and size frequency data from the various fisheries, a model of the migration of albacore in the North Pacific Ocean has been developed. This model is consistent with the hypothesis that there is a single population of albacore in the North Pacific Ocean.

The model depicts extensive migrations of the albacore from one fishery to another and from one side of the North Pacific to the other side. In general it is shown that albacore recruitment into the commercial fisheries takes place largely in the eastern Pacific, and that there is a greater volume of migration of the commercial sizes of fish in the westerly direction from the American fishery into the Japanese fisheries, than vice versa. There is a tendency for the youngest fish in the American fishery to return to the same fishery the following season rather than to migrate across into the

Japanese fisheries. This tendency is reduced in the older fish. Some albacore may be available to the American fishery for as many as four or five successive seasons.

As the albacore attain sexual maturity in temperate waters (6-year-olds and older) they move south into subtropical waters, where they make up the reproductive unit of the North Pacific population. This movement south takes place in the spring at the end of the Japanese winter longline season. It is hypothesized that spawning occurs in subtropical waters during the summer, and that the larval and early juvenile stages are spent in these waters. When about 1 year old, the fish migrate into temperate waters, but do not immediately join the exploited stock. The albacore are generally not available to the commercial fisheries until they are 2 or 3 years old.

On the basis of tag recovery data, age and growth information, and distribution and size frequency data from the various fisheries, a model of the migration of the albacore, *Thunnus germon* (Lacépède), in the North Pacific Ocean is proposed. This model is consistent with the hypothesis that there is a single population of albacore in the North Pacific and that the North Pacific albacore fisheries, both American and Japanese, are exploiting a common resource. The model is presented with the hope that critical examination

and testing of it may lead to a better understanding of the albacore resource of the North Pacific Ocean.¹

NORTH PACIFIC ALBACORE FISHERIES

The three major albacore fisheries in the North Pacific are: (1) The Japanese livebait fishery during April–July off the coast of Japan (Van Campen, 1960); (2) the Japanese longline fishery during October–March from the coast of Japan east to about longitude 170° W. (Nankai Regional Fisheries Research Laboratory, 1954); and (3) the U.S. west coast trolling and livebait fishery during June–November between Baja California and the Pacific Northwest (Clemens, 1955). The

NOTE.—Approved for publication January 18, 1962.

¹ A recent publication by Clemens, Harold B. (1961) ("The Migration, Age, and Growth of Pacific Albacore (*Thunnus germon*), 1951–1958." California Department of Fish and Game, Fish Bulletin 115, 128 pp.) carries a discussion on the same subject of oceanwide migrations of the albacore.

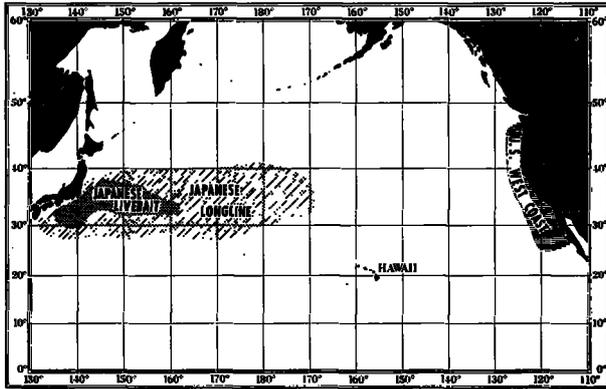


FIGURE 1.—The three major North Pacific fisheries for albacore.

general areas of the three fisheries are shown in figure 1.

SEASONAL DISTRIBUTION AND MOVEMENTS OF THE FISHING GROUNDS

The seasonal shifting of the fishing grounds within the Japanese livebait fishery (fig. 2), Japanese winter longline fishery (fig. 3), and the American west coast fishery (fig. 4) reflects the pattern of the albacore migration within these respective grounds. The Japanese livebait fishery begins off southern Japan in late April or May and gradually moves north and northeast. The fishery reaches its peak in June and rapidly declines in July, as the fish move farther offshore to the eastward.

The Japanese winter longline fishery begins in October, with its center of abundance located in midocean generally between 170° E. and 180° and along latitude 38° N. There is a gradual south-

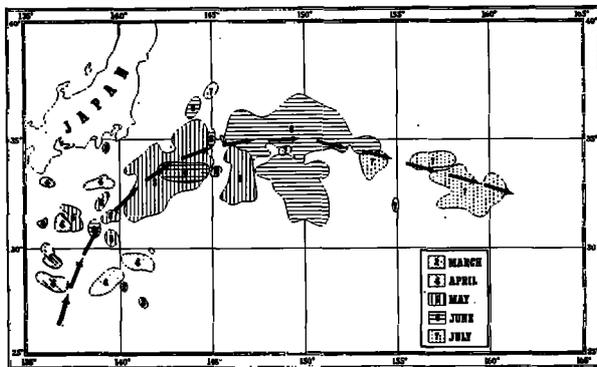


FIGURE 2.—Seasonal pattern of movement of the Japanese livebait fishery. (After Van Campen, 1960, fig. 2.) (The general direction of movement is indicated by the arrow.)

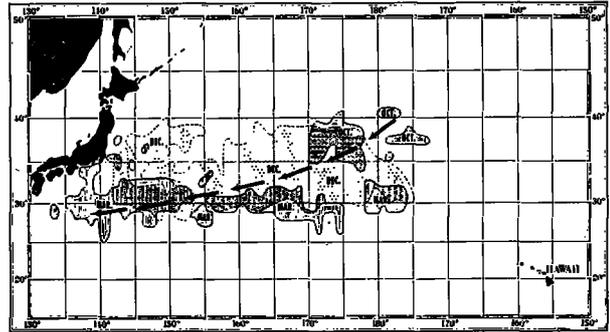


FIGURE 3.—Seasonal pattern of movement of the Japanese winter longline fishery, as constructed from data of the Nankai Regional Fisheries Research Laboratory (1959). (The general direction of movement is indicated by the arrow.)

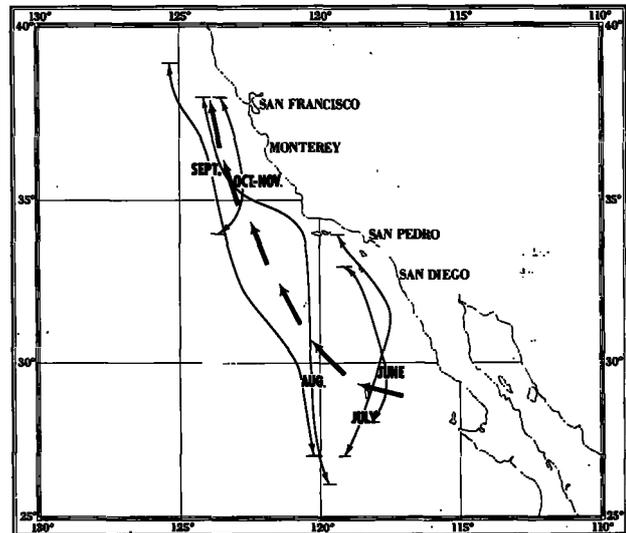


FIGURE 4.—Seasonal movement of the California albacore fishery in 1953. Each line extends over the total area fished during the month and describes diagrammatically the northward expansion of the fishery as the season progresses. (From Clemens, 1955, fig. 24.) (The general direction of movement is indicated by the arrow.)

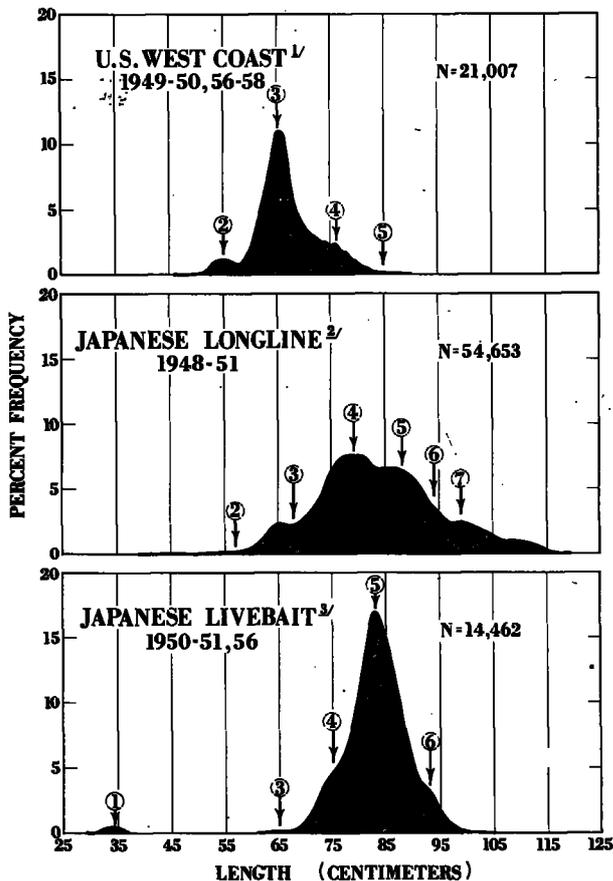
westward shift of the areas of highest catch rates (Nankai Regional Fisheries Research Laboratory, 1959) which continues through March. Thereafter the fishery declines very rapidly. Towards the end of the fishing season, in March, the center of concentration shifts to around latitude 30° N., longitude 140° E.

The American fishery tends to move northward along the coast as the season progresses (Clemens, 1955). This tendency is indicated in figure 4, which is a partial reproduction of Clemens' figure 24.

SIZES AND ESTIMATED AGES OF FISH EXPLOITED

A composite length frequency distribution for each of the fisheries is shown in figure 5. The modal lengths of the age groups are approximations based on the appearance of the modes in the length frequency distributions, as well as on an albacore growth curve derived from tag recovery data (Otsu, 1960).

Studies to date have not yielded a satisfactory method for assigning absolute ages to the albacore. Growth curves have been constructed (Otsu, 1960), but the early growth, below the point of



¹ Compiled from Graham (1959); and from unpublished data of the Fish Commission of Oregon, California Department of Fish and Game, and the Washington State Department of Fisheries.

² Compiled from data in Nankai Regional Fisheries Research Laboratory (1950) and (1951).

³ Compiled from data in Nankai Regional Fisheries Research Laboratory (1951) and Mie Prefectural Fisheries Experimental Station (1957).

FIGURE 5.—Length frequency distributions of albacore taken in the three major fisheries. (The ages (encircled) are shown at the approximate modal size of each age group.)

inflection on the curve, remains questionable. By means of a Gompertz equation, Otsu (1960) attempted to describe the entire growth curve of the albacore but concluded that the initial growth as shown by the resulting curve seemed unreasonably slow, since it required about 3 years for the fish to attain a weight of 1 pound (about 30 cm.). He suggested a possible error of 1 or 2 years in the ages assigned by this method.

A group of 30–35 cm. fish occasionally enters the commercial catches. It is possible that these are the first-year fish, and assuming that they are, it is postulated that the albacore are about 2 years old when (at a length of about 50 cm.), they first enter the fisheries in significant numbers. On this assumption, the Japanese livebait fishery generally exploits three age groups, 4-, 5-, and 6-year-olds, whose modal lengths are approximately 75, 83, and 93 cm. Occasionally 1-year-old fish (around 35 cm.) are taken, but not in great numbers, and 2-year-olds are usually absent from the catches. Three-year-old fish appear in small numbers.

The winter longline fishery exploits a wide range of ages, from 2- to 8- or 9-year-old fish. Generally, the catches are composed of the following modal sizes, corresponding to the age groups within this range: 57, 68, 79, 88, 94, 99 cm., and a few fish of larger groups. Most abundant are the 4- and 5-year-old fish (79- and 88-cm. groups).

The American fishery is generally based on three groups, which are approximately 2-, 3-, and 4-year-old fish (55, 65, and 76 cm.), but small numbers of older groups (5- and 6-year-olds) also appear. The 3-year-old fish are usually the most abundant in the catches. Aside from the infrequent occurrence of 1-year-old fish in the Japanese livebait fishery, the youngest members of the albacore population are exploited by the American fishery since here, for the first time, 2- and 3-year-old fish appear in significant quantities.

MIGRATION OF ALBACORE BETWEEN FISHERIES

Until recently little was known of the distribution of albacore in the approximately 2,000 miles of open ocean between the Japanese winter longline grounds and the west coast of North America. Since 1954, the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, has conducted 10 exploratory fishing and 6 hydro-

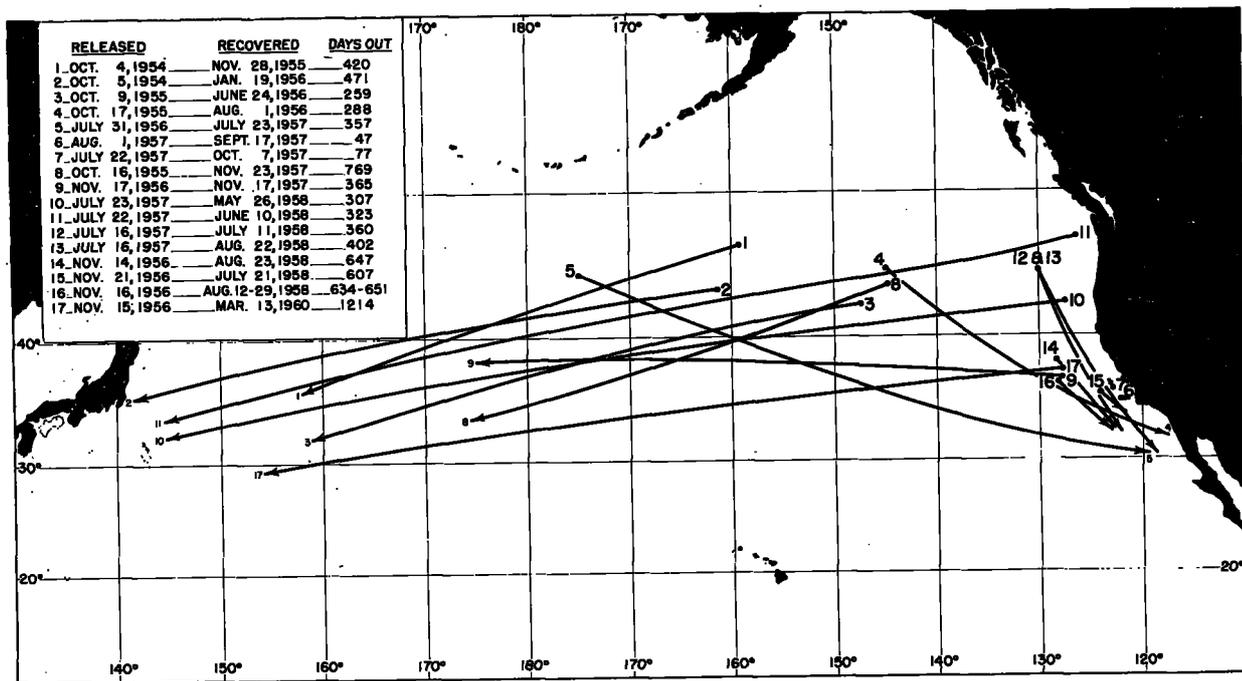


FIGURE 6.—Net movements of albacore tagged by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu. (The lines connect the points of release and recovery of each fish, and the numbers correspond to the "Recovery Number" in table 1).

graphic cruises in that area. The results of these cruises are described by Shomura and Otsu (1956), Graham (1957), and Graham (MS).² By long-lining, trolling, and gillnetting, it was shown that albacore are generally scarce in this extensive area during the winter and spring. In summer, the surveys disclosed localized areas of abundance between longitudes 160° W. and 175° W., but farther to the east albacore occurrence was sparse. In the fall, the catches indicated a continuous distribution of fish, although not in great abundance, between the declining American fishery and the developing Japanese longline fishery.

The migration of the albacore between the west coast of the United States and the Pacific coast of Japan has been shown in the results of tagging experiments (Otsu, 1960). Data on the size and age composition of fish exploited in the different fisheries provide supplementary evidence on the migrations of albacore among the areas of the North Pacific fisheries.

The Bureau of Commercial Fisheries Biological Laboratory, Honolulu, tagged a total of 934 albacore between January 1954 and September

² Graham, Joseph J., Manuscript. The macroecology of the albacore tuna, *Thunnus germon* (Lacépède), in the central North Pacific. Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

1958 in the temperate North Pacific between the U.S. west coast and longitude 179° E. (Otsu, 1960). In addition, 270 albacore were tagged in the Japanese livebait fishing grounds in the spring of 1956 (Van Campen and Murphy, 1957). Of the 934 releases in the central and eastern North Pacific, 17 recoveries (1.8 percent) had been reported as of August 1961 (table 1 and fig. 6). To date no recoveries have been made of the 270 fish tagged in the Japanese fishery.

Recoveries of albacore tagged by other research agencies (nine by the Nankai Regional Fisheries Research Laboratory, five by the California Department of Fish and Game, and four by the Fish Commission of Oregon) are listed in table 2 and illustrated in figure 7.

Tag recoveries have shown transpacific movements of fish from the American fishery into the Japanese longline fishery (fig. 6 Nos. 9 and 17; fig. 7, Nos. 19, 20, and 21) and into the Japanese livebait fishery (fig. 6, Nos. 10 and 11; fig. 7, Nos. 18, 22, 23, and 33). There have been movements from the midocean area between the American fishery and the Japanese longline fishery into the American fishery (fig. 6, Nos. 4 and 5), as well as into both Japanese fisheries (fig. 6, Nos. 1, 2, 3,

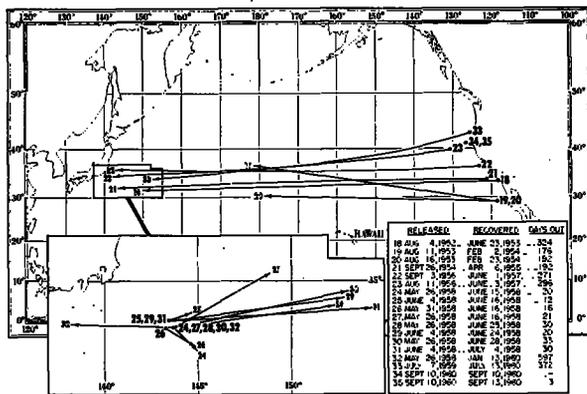


FIGURE 7.—Net movements of albacore tagged by the Nankai Regional Fisheries Research Laboratory, the California Department of Fish and Game, and the Fish Commission of Oregon. (The lines connect the points of release and recovery of each fish, and the numbers correspond to the "Recovery Number" in table 2).

and 8). Tagging in the Japanese livebait fishery has resulted in recaptures which showed a generally easterly movement away from Japan (fig. 7, Nos. 24-31), and one such recovery has been made in the winter longline fishery (fig. 7, No. 32). None of the albacore tagged in the Japanese livebait fishery has been retaken in the American fishery, but, as will be shown later, this probably does not mean that there is a complete lack of migration in that direction.

MODEL OF MIGRATION

Interpretation of the pattern of tag returns indicates that albacore undertake no more than one transpacific crossing during a 1-year period. These movements are considered to be rapid between the established fisheries, and slow within the areas of the fisheries.

TABLE 1.—Recoveries of albacore tagged by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu

Recovery No.	Release		Recapture			
	Date	Fishing gear	Date	Fishermen	Vessel	Fishing gear
1	Oct. 4, 1954	Longline	Nov. 28, 1955	Japanese	No. 1 Seifuku Maru	Longline.
2	Oct. 5, 1954	Trolling	Jan. 19, 1956	do.	unknown	Do.
3	Oct. 9, 1955	do.	June 24, 1956	do.	No. 6 Usa Maru	Livebait.
4	Oct. 17, 1955	do.	Aug. 1, 1956	American	unknown	Trolling.
5	July 31, 1956	do.	July 23, 1957	do.	Carol Virginia	Livebait.
6	Aug. 1, 1957	do.	Sept. 17, 1957	do.	Crisella	Livebait.
7	July 22, 1957	do.	Oct. 7, 1957	do.	Mercator	Trolling.
8	Oct. 18, 1955	do.	Nov. 23, 1957	Japanese	No. 3 Hoju Maru	Longline.
9	Nov. 17, 1956	do.	Nov. 17, 1957	do.	unknown	Do.
10	July 23, 1957	do.	May 26, 1958	do.	do.	Livebait.
11	July 22, 1957	do.	June 10, 1958	do.	No. 2 Zenshin Maru	Do.
12	July 16, 1957	do.	July 11, 1958	American	Lococo Brothers	Trolling.
13	July 16, 1957	do.	Aug. 22, 1958	do.	Bernard Pedro	Do.
14	Nov. 14, 1956	do.	Aug. 23, 1958	do.	Paul C.	Do.
15	Nov. 21, 1956	do.	July 21, 1958	do.	Mable	Livebait.
16	Nov. 16, 1956	do.	Aug. 12-29, 1958	do.	Datho II	Do.
17	Nov. 15, 1956	do.	Mar. 13, 1960	Japanese	No. 3 Hayatori Maru	Longline.

Recovery No.	Release			Recapture		
	Position		Size (cm.)	Position		Days out
	Latitude	Longitude		Latitude	Longitude	
1	46°30' N	159°18' W	78.2	35°45' N	157°39' E	420
2	43°31' N	161°16' W	68.0	35°23' N	141°20' E	471
3	42°16' N	147°18' W	63.4	31°54' N	158°37' E	269
4	44°55' N	144°48' W	59.9	31°21' N	117°17' W	288
5	44°31' N	174°55' W	68.4	30°08' N	119°03' W	357
6	34°49' N	121°57' W	66.5	34°49' N	121°26' W	47
7	35°43' N	122°58' W	65.5	36°24' N	123°07' W	77
8	43°40' N	144°40' W	65.1	33°22' N	174°07' E	769
9	36°44' N	127°37' W	85.2	33°08' N	174°53' E	365
10	42°20' N	127°33' W	78.0	32°15' N	144°15' E	307
11	47°00' N	126°18' W	75.0	33°40' N	144°00' E	323
12	44°47' N	130°04' W	65.0	30° N	118°45' W ¹	360
13	44°47' N	130°04' W	75.0	32° N	122° W ¹	402
14	38°00' N	128°25' W	79.4	32°15' N	122°30' W	647
15	35°21' N	123°57' W	68.6	34°00' N	123°10' W	607
16	36°48' N	127°33' W	65.9	32°38' N	123°00' W	81.2
17	37°12' N	127°41' W	60.8	29°28' N	153°45' E	ca. 90

¹ Approximate position of recapture.

TABLE 2.—Recoveries of albacore tagged by the California Department of Fish and Game, the Fish Commission of Oregon, and the Nankai Regional Fisheries Research Laboratory

Recovery No.	Release			Recapture			
	Date	Agency ¹	Fishing gear	Date	Fishermen	Vessel	Fishing gear
18.....	Aug. 4, 1952	CFG ²	Trolling.....	June 23, 1953	Japanese.....	No. 5 Chosho Maru.....	Livebait.
19.....	Aug. 11, 1953	CFG.....	do.....	Feb. 2, 1954	do.....	No. 1 Konpira Maru.....	Long line.
20.....	Aug. 16, 1953	CFG.....	do.....	Feb. 23, 1954	do.....	Sin-o Maru.....	Do.
21.....	Sept. 28, 1954	CFG.....	do.....	Apr. 6, 1955	do.....	No. 5 Shoyei Maru.....	Do.
22.....	Sept. 3, 1956	CFG.....	do.....	June 1, 1957	do.....	unknown.....	Livebait.
23.....	Aug. 11, 1956	OFC.....	do.....	June 3, 1957	do.....	do.....	Do.
24.....	May 26, 1958	NRFRLL.....	Livebait.....	June 15, 1958	do.....	No. 15 Hoko Maru.....	Do.
25.....	June 4, 1958	NRFRLL.....	do.....	June 16, 1958	do.....	No. 5 Wasumi Maru.....	Do.
26.....	May 31, 1958	NRFRLL.....	do.....	June 16, 1958	do.....	No. 7 Kyowa Maru.....	Do.
27.....	May 26, 1958	NRFRLL.....	do.....	June 16, 1958	do.....	No. 8 Fukuichi Maru.....	Do.
28.....	May 26, 1958	NRFRLL.....	do.....	June 25, 1958	do.....	Chiyo Maru.....	Do.
29.....	June 4, 1958	NRFRLL.....	do.....	June 24, 1958	do.....	unknown.....	Do.
30.....	May 26, 1958	NRFRLL.....	do.....	June 28, 1958	do.....	do.....	Do.
31.....	June 4, 1958	NRFRLL.....	do.....	July 4, 1958	do.....	do.....	Do.
32.....	May 26, 1958	NRFRLL.....	do.....	Jan. 13, 1960	do.....	do.....	Longline.
33.....	July 7, 1959	OFC.....	Trolling.....	July 13, 1960	do.....	Taiwa Maru.....	Livebait.
34.....	Sept. 10, 1960	OFC.....	Seine.....	Sept. 10, 1960	American.....	unknown.....	Do.
35.....	Sept. 10, 1960	OFC.....	do.....	Sept. 13, 1960	do.....	do.....	Do.

Recovery No.	Release			Recapture			Days out
	Position		Size (cm.)	Position		Size (cm.)	
	Latitude	Longitude		Latitude	Longitude		
18.....	33°25' N	118°15' W	76.0	31°30' N	149°40' E		324
19.....	29°00' N	118°30' W	84.0	36°40' N	178°12' E	85.0	176
20.....	29°00' N	118°30' W	91.0	30°10' N	178°54' W	93.0	182
21.....	33°42' N	121°15' W		31°55' N	143°15' E	ca. 75	192
22.....	36°39' N	123°16' W		35°50' N	142°50' E		271
23.....	36°57' N	130°38' W		34°30' N	142°50' E	75.7	286
24.....	33°00' N	143°45' E	ca. 81	32°01' N	144°58' E		20
25.....	33°18' N	143°31' E	ca. 81	33°40' N	144°40' E	79.1	12
26.....	32°59' N	143°19' E	ca. 81	32°07' N	144°52' E		16
27.....	33°00' N	143°45' E	ca. 87	35°23' N	148°54' E	84.8	21
28.....	33°00' N	143°45' E	ca. 82	33°58' N	152°20' E	81.5	30
29.....	33°18' N	143°31' E	ca. 85	34°18' N	152°51' E		30
30.....	33°00' N	143°45' E		34°37' N	153°03' E	76.5	83
31.....	33°18' N	143°31' E	ca. 83	33°52' N	154°21' E		30
32.....	33°00' N	143°45' E	ca. 70	33°08' N	138°15' E	ca. 92	57
33.....	43°01' N	125°34' W	67.0	33°53' N	152°23' E		372
34.....	46°01' N	126°30' W	66.0	46°04' N	126°27' W		4 hr.
35.....	46°04' N	126°27' W	68.0	46°10' N	126°10' W		3

¹ CFG=California Department of Fish and Game; OFC=Fish Commission of Oregon; and NRFRLL=Nankai Regional Fisheries Research Laboratory
² Data of the California tag recoveries were reported by Ganssle and Clemens (1953), Blunt (1964), Investigative Society of Tuna Fishery (1955), and in personal correspondence from H. B. Clemens dated July 9, 1967.

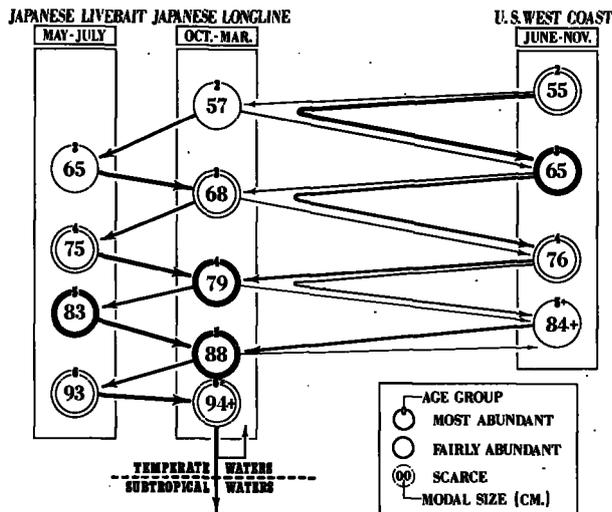


FIGURE 8.—Diagrammatic representation of albacore migration, by size (age) groups.

Figure 8 is a diagrammatic representation of the movements of albacore among the three fisheries. Since the sizes of the fish differ from one fishery to another (fig. 5), the migration of the albacore is hypothesized on the basis of size (age) groups. The approximate modal size for each year class in the catch is shown for each fishery. While it is not possible to describe quantitatively the movements among the fisheries, the following types or patterns of movements are the major elements in our suggested model of North Pacific albacore migrations:

I-a. This is the westward migration, in the fall, of 2-year-old (55 cm.) fish from the area of the American fishery. These albacore have been only partly recruited into the exploited stock at age 2; their recruitment will be completed when they are 3 years old. The majority of 2-year-olds do not

get far enough west to reach the center of the Japanese winter longline fishery, and they may not even reach the eastern fringe of the developing winter longline grounds. In either case they do not migrate with the main body of southwesterly migrating fish in the longline fishery, but remain outside the area of any fishery until they return to the American fishery the following season as 3-year-olds.

I-b. The remaining 2-year-olds, those that do reach the center of the Japanese longline fishery, continue moving in a southwesterly direction between October and March and enter the Japanese livebait fishery in the spring as 3-year-olds. This group is apparently small, judging by the small numbers of 3-year-olds in the Japanese livebait catch.

II-a. The 3-year-olds (65 cm.), which are the major components of the American catch, may begin their westerly migration as early as August or September, but a significant portion of this group departs later in the season and does not reach the center of the Japanese longline fishery. These fish return to the American fishery the following summer as 4-year-olds.

II-b. The rest of the 3-year-olds, perhaps an equally significant portion, judging from the numbers of this year class in the American fishery and the Japanese longline fishery (fig. 5), enter the Japanese longline fishery by early winter. These fish continue westward to enter the Japanese livebait fishery the following spring as 4-year-olds.

III-a. The bulk of the third age group in the American catch, the 4-year-olds (76 cm.), migrate westward from the American fishery into the Japanese longline fishery and subsequently continue into the Japanese livebait fishery as 5-year-olds.

III-b. A small fraction of the 4-year-olds separates from the others and returns to the American fishery the following summer as 5-year-olds. This is only a small fraction, however, since 5-year-olds are an insignificant proportion of the American catch.

IV-a. Nearly all of the 5-year-old and older fish in the American fishery migrate into the Japanese livebait fishery by way of the Japanese longline fishery.

IV-b. A few of these older fish do separate and return to the American fishery. This is indicated

by a tag recovery (table 1 and fig. 10, Recovery No. 14).

V-a. The Japanese livebait fishery is notably lacking in 2- and 3-year-old fish, which are fairly abundant in the American fishery. Such small fish, when present, may migrate into the American fishery after spending a part of the season in the longline fishery.

V-b. Of the more common sizes of fish in the Japanese livebait fishery, only the two youngest groups (the 4- and 5-year-olds) provide some fish which migrate into the American fishery. However, these are few, since by the time they enter the American fishery they are already 5- and 6-year-olds, and these age groups make an insignificant contribution to the American catch.

VI. The Japanese winter longline fishery receives fish from both the Japanese livebait fishery and the American fishery. From the longline fishery, the greater part of the albacore move into the Japanese livebait fishery, while the rest migrate east into the American fishery.

VII. The 6-year-olds (94 cm.) and older age groups in the winter longline fishery do not enter into either of the other two fisheries. A portion of these fish, having attained sexual maturity in temperate waters (albacore mature at around 90 cm.), move south into subtropical waters in the spring to form the reproductive unit of the North Pacific population (Ueyanagi, 1957; Otsu and Uchida, 1959). Since these older fish are always present in the winter longline fishery, it is apparent that at least some of them return north in the spring, possibly to the east of and beyond reach of the Japanese livebait fishery.

VIII. Most of the groups of fish exploited in the Japanese livebait fishery move from that fishery into the winter longline fishery and then back into the livebait fishery, thus remaining in the western North Pacific. Judging by the sizes of fish exploited, it is clear that only a small fraction of the fish in the livebait fishery migrate across the Pacific into the American fishery.

The above model is summarized in table 3, and the general pattern of migration of albacore in the North Pacific is illustrated in figure 9.

DISCUSSION

Data from tag recoveries support the model and thus the underlying hypothesis that there is a single population of albacore in the North Pacific

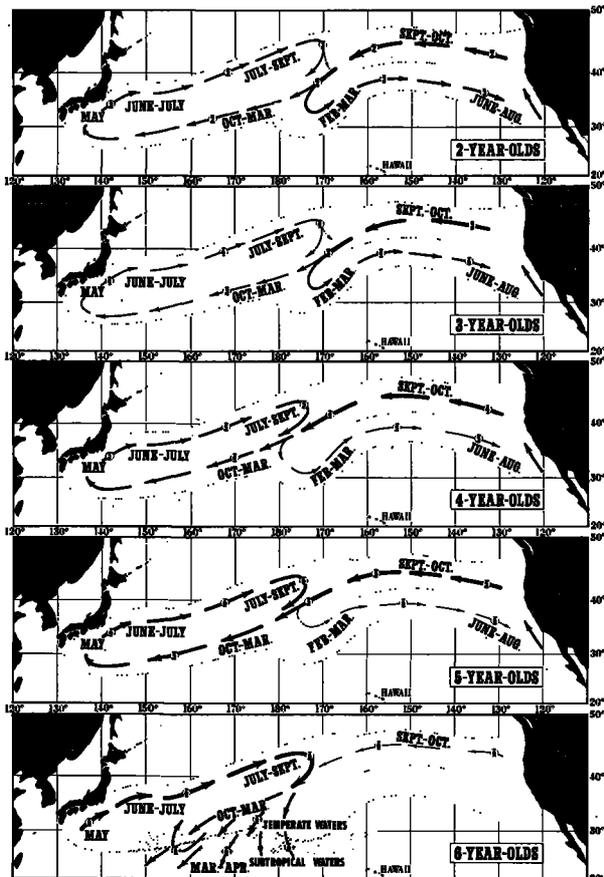


FIGURE 9.—Model of albacore migrations in the North Pacific Ocean, by age groups (ages encircled).

Ocean. In figure 10 and table 4 are shown the postulated migrations of each of the tagged fish recovered to date. The migration believed undertaken by each fish between tagging and recovery is related to one or more of the types of movement described in the preceding section and summarized in table 3.

There has not been any recovery of fish tagged as 2-year-olds in the American fishery, but this is understandable in view of their small number. Of 218 fish tagged by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, in the general area of this fishery between longitudes 110° W. and 127° W., only 11 were 2-year-old fish. Judging from the fact that this age group is poorly represented in the Japanese longline fishery and that 3-year-olds are very scarce in the Japanese livebait fishery, it can be assumed that most of the fish return to the American fishery the following season and, along with new recruits, form the

dominant 3-year-old age group (type I-a). The others probably constitute the 2-year-olds in the longline catch and the 3-year-olds in the following year's Japanese livebait catch (type I-b).

It has been hypothesized that a portion of the large adults occurring in the Japanese winter longline fishery move south during the spring into subtropical waters to form the reproductive part of the North Pacific population (Ueyanagi, 1957; Otsu and Uchida, 1959). We believe that it is fish from this group that appear in the Hawaiian longline fishery each year and contribute to an increase in landings beginning around April. However, since the annual landings of albacore in Hawaii are very small (between 10,000 and 21,000 pounds during the 1955-59 period), it is possible that the Hawaiian Islands are on the eastern fringe of this southward migration.

Otsu and Uchida (1959) have suggested that the albacore occurring in Hawaiian waters are a segment of the North Pacific spawning population. They also agree with Ueyanagi (1957) that albacore spawning probably takes place in subtropical waters in the areas under the influence of the

TABLE 3.—Summary of the model of albacore migrations in the North Pacific Ocean

Type of movement	Pattern of movement among fisheries
I-a-----	U.S. west coast (2-year-olds) → midocean (most) → U.S. west coast (3-year-olds)
I-b-----	U.S. west coast (2-year-olds) → Japanese longline → Japanese livebait (3-year-olds)
II-a-----	U.S. west coast (3-year-olds) → midocean → U.S. west coast (4-year-olds)
II-b-----	U.S. west coast (3-year-olds) → Japanese longline → Japanese livebait (4-year-olds)
III-a-----	U.S. west coast (4-year-olds) → Japanese longline (most) → Japanese livebait (5-year-olds)
III-b-----	U.S. west coast (4-year-olds) → midocean (few) → U.S. west coast (5-year-olds)
IV-a-----	U.S. west coast (5-year-olds and older) → Japanese longline (most) → Japanese livebait (6-year-olds and older)
IV-b-----	U.S. west coast (5-year-olds and older) → midocean (few) → U.S. west coast (6-year-olds and older)
V-a-----	Japanese livebait (2, 3-year-olds) → Japanese longline → U.S. west coast (3-, 4-year-olds) (few)
V-b-----	Japanese livebait (4-, 5-year-olds) → Japanese longline → U.S. west coast (5-, 6-year-olds) (few)
VI-----	U.S. west coast (2-, 3-, 4-, 5+- year-olds) → Japanese longline (Mixing) ← Japanese livebait (3-, 4-, 5-, 6-year-olds)
VII-----	Japanese longline (6-year-olds and older) → Subtropical Convergence spawning → Subtropical waters spawning
VIII-----	U.S. west coast (few) → Japanese longline ← Japanese livebait (most)

¹ This term refers to the general area between the center of the Japanese longline fishery and the U.S. west coast, and including the eastern fringe of the longline fishery.

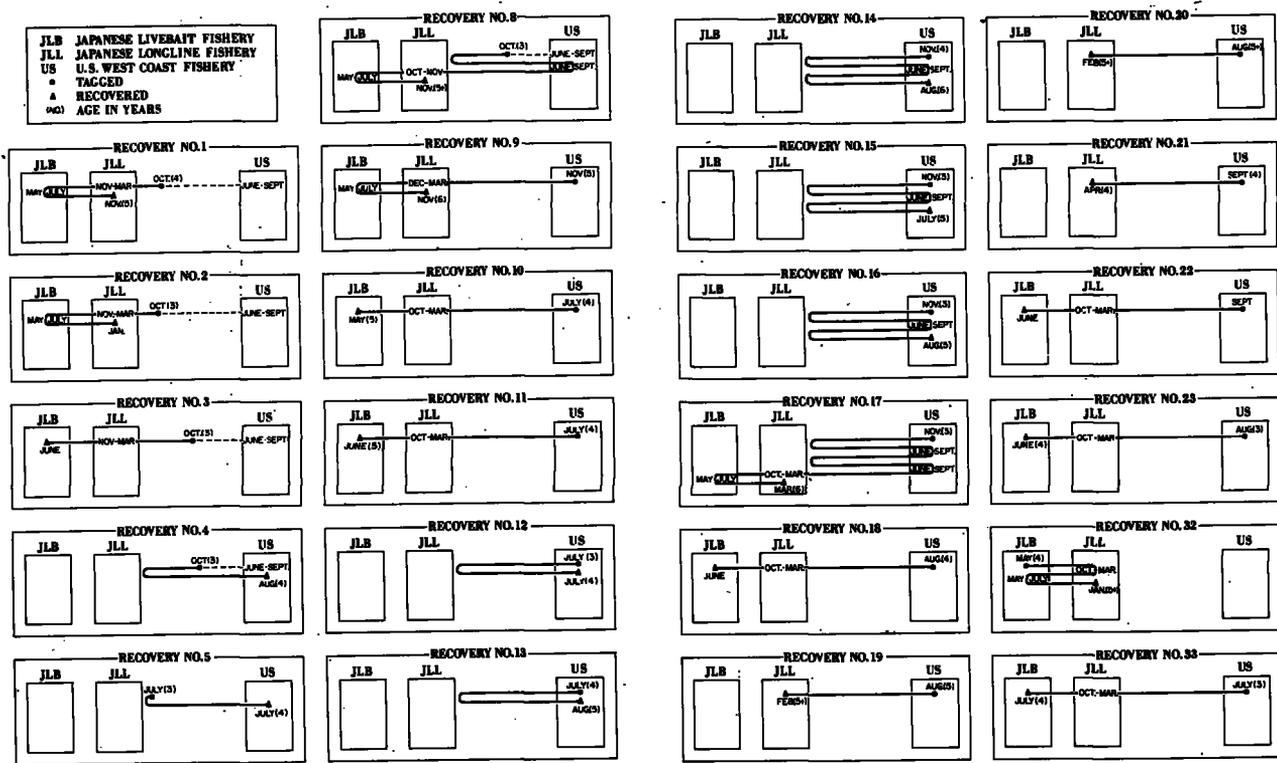


FIGURE 10.—Diagrammatic representation of the postulated migrations of albacore between tagging and recovery (see table 4).

North Equatorial Current. It seems a reasonable hypothesis that spawning occurs during the summer in subtropical waters (the exact spawning grounds have not yet been defined), and that the larval and early juvenile stages are spent in these waters. The collection of young albacore from stomach contents of predator species (Yabe et al., 1958) indicates the occurrence of these stages in subtropical waters. At a later stage, perhaps when the fish are about a year old, they migrate into temperate waters but do not immediately join the exploited stock (Suda, 1958).

As stated previously the Japanese livebait fishery occasionally encounters 1-year-old fish (about 35 cm.). There have been similar occurrences of small fish in the American fishery, for example, during the summer of 1954, when the fishery was reportedly characterized by the appearance of small fish (personal communications, Inter-American Tropical Tuna Commission). Such small fish are probably abundant generally throughout temperate waters, but are not available to the commercial fisheries until they reach the age of 2 or 3.

The virtual absence of 2-year-olds in the Japanese livebait catch, and the relatively small number of this age group in the longline fishery, seem to indicate that recruitment into the exploited stock occurs primarily in the American fishery. This apparent concentration of recruitment in the eastern Pacific may be exaggerated by gear selectivity, as the longline gear used in the central Pacific would not be expected to sample such small fish effectively for several reasons. This objection would not hold, however, in the Japanese livebait fishery, and so it is apparent that the major portion of the recruitment is taking place in the eastern rather than the western North Pacific.

In general, our model indicates a greater volume of migration of the commercial sizes of albacore in the westerly direction, from the American fishery into the Japanese fisheries, than vice versa. At the same time, it indicates that a significant portion of the fish entering the American fishery does not migrate directly into the Japanese fisheries, but instead is exploited over 3 or 4 seasons in the American fishery. Furthermore, the sizes

TABLE 4.—Postulated migration of albacore between tagging and recovery

[Each recovery is related to a "type of movement," shown in table 3.]

Recovery No.	Type of movement	Postulated migration ¹
1	III-a, VIII	US (June-Sept.) → MO (tagged) (Oct.) (78.2 cm.) → JLL (Nov.-Mar.) → JLB (May-July) → JLL (recovered) (Nov.) (size unknown)
2	II-b, VIII	US (June-Sept.) → MO (tagged) (Oct.) (68 cm.) → JLL (Nov.-Mar.) → JLB (May-July) → JLL (recovered) (Jan.) (size unknown)
3	II-b	US (June-Sept.) → MO (tagged) (Oct.) (63.4 cm.) → JLL (Nov.-Mar.) → JLB (recovered) (June) (size unknown)
4	II-a	US (June-Sept.) → MO (tagged) (Oct.) (59.9 cm.) → US (recovered) (Aug.) (72.3 cm.)
5	II-a	MO (tagged) (July) (83.4 cm.) → MO (Oct.-Mar.) → US (recovered) (July) (78.0 cm.)
6		Tagged and recovered in American fishery during same season.
7		
8	II-a, III-a, VIII	US (June-Sept.) → MO (tagged) (Oct.) (65.1 cm.) → US (June-Sept.) → JLL (Oct.-Mar.) → JLB (May-July) → JLL (recovered) (Nov.) (94.8 cm.)
9	IV-a, VIII	US (tagged) (Nov.) (85.2 cm.) → JLL (Dec.-Mar.) → JLB (May-July) → JLL (recovered) (Nov.) (97.5 cm.)
10	II-a	US (tagged) (July) (78 cm.) → JLL (Oct.-Mar.) → JLB (recovered) (May) (85.2 cm.)
11	III-a	US (tagged) (July) (75 cm.) → JLL (Oct.-Mar.) → JLB (recovered) (June) (size unknown)
12	II-a	US (tagged) (July) (65 cm.) → MO (Oct.-Mar.) → US (recovered) (July) (77.3 cm.)
13	III-b	US (tagged) (July) (75 cm.) → MO (Oct.-Mar.) → US (recovered) (Aug.) (84.5 cm.)
14	II-b, IV-b	US (tagged) (Nov.) (79.4 cm.) → MO (Dec.-Mar.) → US (June-Sept.) → MO (Oct.-Mar.) → US (recovered) (Aug.) (92.6 cm.)
15	II-a, III-b	US (tagged) (Nov.) (88.6 cm.) → MO (Dec.-Mar.) → US (June-Sept.) → MO (Oct.-Mar.) → US (recovered) (July) (86.4 cm.)
16	II-a, III-b	US (tagged) (Nov.) (85.9 cm.) → MO (Dec.-Mar.) → US (June-Sept.) → MO (Oct.-Mar.) → US (recovered) (Aug.) (81.2 cm.)
17	II-a, III-b, IV-a, VIII	US (tagged) (Nov.) (80.8 cm.) → MO (Dec.-Mar.) → US (June-Sept.) → MO (Oct.-Mar.) → US (June-Sept.) (Mar.) (90 cm.)
18	III-a	US (tagged) (Aug.) (76.0 cm.) → JLL (Oct.-Mar.) → JLB (recovered) (June) (size unknown)
19	IV-a	US (tagged) (Aug.) (84 cm.) → JLL (recovered) (Feb.) (88 cm.)
20	IV-a	US (tagged) (Aug.) (91 cm.) → JLL (recovered) (Feb.) (93 cm.)
21	III-a	US (tagged) (Sept.) (size unknown) → JLL (recovered) (Apr.) (ca. 75 cm.)
22		US (tagged) (Sept.) (size unknown) → JLL (Oct.-Mar.) → JLB (recovered) (June) (size unknown)
23	II-b	US (tagged) (Aug.) (size unknown) → JLL (Oct.-Mar.) → JLB (recovered) (June) (76.7 cm.)
24-31		Tagged and recovered in livebait fishery during same season.
32	VIII	
33	II-b	US (tagged) (July) (87 cm.) → JLL (Oct.-Mar.) → JLB (recovered) (July) (size unknown)
34-35		Tagged and recovered in American fishery during same season.

¹ US=American fishery; JLL=Japanese longline fishery; JLB=Japanese livebait fishery; MO=midocean between Japanese longline fishery and U.S. west coast, or on eastern fringe of Japanese longline fishery.

of fish commonly exploited by the Japanese livebait fishery (4-, 5-, and 6-year-olds) are such that only a small percentage would appear later in the American fishery. This is, to a large extent, also true of the Japanese longline fishery, which takes largely the 4-, 5-, and 6-year-old fish.

It is therefore easy to understand why tagging in the Japanese livebait fishery has not resulted in any recoveries in the American fishery. The chances of such recoveries are slim because of the small number of fish of these older age groups appearing in the American catch. Tagging of the less common smaller fish in the livebait or longline fisheries should increase the chances of recoveries in the American fishery.

SUMMARY

1. A model of the migration of albacore in the North Pacific Ocean is proposed on the basis of tag recovery data, age and growth information, and distribution and size frequency data from various fisheries. This model is consistent with the hypothesis that there is a single population of albacore in the North Pacific Ocean.

2. The migration of albacore within the areas of the three major fisheries is in general reflected by the seasonal shifting of the respective fishing grounds. The Japanese livebait fishery begins off southern Japan in late April or May and gradually moves in the north and northeasterly directions. In July the fishery rapidly declines

as the fish move offshore from central Japan in an easterly direction.

The Japanese longline fishery begins in October with its center of abundance located in midocean between longitudes 170° E. and 180°; and along latitude 38° N. The fishery generally shifts in a southwesterly direction with the advance of the season. At the end of the season, in March, the center of concentration is located around 30° N., 140° E.

The American fishery begins off Baja California in June and gradually shifts north along the coast, as well as offshore, as the season progresses.

3. Tag recoveries have shown transpacific movements of albacore from the American fishery into the Japanese longline and livebait fisheries and from midocean into both the American and Japanese fisheries. Tagging in the Japanese livebait fishery has produced one recapture in the longline fishery.

4. The three North Pacific fisheries exploit different sizes of fish. Assuming that the first year's growth of albacore is about 30 cm., it is postulated that the fish are 2-years-old (about 50 cm.) when they first enter the commercial fisheries. On this basis it is shown that the Japanese livebait fishery takes four groups, which are approximately 3-, 4-, 5-, and 6-year-old fish, with modal lengths of 65, 75, 83, and 93 cm. Five-year-old fish are usually the principal component of the catch. The catches in the winter longline fishery are composed of 2- to 8- or 9-year-old fish, with modal lengths of approximately 57, 68, 79, 88, 94 cm., and larger. The 4- and 5-year-old fish are most numerous in the catch. The American fishery usually exploits 2-, 3-, and 4-year-old fish (55, 65, 76 cm.), but small numbers of older age groups (5- and 6-year-olds) also appear in the catches. The 3-year-old fish are generally most abundant. These differences in sizes among the fisheries are considered in developing the model of albacore migration.

5. It is postulated that albacore undertake no more than one transpacific migration within a 1-year period.

6. The model of the migration of albacore among the fisheries is briefly as follows: a varying portion of the 2-, 3-, and 4-year-old fish and nearly all of the older fish in the American fishery migrate westward into the Japanese longline fishery, and subsequently into the Japanese live-

bait fishery the following spring. The remainder either do not reach, or may possibly enter the fringe of the Japanese longline fishery, and return to the American fishery the following summer. Consequently, some of the fish may be available to the American fishery for as many as four or five seasons (fig. 8).

The Japanese livebait fishery is notably lacking in 2- and 3-year-old fish. Such small fish, when present, may migrate into the American fishery after spending a part of the season in the winter longline fishery. Of the more common sizes in the livebait fishery, only the 4- and 5-year-old groups provide some fish that enter the American fishery the following summer, but these are few since 5- and 6-year-old fish comprise only a very small proportion in the American catch. The bulk of the fish from the livebait fishery migrate into the longline fishery in the fall and return to the livebait fishery the following spring.

Fish enter the winter longline fishery from both the American fishery and the Japanese livebait fishery. A large part of these fish migrate southward in the winter longline fishery, and subsequently enter the livebait fishery in the spring, while a few separate and migrate into the American fishery by summer.

A portion of the large adults occurring in the Japanese winter longline fishery (6-year-olds and older) move south during the spring into subtropical waters, where they make up the reproductive unit of the North Pacific population.

7. It is hypothesized that spawning occurs in subtropical waters during the summer, and that the larval and early juvenile stages are spent in these waters. When about a year old, the fish migrate into temperate waters, but they do not immediately join the exploited stock. The albacore are generally not available to commercial fisheries until they reach the age of 2 or 3.

8. It appears that most of the recruitment into the exploited stock takes place in the eastern rather than the western North Pacific. There is a greater volume of migration of the commercial sizes of albacore in the westerly direction from the American fishery into the Japanese fisheries, than vice versa.

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LITERATURE CITED

- BLUNT, CLARKE E., JR.
1954. Two mid-Pacific recoveries of California-tagged albacore. *California Fish and Game*, vol. 40, no. 3, pp. 339.
- CLEMENS, HAROLD B.
1955. Catch localities for Pacific albacore (*Thunnus germo*) landed in California, 1951 through 1953. *California Department of Fish and Game, Fish Bulletin* 100, 28 pp.
- GANSSLE, DAVID, and HAROLD B. CLEMENS.
1953. California-tagged albacore recovered off Japan. *California Fish and Game*, vol. 39, no. 4, pp. 443.
- GRAHAM, JOSEPH J.
1957. Central North Pacific albacore surveys, May to November 1955. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries 212, 38 pp.
1959. Northeastern Pacific albacore survey. Part I. Biological observations. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries 310, 33 pp.
- INVESTIGATIVE SOCIETY OF TUNA FISHERY.
1955. On the recapture of an American-tagged albacore. *Tuna Fishing*, no. 21, pp. 37. [In Japanese.]
- MIE PREFECTURAL FISHERIES EXPERIMENTAL STATION.
1957. *Katsuo gyogyō shiken chōsa hōkoku* [Reports of skipjack fishery investigations], no. 12, 86 pp. [In Japanese.]
- NANKAI REGIONAL FISHERIES RESEARCH LABORATORY.
1950. *Katsuo-maguro shigen chōsa yōhō* [Summary report of tuna resource investigations]. 70 pp. [In Japanese.]
1951. Supplementary Report No. 1. 194 pp. [In Japanese.]
1954. Average year's fishing condition of tuna longline fisheries, 1952 edition, albacore section. Published by Federation of Japan Tuna Fishermen's Cooperative Associations, Tokyo. [In Japanese; English translation] U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries 169, 131 pp.
1959. Average year's fishing condition of tuna longline fisheries, 1958 edition. (Text and Atlas). Published by Federation of Japan Tuna Fishermen's Cooperative Associations, Tokyo. [In Japanese with English figure and table captions.]
- OTSU, TAMIO.
1960. Albacore migration and growth in the North Pacific Ocean as estimated from tag recoveries. *Pacific Science*, vol. 14, no. 3, pp. 257-266.
- OTSU, TAMIO, and RICHARD N. UCHIDA.
1959. Sexual maturity and spawning of albacore in the Pacific Ocean. U.S. Fish and Wildlife Service, *Fishery Bulletin* 148, vol. 59, pp. 287-305.
- SHOMURA, RICHARD S., and TAMIO OTSU.
1956. Central North Pacific albacore surveys, January 1954-February 1955. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries 173, 29 pp.
- SUDA, AKIRA.
1958. Catch variations in the North Pacific albacore. . . I. Recruitment and dispersion of the North Pacific albacore. Report of Nankai Regional Fisheries Research Laboratory, no. 9, pp. 103-116. [In Japanese with English abstract and table and figure captions.]
- UEYANAGI, SHOJI.
1957. Spawning of the albacore in the western Pacific. Report of Nankai Regional Fisheries Research Laboratory, no. 6, pp. 113-124. [In Japanese with English abstract and table and figure captions.]
- VAN CAMPEN, WILVAN G.
1960. Japanese summer fishery for albacore (*Germo alalunga*). U.S. Fish and Wildlife Service, Research Report 52, 29 pp.
- VAN CAMPEN, WILVAN G., and GARTH I. MURPHY.
1957. Tagging albacore on a Japanese bait boat. *Pacific Fisherman*, vol. 55, no. 3, pp. 37-43.
- YABE, HIROSHI, SHOJI UYANAGI, SHOJI KIKAWA, and HISAYA WATANABE.
1958. Young tunas found in the stomach contents. Report of Nankai Regional Fisheries Research Laboratory, no. 8, pp. 31-48. [In Japanese with English abstract and table and figure captions.]

FURTHER STUDIES ON FISHWAY SLOPE AND ITS EFFECT ON RATE OF PASSAGE OF SALMONIDS

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ABSTRACT

The rates of passage of chinook (*Oncorhynchus tshawytscha*) and sockeye (*O. nerka*) salmon and steelhead trout (*Salmo gairdneri*) were studied in 1:16- and 1:8-slope, pool-and-overfall fishways. In general, the passage of salmonids through the 1:8-slope fishway with a 1.0-foot rise between pools was as fast as, or faster than, in the 1:16-slope fishway with a 1.0-foot

rise. When the rise between pools was increased to 1.5 feet in the 1:8-slope fishway, chinook and sockeye were slower. The "Dalles-type" weir crests in a 1:16-slope fishway appeared to accelerate chinook passage. Chinook and sockeye displayed seasonal differences in times within the species.

The effect of fishway slope¹ on the passage of fish is an important factor in fishway design. Of equal importance is the potential saving in construction costs which will accrue if it can be demonstrated that fishways with steeper slopes pass fish equally as well as the presently accepted standard designs.

Years of water resource development on the Columbia River for irrigation, power, and flood control have produced a multitude of problems relating to the passage of anadromous fishes.

Fish passage requirements and criteria constitute a continuing problem in fishway construction. Varying physical and biological conditions require constant research to meet the demands in each specific instance. Intensive efforts to provide an economical solution to our fish passage problems at dams bring into focus the need for basic information on the reaction of upstream migrant salmon to various physical

characteristics of fishways. Until recently little research has been done on fish passage requirements.

Slopes of 1:20, 1:16, and 1:10 are found in existing fishways on the Columbia River. The 1:16 slope has come to be the accepted standard for the larger fishways. If a steeper slope shows equal fish-passing ability, fishway construction costs can be reduced. Scientists at the fisheries-engineering research project, located at Bonneville Dam on the Columbia River, are studying the reaction of migrating salmon to different fishway slopes and other factors that may influence the passage of salmon at dams.²

This paper presents a continuation of research, reported by Gauley (1960) on the effect of fishway slope and other factors on the rate of passage of salmonids. The results of this research provide basic information for the solution of fishway problems.

EXPERIMENTAL EQUIPMENT

LABORATORY

The research facilities are adjacent to the Washington shore fishways (figs. 1 and 2). Collins and Elling (1960) present a detailed descrip-

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¹ Fishway slope is defined as the ratio of the rise or vertical distance to the run or horizontal distance.

² This project was financed by the U.S. Army Corps of Engineers as part of a broad program of fisheries-engineering research for the purpose of providing design criteria for more economical and more efficient fish-passage facilities at Corps projects on the Columbia River.

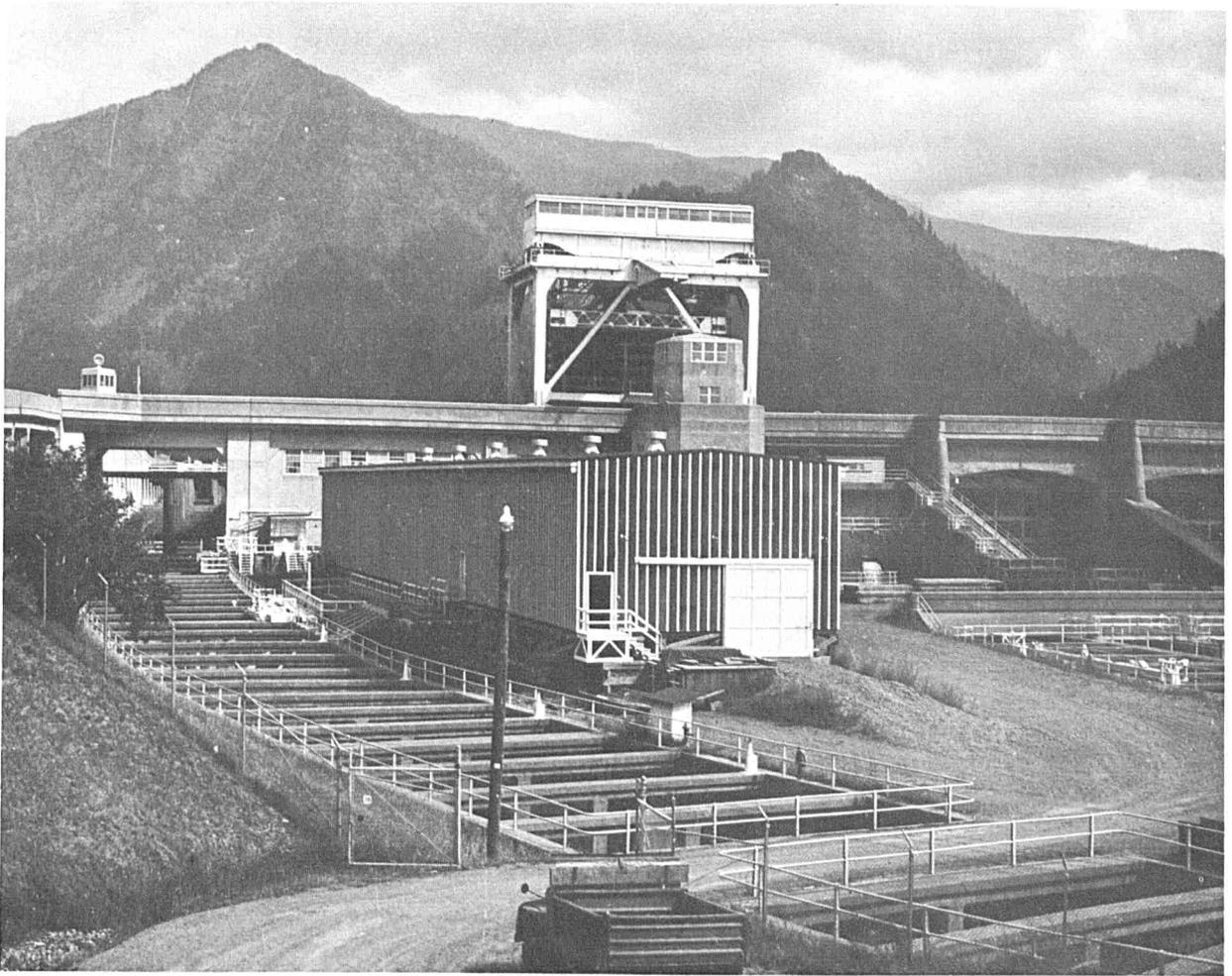


FIGURE 1—Research facilities at Bonneville Dam. The north end of the main dam is shown in the background and part of the Washington shore fishway in the foreground.

tion of the laboratory. In brief, the key features for operation of the facility are (1) the procurement of fish and (2) the introduction and control of water.

A removable picketed lead blocks a small portion of the Washington shore fishway, thus diverting fish into a short entrance fishway leading to a collecting pool in the laboratory. Test fish leave the laboratory through a short exit fishway which returns them to the main fishway.

The water is supplied by two sources and controlled by a system of pipes and valves. Most of the water is supplied from the forebay through a large conduit to the flow introduction pool in the laboratory. The maximum flow is about 200 cubic feet per second (c.f.s.). Water from the main fishway (about 20 c.f.s.) supplies the exit fishway.

A series of valves control the inflow of water, and drain valves control the outflow so that hydraulic conditions in the test and control fishway can be accurately controlled.

FISHWAYS

Fish passage was studied in two pool-and-overfall fishways without submerged orifices. The total gain in elevation was the same for both fishways, although physical characteristics of each could be altered independently.

Slopes

The experimental fishways were constructed of prefabricated frames and heavy plywood panels. By erecting a center wall, the test area was divided into two passageways 11.5 feet wide. The slopes in both passageways could be made identical, or

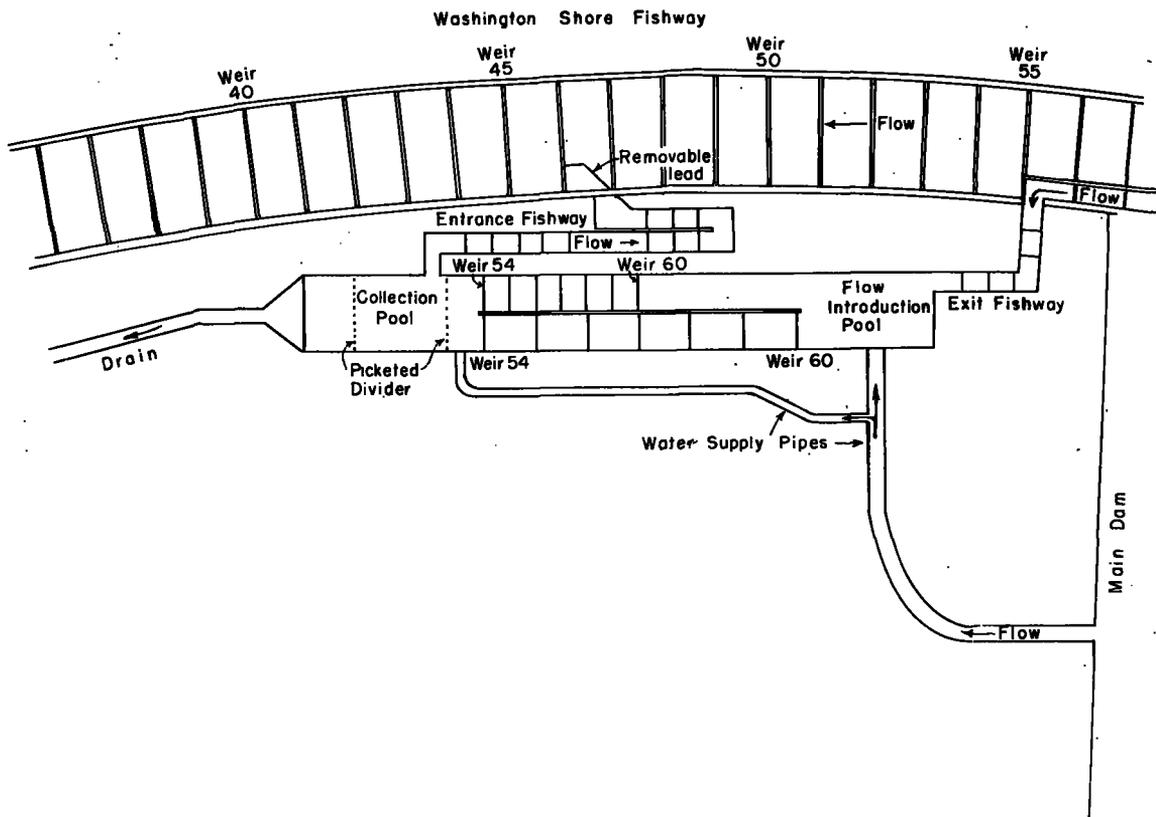


FIGURE 2—General plan of the laboratory, bypass, and associated experimental components. Weir designations indicate elevation in feet above mean sea level.

one could be altered independently without disturbing the other by installing the fishway floors in previously constructed sections to give the desired slope (figs. 3 and 4).

The fishway weirs which were transferable were constructed with concrete bases to reduce buoyancy. By the addition or removal of weirs, rise between pools could be changed. Such changes were made only in the test fishway.

The course of studies utilized two fishway slopes—1:16 (control) and 1:8 (test). The control fishway remained unchanged throughout the

TABLE 1.—Dimensions of fishways used in the slope studies during 1957

Fishway type	Slope	Number of pools	Pool length	Pool width	Mean pool depth	Rise between pools	Elevation gained
			Feet	Feet	Feet	Feet	Feet
1.....	1:16	6	16.0	11.5	6.30	1.0	6
1 B ¹	1:16	6	16.0	4.0	6.30	1.0	6
2.....	1:8	6	8.0	11.5	6.30	1.0	6
3.....	1:8	4	12.0	11.5	6.05	1.5	6

¹ The Dalles-type weir crest (fig. 12) used in this fishway.

season except during a brief period of altered fishway width and weir crests. During the season 1.0-foot and 1.5-foot rises between pools were tested in the 1:8-slope fishway.

Table 1 and figure 5 give the dimensions of fishways used during the 1957 experiments. Hereafter, in the interest of brevity, fishway type numbers will be used to identify the various fishway dimensions and slopes.

Lighting

Controlled light conditions were provided by a battery of 1,000-watt mercury-vapor lamps (fig. 6) which could be adjusted vertically above the water surface, so that identical light intensities prevailed in both fishways. The lamps were suspended vertically 6 feet above the water surface where they produced an average incident light intensity of 700 foot-candles. The range was 300 to 1,000 foot-candles. Light measurements directly beneath the reflectors were highest, whereas the

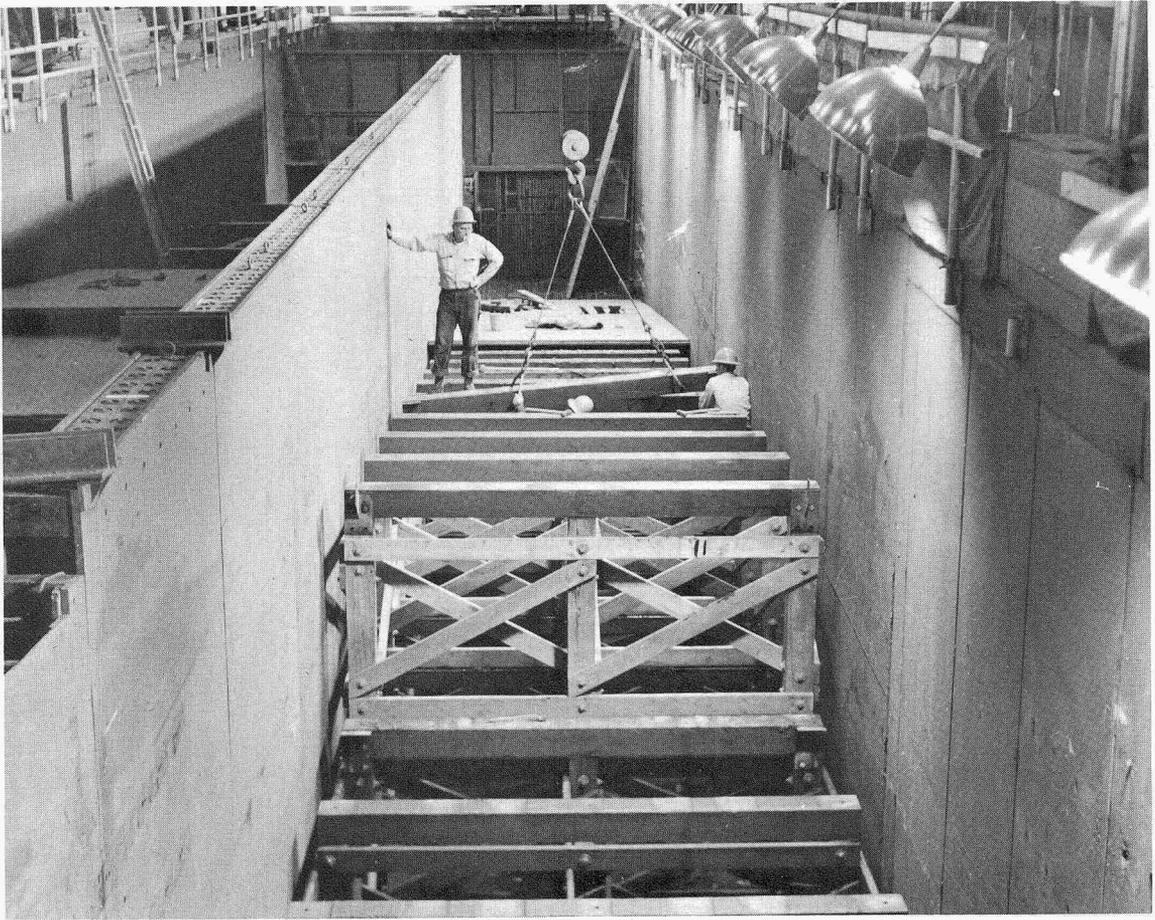


FIGURE 3—Installation of floor frames for the 1:8-slope fishway. A section of floor is in place at the lower end of the fishway.

lower readings were recorded along the walls. These light conditions were comparable to lighting in the main Bonneville fishway during a bright cloudy day.

Hydraulic Conditions

Waterflow through the test area was maintained by regulating the flow of water into the flow introduction pool. Keeping a constant head on the uppermost weir crest permitted maintenance of the water flowing over the fishway weirs at a head of 0.8 foot measured 4 feet upstream from the weir crest. This was the maximum depth at which the desired plunging flow over the weir crests could be stabilized. More water caused a streaming flow in the fishways, which had been demonstrated to temporarily interrupt fish passage (Elling and Raymond, 1959).

METHODS

Release and timing of fish

To evaluate properly the effects of fishway slope on salmonids, the performance of each species both as an individual and in groups, as well as the composite performance of all species must be considered. With this in mind we employed the following three types of releases: (1) an individual fish ascending the fishway alone, (2) groups in which 21 fish of the same species were timed as a group, and (3) mass releases representing all species available.

Individuals

Fish were released into both fishways through the picketed divider at the upstream end of the collection pool. Figure 7 is a side view looking down on the release compartment. The collection

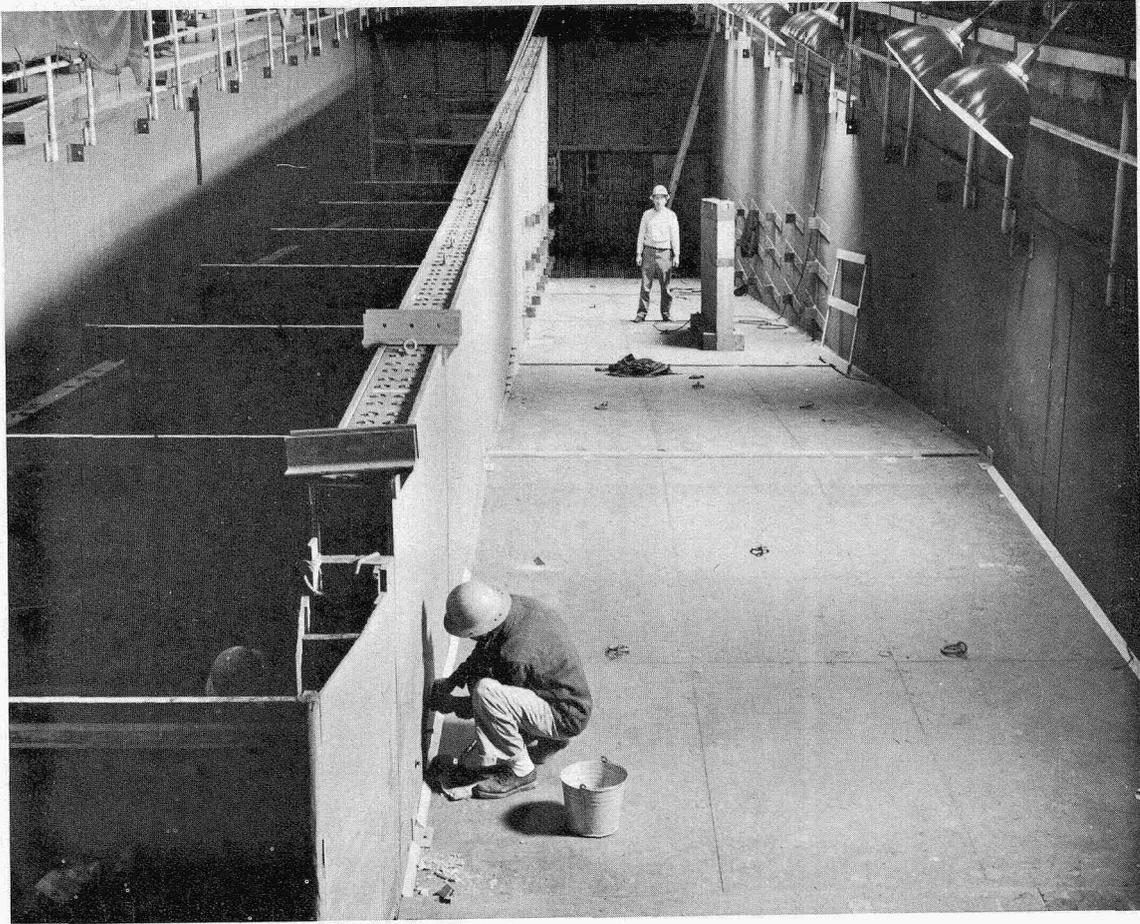


FIGURE 4—The 1:8-slope fishway floor. Wall brackets mark the locations for weirs.

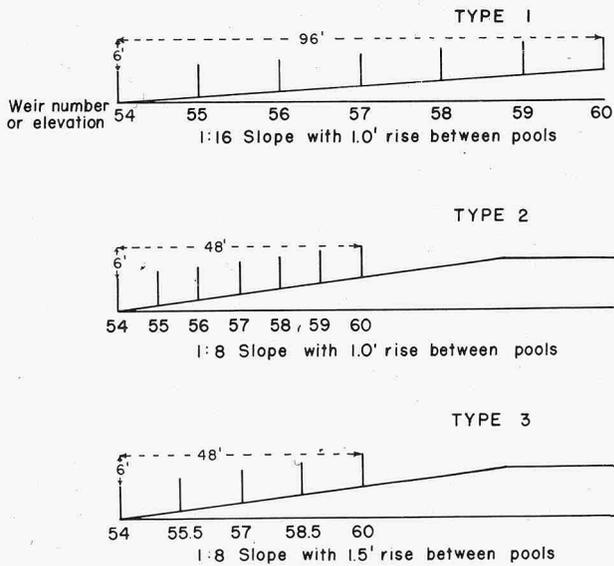


FIGURE 5.—Diagrammatic drawing showing weir placement for the two fishway slopes.

pool is visible at the left margin behind the divider.

The operator at the left has raised the entrance gate to the release compartment to admit a fish from the collection pool, while the operator on the right is preparing to raise the exit gate to the introductory area leading to the test fishway. The second exit gate leads to the control fishway. As each fishway was vacated, another fish was released into the vacant fishway.

During the brief passage through the release compartment each fish was identified by species, and its length was estimated.

The time spent in each pool (pool time) and the total time required to ascend the fishway were kept on separate stop watches. Pool times were obtained by an observer starting one watch and stopping a second one simultaneously as the fish crossed each weir. A second observer timed

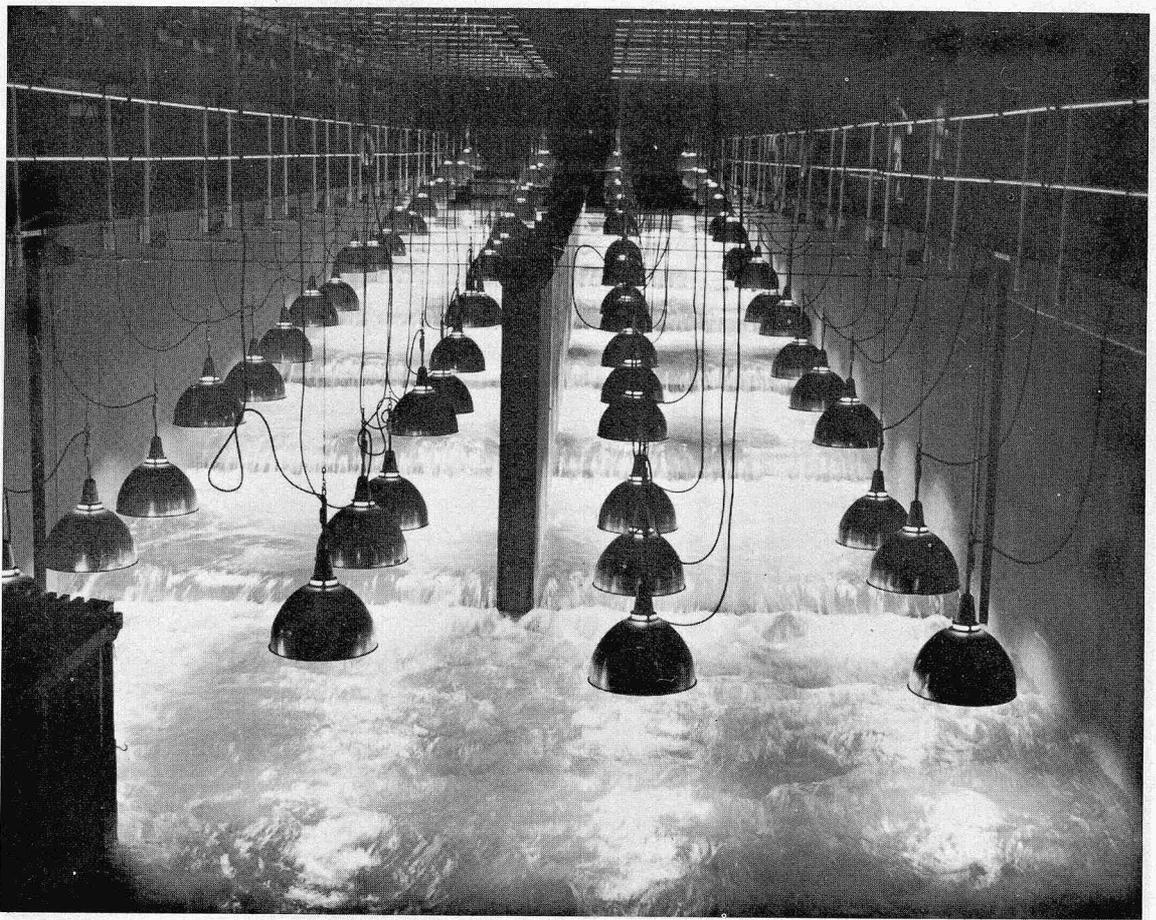


FIGURE 6.—Identical type-1 fishways with 1,000-watt mercury-vapor lights in place. Each light was 6 feet from the water surface.

the fish as it entered and left the fishway, thus obtaining total time spent in the fishway, which could be checked against the sum of the pool times. This method for timing individuals was used by Gauley (1960) for fishway slope experiments at Bonneville.

Groups

Rapid releases of individuals of the same species were made until 21-fish groups were introduced into each fishway. The releasing procedure was similar to that used for individual releases. Fish were released alternately into the test and control fishway until a total of 21 fish had been introduced into each fishway. Lengths were again noted for all fish that entered.

Passage time for group releases was recorded by a 20-pen recorder (fig. 8). The electrically operated recorder was used to tally on a chart all fish entering and leaving each fishway. When con-

tact buttons were pressed at the counting station, a mark was made on the chart. A button at each counting station activated a different pen on the chart. Passage time of the fish was then determined from recorded chart times.

Two observers were stationed at the downstream and upstream ends of each fishway. At the lower end (weir 54) one counter tallied successful passages, while the second counter tallied fish that dropped back out of the test area.

Mass Releases

For these tests, fish were admitted to the introductory pool by raising a section of the picketed divider below each fishway. Thus a number could enter the control and test fishways simultaneously.

To control the number of fish entering, two sizes of release gates were used: A 10-inch wide

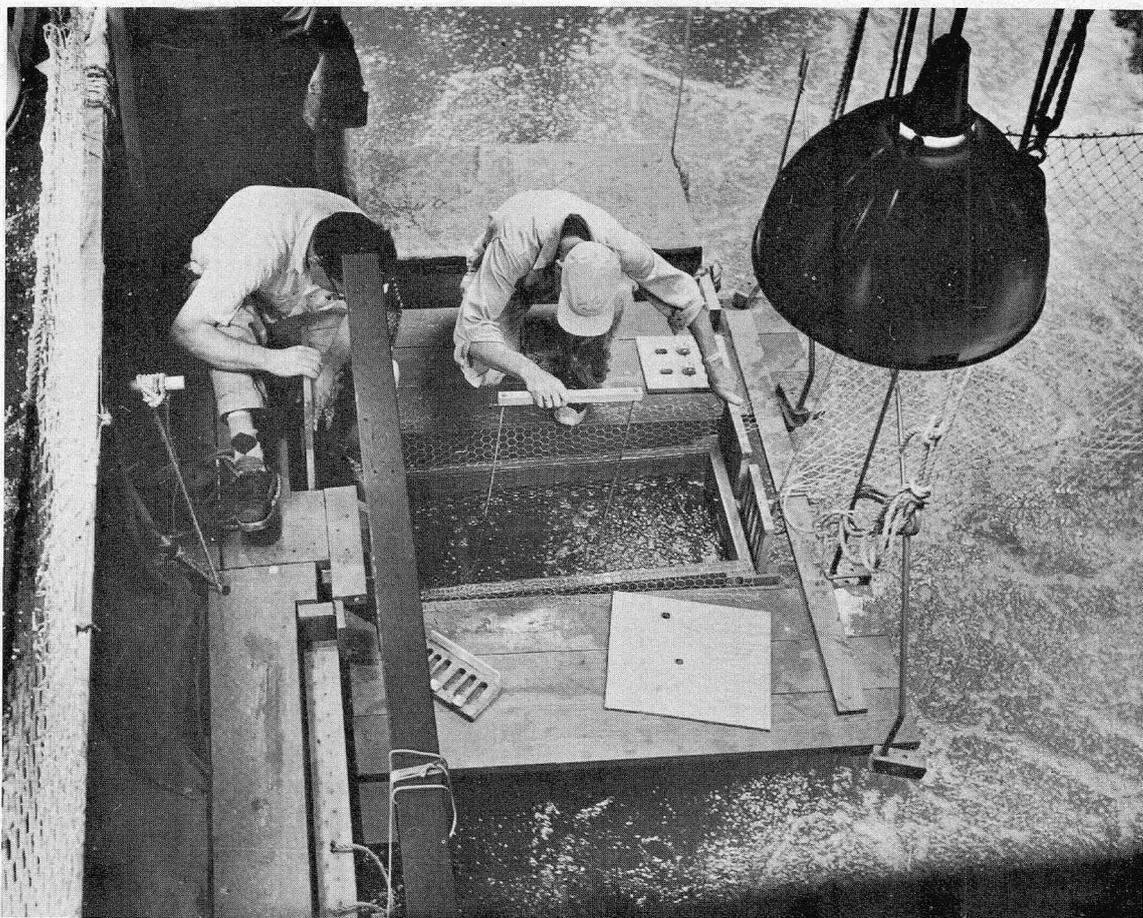


FIGURE 7.—The release compartment. The two exit gates are below the lamp reflector.

opening when fish were in ample supply and a 5-foot opening when fish were less plentiful.

The mass release timing procedure was essentially the same as that used for group releases. Because mass releases were composed of mixed species, it was necessary to identify each fish as it left the fishway at weir 60.

ANALYSIS OF PASSAGE TIMES

Passage time was used as a measure of performance of salmonids in the different fishways tested. The statistic employed and method of analysis varied among individuals, groups, and mass releases, depending on the adaptability of the data to statistical treatment.

Individuals

Median passage times of individuals were compared, and differences between fishways were determined by using 95 percent confidence in-

tervals for the median (Dixon and Massey, 1951). Median passage times with the upper and lower limits are shown in table 2. The median was used in preference to the mean because of the high variance which generally occurred within the passage times in each fishway.

Groups

Both the median elapsed and the mean times were used to evaluate group (21 fish) passage times.

The median elapsed time is defined as the time differences between the median fish entering the fishway and the median fish existing at weir 60. This was determined simply by subtracting the time of the median fish over weir 54 from the time of the median fish over weir 60.

The application of median elapsed time to group releases occasionally appeared to be of limited value as a measure of passage time, because of aberrant values resulting when entry times into

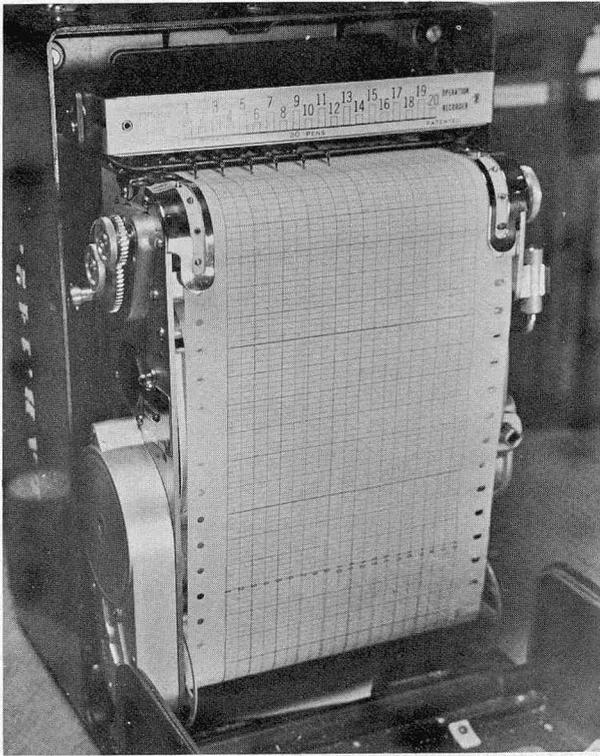


FIGURE 8.—The 20-pen operation recorder used to record passage times during group and mass releases. Six pens are in operation.

the release compartment were prolonged. This situation occurred only when fish were scarce or were reluctant to enter and pass through the

release compartment. Consequently, the analysis of median elapsed time of group releases was limited to releases in which the introductory time was less than 1 hour.

The mean passage time is the difference between the mean time of the group over weir 54 and the mean time of the group over weir 60. In some instances it was necessary to assign an arbitrary exit time for individuals that did not cross weir 60.

If a fish had not passed weir 60 one hour after the last fish had gone over weir 54, one more hour was added and the resulting exit time was used in the determination of the mean exit time for all fish. Differences between passage times in the two fishways were tested by a *t* test on the means or medians at the 95 percent level.

Mass Releases

Mass releases were evaluated by comparing median elapsed times only. Again *t* tests were applied to determine if differences existed between the passage times of the test and control fishways. Here, *t* tests were applied to means of the median elapsed times.

The analysis of passage time for each mass release was accepted as being applicable to the dominant species of salmon. As pointed out earlier, however, mass releases included all species available so that the presence of minority species may have influenced the passage times during

TABLE 2.—Median passage times with lower and upper limits of the 95 percent confidence intervals for chinook, sockeye, and steelhead individuals

[Table A-25 Dixon and Massey, 1951]

Species	Date	Fishway type ¹	No. in sample	Passage time (minutes)			
				Lower limit	Median	Upper limit	
Chinook:							
North.....	April 16-25.....	{	1	38	12.53	17.22	29.46
South.....			1	52	8.58	14.18	18.30
Test.....	May 15-16.....	{	² 1	13	3.47	6.23	24.73
Control.....			1	10	8.15	12.68	70.08
Test.....	April 29-May 7.....	{	² 1 B	69	4.65	6.22	9.02
Control.....			1	39	7.82	12.97	17.75
Test.....	May 31-June 7.....	{	2	74	7.33	9.88	12.03
Control.....			1	56	10.50	13.80	16.88
Test.....	June 12-July 9.....	{	3	46	9.73	15.10	31.37
Control.....			1	68	6.90	10.26	12.37
Sockeye:							
Test.....	July 12-18.....	{	2	111	1.20	1.40	1.90
Control.....			1	72	11.45	14.66	16.43
Test.....	June 13-July 9.....	{	3	65	7.85	12.30	15.42
Control.....			1	82	7.53	9.28	9.83
Steelhead:							
Test.....	April 29-May 7.....	{	² 1 B	10	5.90	11.26	15.08
Control.....			1	15	5.35	11.88	18.55
Test.....	May 31-June 6.....	{	2	8	4.12	9.98	28.97
Control.....			1	6	2.42	10.04	15.17
Test.....	June 12-July 9.....	{	3	33	2.95	6.68	11.22
Control.....			1	29	2.38	6.48	8.87

¹ See table 1.

² The Dalles-type weir crests installed.

these releases. This factor was not present during individual and group releases.

RESULTS

1:16-SLOPE, 1.0-FOOT RISE

Before attempting to determine the effect of slope on the rate of passage of salmonids, we designed an experiment to determine whether passage times were the same in both channels of the experimental flume. If passage times were equal, then any difference found after slope had been altered could be attributed to factors resulting from the difference in slope. Two conventional 1:16-slope fishways with a 1.0-foot rise between pools were installed, one in each channel (fig. 9), and a series of tests, using individuals, groups, and mass releases, were conducted. Results are based mainly on chinook (*Oncorhynchus tshawyts-*

cha), the dominant species in the fish run at the time the tests were conducted.

Thirty-eight individual chinook were tested in the north fishway and 52 in the south fishway. The median passage time was 17.22 minutes in the north fishway and 14.18 minutes in the south. Although the median time was slightly less in the south fishway, it was not significantly so.

Five groups of 21 chinook were timed in their passage through each fishway. The median elapsed passage times are given in table 3. A *t* test on the mean of the median elapsed times indicated there was no significant difference between the passage times in the two fishways.

The results of two mass releases comprised mainly of chinook (table 4) were similar to the individual and group tests which indicated that no difference existed between passage times in the two fishways.



FIGURE. 9—Identical type-1 fishways used to test for equal passage times in the north (on the left) and south channels. The mercury-vapor lamps were removed to provide an unobstructed view of the fishways.

TABLE 3.—Median elapsed passage times of 5 groups of 21 chinook in two type-1 fishways, Apr. 23–26, 1957

Date	North fishway	South fishway
	<i>Minutes</i>	<i>Minutes</i>
Apr. 23.....	17.80	18.17
Apr. 24.....	13.02	24.78
Apr. 25.....	18.68	12.92
Do.....	15.43	16.75
Apr. 26.....	26.11	23.41
Mean.....	18.21	19.22
	<i>t</i>	.617
	<i>P</i>	>.05

1:8-SLOPE 1.0-FOOT RISE

Since the two sides (north and south) must be considered uniform on the basis of the tests, the 1:16-slope fishway in the north channel was removed and a 1:8-slope fishway with a 1.0-foot rise between pools (type 2) was installed (fig. 10). The south fishway was left unchanged to be used as the control fishway. Table 1 gives comparisons of the physical characteristics of the two fishways.

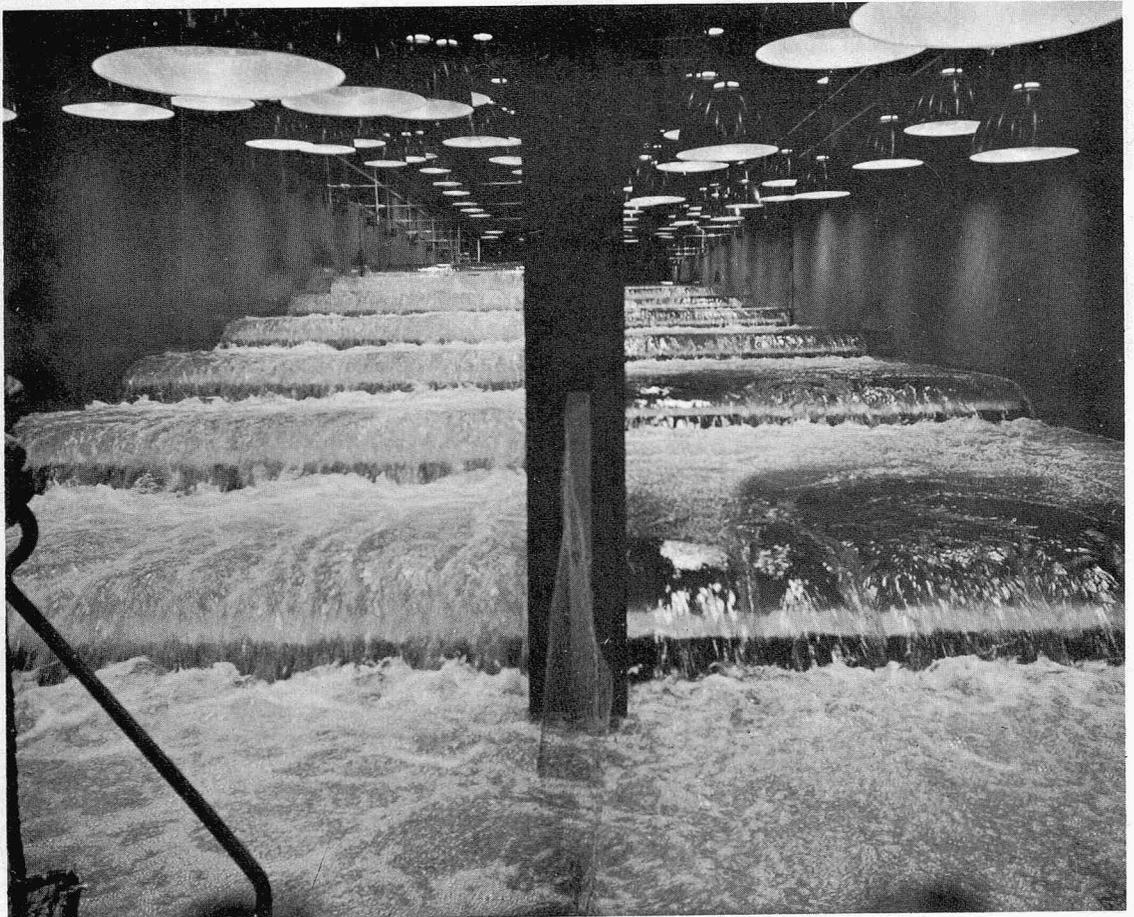


FIGURE 10.—A type-2 fishway on the left and a type-1 on the right. Note the greater turbulence in the type-2 fishway.

TABLE 4.—Median elapsed passage times and species composition¹ of two mass releases in two type-1 fishways, Apr. 19 and 26, 1957

Date	North fishway			South fishway		
	Species composition		Median elapsed time	Species composition		Median elapsed time
	Chinook	Steelhead		Chinook	Steelhead	
Apr. 19.....	<i>Number</i>	<i>Number</i>	<i>Minutes</i>	<i>Number</i>	<i>Number</i>	<i>Minutes</i>
Apr. 26.....	61	18	29.53	68	6	33.87
	111	10	34.55	132	10	29.51
Mean.....			32.04			31.69

¹ Species identification was made as fish left the fishway at weir 60.

Chinook

Seventy-four individual chinook were timed in the test fishway and 56 in the control fishway from May 31 to June 7. The median passage times were 9.88 and 14.00 minutes, respectively. A table of confidence intervals for the median indicates that the passage time was significantly less in the test fishway.

TABLE 5.—Median elapsed and mean passage times of 4 groups of 21 chinook timed in type 2 and type-1 fishways, May 29 and June 5, 1957

Date	Median elapsed time		Mean time	
	Test type-2 fishway	Control type-1 fishway	Test type-2 fishway	Control type-1 fishway
	Minutes	Minutes	Minutes	Minutes
May 29.....	11.37	12.33	8.38	18.70
Do.....	15.08	14.60	20.20	19.05
Do.....	19.57	19.19	17.73	15.27
June 5 ¹			17.79	13.05
Mean.....	15.34	15.37	16.00	16.52

^t P > .001 > .05 > .299 > .05
¹ Median elapsed times were not used because entry period exceeded 1 hour.

A comparison of the median elapsed and mean passage times of four groups of 21 chinook timed through the test and control fishways is given in table 5. A *t* test on the means of the median elapsed times indicated there was no significant difference between passage times in the two fishways. Likewise, an analysis on the means of the mean passage times gave similar results.

A comparison of the median elapsed passage times of six mass releases comprised chiefly of chinook salmon timed through the test and control fishways is given in table 6. Species composition

TABLE 6.—Median elapsed times of six mass releases tested in type 2 and type-1 fishways, May 29 to June 7, 1957

Date	Test type-2 fishway	Control type-1 fishway
	Minutes	Minutes
May 29.....	13.76	11.18
June 3.....	15.79	10.89
June 5.....	23.42	18.67
June 6.....	21.00	22.48
Do.....	21.47	17.13
June 7.....	13.64	12.52
Mean.....	18.01	15.48

^t P > .952 > .05

of these releases is given in table 7. A *t* test on the means of the median times indicated there was no significant difference between the passage times in the test and control fishways.

At the present time, we cannot offer an explanation for the difference between results obtained from individual chinook passage times and chinook released as a group and those released en masse. Individual passage times were significantly less in the test fishway than in the control fishway, but group and mass releases indicated no significant

TABLE 7.—Species composition¹ of mass releases tested in type 2 and type-1 fishways, May 29 to June 7, 1957

Date	Test type-2 fishway			Control type-1 fishway		
	Chinook	Steelhead	Other ²	Chinook	Steelhead	Other ²
	Number	Number	Number	Number	Number	Number
May 29.....	65	3		36	2	1
June 3.....	35	1	16	39	4	7
June 5.....	13	2	3	37	1	2
June 6.....	40	1	2	48	3	3
Do.....	67	1		88	4	1
June 7.....	33		1	29	2	1

¹ Species identification was made as fish left the fishway at weir 60.
² Mostly suckers (*Catostomus sp.*) and squawfish (*Pygocottus sp.*).

difference between passage times in the two fishways.

Sockeye

Tests were conducted on individual sockeye (Columbia River blueback) from July 12 through July 18. A scarcity of this species at this time precluded the use of group or mass releases for comparative purposes. Seventy-two sockeye were timed in the control fishway and 111 in the test fishway. The median times were 14.66 minutes and 1.40 minutes, respectively. Based on the confidence intervals about the medians, a significantly faster ascent was achieved in the test fishway than in the control. Note the striking differences in passage times between the two fishways. This difference was also apparent in the mean passage times (5.98 minutes in the test compared to 16.06 minutes in the control).

This rapid passage time in the test fishway gives rise to several questions. Would these fish react the same way in a longer fishway surmounting a dam? Could they continue at the same rate in a longer fishway, and if so, would this impair their ability to reach the upriver areas and spawn? Examination of these questions will be undertaken in future experiments.

Steelhead

Only 14 individuals were tested during May 31 to June 6, eight in the test fishway and six in the control fishway. The median times based on these small samples are 9.98 and 10.04 minutes respectively, indicating no difference between passage times.

Four mass releases were made in which steelhead comprised the principal species passed (table 8).

The median elapsed times in the test and control fishways are given in table 9. A *t* test on the

TABLE 8.—Species composition ¹ of four mass releases timed through type-2 and type-1 fishways, July 15-18, 1957

Date	Test type-2 fishway				Control type-1 fishway			
	Chinook	Steelhead	Sockeye	Other ²	Chinook	Steelhead	Sockeye	Other ²
	Number	Number	Number	Number	Number	Number	Number	Number
July 15.....	111	173	9	16	39	115	6	4
July 16.....	38	114	10	3	24	80	7	2
July 17.....	42	85	7	-----	12	77	8	3
July 18.....	25	111	12	6	9	67	3	2

¹ Species identification was made as fish left the fishway at weir 60.
² Carp (*Cyprinus* sp.), squawfish (*Ptychocheilus* sp.), and suckers (*Catostomus* sp.).

TABLE 9.—Median elapsed times of four mass releases timed through type-2 and type-1 fishways, July 15-18, 1957

Date	Test, type-2 fishway	Control, type-1 fishway
	Minutes	Minutes
July 15.....	8.98	16.02
July 16.....	9.22	11.59
July 17.....	7.75	12.23
July 18.....	6.50	13.75
Mean.....	8.11	13.35

t
P 4.492 <.05

means of the median elapsed times for the two fishways indicated that the passage time through the test fishway was significantly less. This agrees with the conclusion drawn from research in 1956 (Gauley, 1960); groups of 20 steelhead ascended a similar test fishway in less time than they did the control fishway.

1:8-SLOPE, 1.5-FOOT RISE

In the following series of experiments the 1:8-slope fishway was modified to the condition employing 12-foot pools with a 1.5-foot rise between pools (type 3). It should be noted that an increase in rise between pools changes the flow over the weirs; water velocity increases, and water depth decreases. The control fishway remained unchanged (type 1). The two fishways are illustrated in figure 11.

Chinook

Individual passage times for two periods (June 12-20 and June 28 to July 9) were combined to provide a larger sample. This combination allows comparison of 46 individuals in the test fishway and 68 in the control fishway. The median time of chinook in the test fishway trials (15.10 minutes) was 5 minutes greater than the median

TABLE 10.—Median elapsed and mean passage times (minutes) of seven groups of 21 chinook tested in type-3 and type-1 fishways, June 13-19, 1957

Date	Median elapsed time		Mean time	
	Test, type-3 fishway	Control, type-1 fishway	Test, type-3 fishway	Control, type-1 fishway
	June 13.....	18.65	10.68	24.16
June 13.....	-----	-----	29.96	9.74
June 14.....	20.19	10.18	48.47	21.21
June 14.....	20.91	10.80	33.38	10.78
Do.....	17.40	13.25	37.23	10.02
June 19.....	18.28	16.05	17.79	14.78
Do.....	15.65	12.96	17.81	19.26
Mean.....	18.51	12.30	29.83	14.40

t
P 5.065 <.05 3.405 <.05
¹ Median elapsed times were not used because entry period exceeded 1 hour.

time of the controls (10.26 minutes). Although there was approximately a 5-minute difference in passage times, this was not statistically significant.

The means of the median elapsed and the mean passage times for seven groups of 21 chinook are given in table 10. A *t* test on the means of the median elapsed times indicated that passage in the test fishway was significantly slower than in the control fishway. A similar analysis on the means of the mean passage times gave the same results.

Four mass releases, containing a preponderance of chinook, were made in the test and control fishways. Species composition for these releases are presented in table 11. Table 12 gives the

TABLE 11.—Species composition ¹ of four mass releases passing through type-3 and type-1 fishways, June 12 to July 1, 1957

Date	Test type-3 fishway			Control type-1 fishway		
	Chinook	Steelhead	Sockeye	Chinook	Steelhead	Sockeye
	Number	Number	Number	Number	Number	Number
June 12.....	44	3	-----	49	5	-----
June 13.....	32	-----	-----	31	4	-----
June 19.....	79	3	3	116	18	12
July 1.....	24	8	9	42	14	14

¹ Species identification was made as fish left the fishway at weir 60.

TABLE 12.—Median elapsed times (minutes) of four mass releases tested in type-3 and type-1 fishways, June 12 to July 1, 1957

Date	Test type-3 fishway	Control type-1 fishway
June 12.....	23.85	20.72
June 13.....	18.46	17.36
June 19.....	25.75	11.05
July 1.....	27.97	23.01
Mean.....	24.01	18.04

t
P 1.798 >.05



FIGURE 11.—A type-3 fishway (left) and a type-1 fishway (right).

median elapsed times for four releases in the test and control fishways. In each of the four releases the passage time was greater in the test fishway but a *t* test on the means of the median elapsed times indicated no significant difference between passage times in the two fishways. Here, as was also the case with individual chinook, passage times in the test fishway (type 3) were greater than in the control fishway (type 1) but not significantly so.

Sockeye

Passage times of individual sockeye for the two periods June 13–20 and June 28 to July 9 were combined into a single sample as was done for chinook. The median passage time of 66 sockeye in the test fishway was 12.30 minutes while in the control fishway the median time of 82 sockeye was 9.28 minutes. Although the median time in the test fishway was greater by 3 minutes, there

was no significant difference between the passage times in the two fishways.

The median and mean passage times of five groups of sockeye are presented in table 13. Although the passage time was consistently greater in the test fishway, a *t* test on the means of the median elapsed times indicated there was no significant difference between passage times in the two fishways. A similar analysis on the means of the mean passage time gave the same results.

Steelhead

These tests comprised only the passages of individual fish. No group or mass releases were made. The passage time for the two periods June 12–20 and June 28 to July 9 were combined. The median passage times of 33 individuals in the test fishway and 29 in the control fishway were 6.68 minutes and 6.48 minutes, respectively. A comparison of these times indicated there was no

TABLE 13.—Median elapsed and mean passage times (minutes) of five groups of 21 sockeye tested in type-3 and type-1 fishways, July 3-10, 1957

Date	Median elapsed time		Mean time	
	Test type-3 fishway	Control type-1 fishway	Test type-3 fishway	Control type-1 fishway
July 3.....	17.19	15.20	25.99	9.64
July 5.....	25.50	9.09	17.75	16.02
July 8.....	15.25	16.19	25.39	18.05
July 9.....	16.72	12.56	14.27	12.12
July 10.....	37.10	25.78	34.88	25.80
Mean.....	22.35	15.76	23.66	16.33
	t	1.330	1.615	
	P	>.05	>.05	

significant difference in the passage time of steelhead in the test (type 3) fishway and the control (type 1) fishway. Previous experiments by Gauley (1960) yielded similar results.

Other Fish

At certain times during the summer fairly large numbers of carp, squawfish, and suckers ascend the Bonneville fishways. It is desirable to know how these species respond to different fishway conditions:

A mass release of June 18 contained a large percentage of squawfish and suckers. A total of 269 fish entered the control fishway, and approximately the same number passed through the fishway. These were identified as they passed out of the fishway at weir 60. Of the 269 fish, 159 (59 percent) were nonsalmonids. In the test fishway, of 196 entering, only 57 went out at weir 60. Of the 57 fish, seven (12 percent) were nonsalmonids. Assuming that equal proportions of nonsalmonids entered both fishways the suggestion is that the 1:8-slope fishway with a 1.5-foot rise between pools inhibits the passage of squawfish and suckers.

Other factors affecting passage time

Throughout the course of experiments and during the analysis of data on fishway passage times, it became apparent that factors other than fishway slope might have affected the passage time of salmonids through a given fishway. The supplementary nature of data concerning these factors preclude a thorough analysis. Numerous factors were considered, but to date only three—(1) the Dalles-type weir crest, (2) seasonal variation, and (3) rise between pools—have yielded enough information for a brief discussion.

The Dalles-Type Weir Crests

The Dalles-type weir crests (fig. 12) were installed in the south fishway in conjunction with other studies. This installation made possible the comparison of the fish-passing ability of this type of weir crest with the conventional square weir crests in the north fishway.² Chinook and steel-

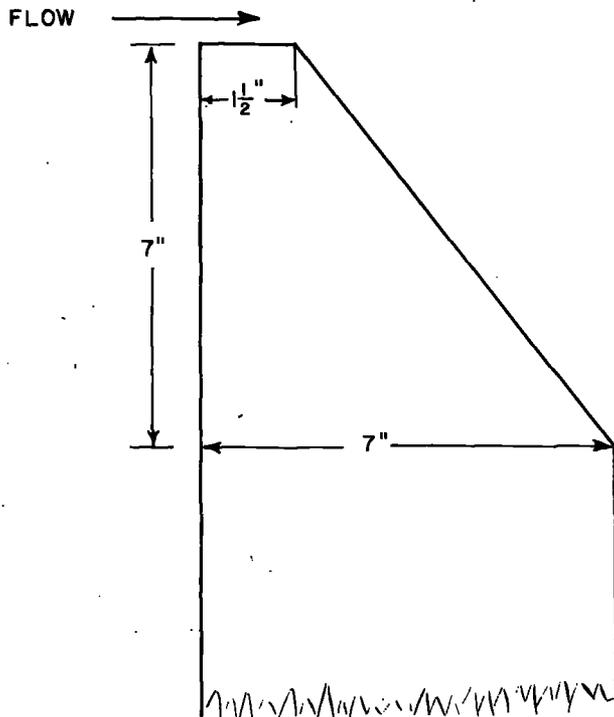


FIGURE 12.—Cross section view of the Dalles-type weir crest.

head individuals were timed through type-1 and type-1, B (fig. 13), fishways. (See table 1 for fishway dimensions.)

Three comparisons between the two weir crests and two fishway types, given in table 14, indicate the following with respect to chinook passage: Case 1—chinook moved faster in a 11.5-foot-wide fishway having Dalles-type weir crests than in a similar fishway having square weir crests; Case 2—chinook moved faster in a 4-foot-wide fishway having Dalles-type weir crests than in a fishway 11.5 feet wide having square weir crests; Case 3—there was no difference between chinook passage times in the wide and narrow fishways with the Dalles-type weir crest. Thus, in case 2, the ac-

² Here, the Dalles-type weir crest is a sharp crested weir and the square weir crest is considered a broad crested weir. With equal heads on both weir types, the flow over the sharp crested weir will be approximately 10 percent greater.

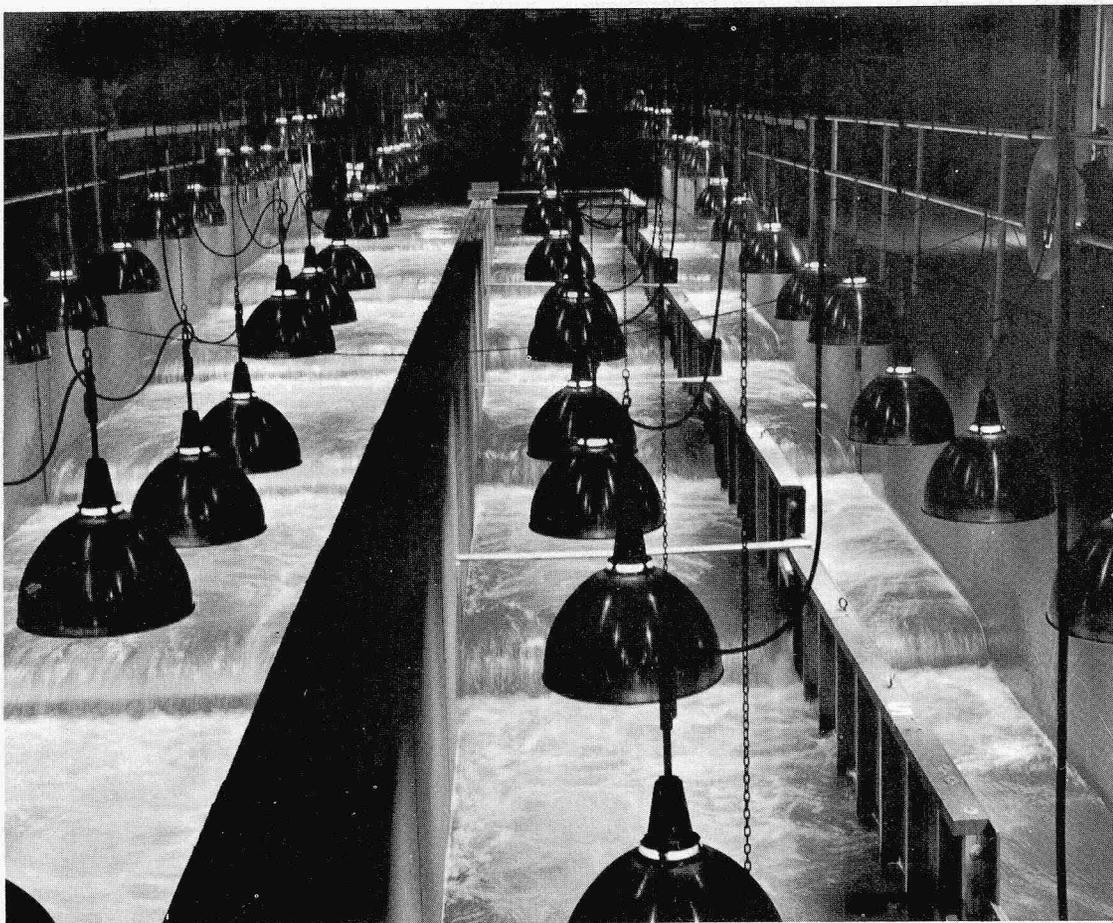


FIGURE 13.—The type-1, B-fishway (extreme right), created by installing a partition wall in a type-1 fishway.

TABLE 14.—Comparisons between the Dalles-type and square type weir crests using individual chinook passage times in type-1 and type-1 B fishways, Apr. 29 to May 16, 1957

Case	Fishway type	Sample size	Lower limit	Median	Upper limit
		<i>Number of fish</i>	<i>Minutes</i>	<i>Minutes</i>	<i>Minutes</i>
1	Type 1, square crests.....	10	8.15	12.68	70.08
	Type 1, Dalles crests.....	13	3.47	6.23	24.73
2	Type 1, square crests.....	39	7.82	12.97	17.75
	Type 1 B, Dalles crests.....	69	4.65	6.22	9.02
3	Type 1, Dalles crests.....	13	3.47	6.23	24.73
	Type 1 B, Dalles crests.....	69	4.65	6.22	9.02

celerated passage of chinook in the type-1, B fishway appears to have been a function of the Dalles-type weir crests rather than fishway width.

By contrast, a comparison between the passage times of 10 steelhead in a type-1, B fishway having Dalles-type weir crests and 15 steelhead in a type-1 fishway having square crests, showed no difference between the median passage times in the two fishways.

The Dalles-type weir crest appeared to be more advantageous for chinook passage than the square-type crest. Perhaps this is due to the greater flow of water over the sharp-crested weir, the oblique plane of the weir crest, or a combination of factors. The fact that steelhead were not accelerated by the Dalles-type crest suggests that some difference in species or size may affect an individual's ability to negotiate weir crests of different designs.

Seasonal Variation

Previous experiments in 1956 (Gauley, 1960) indicated there was a seasonal variation in passage time of steelhead through the control fishway. In the recent experiments, chinook and sockeye were examined to determine if this were also true for these species. Only passage times in the type-1 (control) fishway were used as this fishway was not altered and provided for passage time comparisons during most of the season.

Individual passage times were used to compare three periods of chinook migration, April 16 to May 7, May 31 to June 7, and June 12 to July 9, corresponding roughly to the spring run, an intermediate peak, and the summer run (fig. 14). The

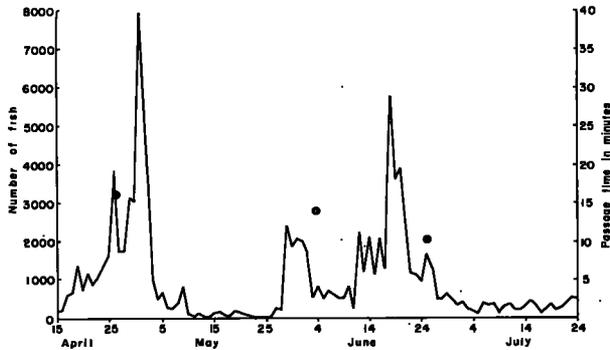


FIGURE 14.—The variation in median passage times (round dots) of chinook individuals during three segments of the run passing Bonneville Dam. The run (solid line) is represented by the daily counts in the Washington shore ladder, 1957. (Daily chinook count obtained from Corps of Engineers.)

median passage times presented in table 15 indicate that individual chinook in the summer period (June 12 to July 9) moved significantly faster than during the other two periods.

TABLE 15.—Median passage times of chinook tested in a type-1 fishway during three periods, Apr. 16 to July 9, 1957

Date	Sample size	Lower limit	Median	Upper limit
	<i>Number of fish</i>	<i>Minutes</i>	<i>Minutes</i>	<i>Minutes</i>
Apr. 16–May 7	129	11.60	15.90	17.75
May 31–June 7	56	10.50	13.80	16.88
June 12–July 9	68	6.90	10.26	13.37

Group releases of chinook revealed basically the same result. An analysis of variance on the means of the median elapsed times (table 16) showed a significant difference between the means of the three periods.

Passage times of individual sockeye in a type-1 fishway are available for comparison throughout most of the run. For analysis, the passage times were divided into two groups: June 13 to July 5 and July 8–18, representing the first and last half of the sockeye run (fig. 15). A comparison of the median passage times presented in table 17 indicates that fish in the first part of the run were

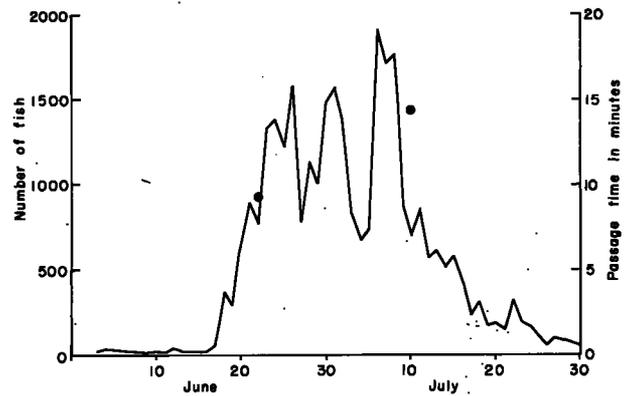


FIGURE 15.—The variation between median passage times (round dots) of sockeye individuals in the first half and the last half of the run passing Bonneville Dam. The run (solid line) is represented by the daily counts in the Washington shore ladder, 1957. (Daily sockeye count obtained from Corps of Engineers.)

TABLE 16.—Median elapsed times (minutes) of groups of chinook tested in a type-1 fishway during three periods, Apr. 23 to June 19, 1957

	April 23–26	May 29–June 7	June 13–19
	18.17	12.33	10.58
	24.78	14.60	17.61
	12.92	19.19	10.18
	16.75	12.90	10.80
	23.41		13.25
			16.05
			12.96
Mean	19.22	14.76	13.06

TABLE 17.—Median passage times of two groups of sockeye tested in a type-1 fishway during June 13–July 18, 1957

Date	Sample size	Lower limit	Median	Upper limit
	<i>Number of fish</i>	<i>Minutes</i>	<i>Minutes</i>	<i>Minutes</i>
June 13–July 5	73	6.00	9.22	11.58
July 8–18	80	11.28	14.30	16.28

significantly faster than those in the last part of the run.

Rise Between Pools

Research on a 1:8-slope fishway by Gauley (1960) indicated a direct relationship between magnitude of rise between pools and passage time. Recent supporting evidence was found by comparing passage times of chinook and sockeye in the 1:8-slope fishway with 1.0- and 1.5-foot rises, respectively.

The median passage times of sockeye individuals timed through type-2 and type-3 fishways are given in table 18. A comparison of these times showed that the passage time was significantly

TABLE 18.—Median passage times of sockeye and chinook individuals ascending 1:8-slope fishways with a 1.5-foot rise (type-3 fishway) and a 1-foot rise (type-2 fishway) between pools

[Passage times in the respective control fishways are included]

Species	Date	Test 1:8-slope					Control 1:16-slope				
		Rise	Sample size	Lower limit	Median	Upper limit	Rise	Sample size	Lower limit	Median	Upper limit
		Feet	Number of fish	Mminutes	Minutes	Minutes	Feet	Number of fish	Mminutes	Minutes	Minutes
Sockeye.....	June 17-July 9.....	1.5	65	7.85	12.30	15.42	1.0	82	7.53	9.28	9.83
	July 12-18.....	1.0	111	1.20	1.40	1.90	1.0	72	11.45	14.66	16.43
Chinook.....	June 12-July 9.....	1.5	46	9.73	16.10	31.37	1.0	68	6.90	10.26	12.37
	May 31-June 7.....	1.0	74	7.33	9.88	12.03	1.0	66	10.50	13.80	16.88

less in a fishway having a 1.0-foot rise than in a fishway having a 1.5-foot rise. Comparative times given for passage through the control fishway suggest that the differences due to rise would have been even more pronounced, if seasonal variation had been taken into account.

The median passage times of chinook individuals in type-2 and type-3 fishways are also presented in table 18. Chinook ascending the type-2 fishway were faster than those ascending the type-3 fishway but not significantly so. Again comparing passage times in the control fishway, the difference would have been more pronounced if seasonal variation had been considered.

SUMMARY

The effects of fishway slope on the rate of passage of chinook, sockeye, and steelhead were studied at the Fisheries-Engineering Research Laboratory at Bonneville Dam, by comparing passage times of salmonids through two fishways with different slopes—a 1:8-slope test fishway and a 1:16-slope control fishway. Both fishways were pool-and-overfall type without submerged orifices, attaining a total gain in elevation of 6 feet. Passage times of individuals, groups, and mass releases were used to compare fishway slopes and incidental factors.

A comparison of passage times between the 1:8-slope test fishway with a 1.0-foot rise between pools and the 1:16-slope control fishway with a 1.0-foot rise between pools demonstrates that chinook, sockeye, and steelhead ascended the test fishway at a faster rate than the control fishway. The passage times, however, were not always significantly faster.

When the rise between pools in the test fishway was increased to 1.5 feet, there was a correspond-

ing increase in passage time. Most of the chinook, sockeye, and steelhead ascended the test fishway at a slower rate than the control fishway but only chinook groups were significantly slower.

Three incidental factors affected passage time: (1) weir crest design, (2) seasonal variation, and (3) rise between pools. Tests in the 1:16-slope fishway with Dalles-type weir crests and square weir crests showed chinook ascended the Dalles crest faster while steelhead ascents were about the same for both weir crest designs. A significant seasonal variation in passage times through fishways occurred within the respective chinook and sockeye salmon migrations. Chinook in the summer run were significantly faster than individuals in the spring run while the first half of the sockeye run was significantly faster than the last half. The median passage time of chinook and sockeye in a 1:8-slope fishway having a 1.0 foot rise between pools was significantly less than in the same fishway having a 1.5-foot rise between pools.

ACKNOWLEDGMENTS

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LITERATURE CITED

COLLINS, GERALD B., AND CARL H. ELLING

1960. Fishway research at the Fisheries-Engineering Research Laboratory. U.S. Fish and Wildlife Service, Circular No. 98, 17 pp.

DIXON, WILFRID J., AND FRANK J. MASSEY, JR.

1951. Introduction to statistical analysis. First edition. McGraw-Hill Book Company, New York, 370 pp.

ELLING, CARL H., AND HOWARD L. RAYMOND

1959. Fishway capacity experiments, 1956. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 299, 26 pp.

GAULEY, JOSEPH R.

1960. Effect of fishway slope on rate of passage of salmonids. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 350, 23 pp.

AGE, GROWTH, AND MATURITY OF ROUND WHITEFISH OF THE APOSTLE ISLANDS AND ISLE ROYALE REGIONS, LAKE SUPERIOR

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ABSTRACT

The round whitefish has been of some commercial importance in the upper Great Lakes but production in Lake Superior has generally been small; the United States average was 26,600 pounds for 1929-59.

This study is based on 1,173 fish collected in the Apostle Islands in 1958-60 and 103 collected at Isle Royale in 1958 and 1960. The average age of 6.0 years at Isle Royale was concluded to be significantly higher than the mean of 4.2 years in the Apostle Islands. The body-scale relation is a straight line with an intercept of 1.1 inches on the length axis. Weight of Apostle Islands round whitefish captured in several months increased as the 3.22 power of the length. Growth in length was relatively slow; nearly or fully 7 years were

required to reach an acceptable commercial length of 14 inches in both the Apostle Islands and at Isle Royale. The calculated weights at the end of the seventh year were 12.6 ounces in the Apostle Islands and 13.8 ounces at Isle Royale. Minimum length at maturity of male round whitefish (7.0-7.4 inches) was less than that of females (8.5-8.9 inches). At age-group II, 11.1 percent of male round whitefish, but only 1.5 percent of the females were mature. All males were mature as age-group V and all females as age-group VI. Males dominated the younger age groups but females were more numerous in the older ones. Estimates of the number of eggs in 37 round whitefish ovaries yielded an average of 5,330 eggs for fish 10.5-17.4 inches long.

The round whitefish, *Prosopium cylindraceum*, is found in all the Great Lakes but Lake Erie. The species ranges north from the Great Lakes to the Arctic, is present in the streams and lakes of eastern Canada, and occurs in both the St. Lawrence and Hudson River drainages (Hubbs and Lagler, 1947).

The present study of age and growth is the first for the round whitefish in Great Lakes waters, but growth studies of the species have been made for other waters by Cooper and Fuller (1945), Kennedy (1949), and Rawson (1951). Information on the age and growth of the related pygmy whitefish, *Prosopium coulteri*, in Lake Superior was published by Eschmeyer and Bailey (1955); this species has not been reported from any other of the Great Lakes.

NOTE.—Approved for publication June 9, 1962.

The round whitefish has some commercial importance. Greatest production has been in Lake Michigan (mostly in the northern part) where the annual catch frequently has approached or exceeded a quarter-million pounds. The U.S. waters of Lake Huron (limited data for Canadian waters) have also produced round whitefish, but the annual catch there has seldom exceeded 100,000 pounds. Production in Lake Superior generally has been small. The catch in U.S. waters of the lake averaged 26,600 pounds in 1929-59. The largest catch most commonly was taken in Michigan waters. The mean landings for the States were: Michigan, 13,600 pounds; Wisconsin, 9,400; Minnesota, 3,700. Production of round whitefish in Canadian (Ontario) waters of Lake Superior averaged 11,000 pounds in 1952-59 (no statistics on the species in earlier years).

Substantial increases in 1959 U.S. landings (to 69,000 pounds), and the estimated 1960 Canadian catch of 58,000 pounds, could mark the beginning of an upward trend in Lake Superior round whitefish production.¹

Despite the highly palatable flesh, the market value of the round whitefish has been limited because of the relatively small average size and the fluctuating supply. Small catches often are sold as part of shipments of other species. This marketing procedure may contribute to an underestimate of the production since "odd poundages" are not always listed by fishermen on their reports.

A major purpose of the present study was the gathering of information on the size, age composition, and growth of round whitefish in Lake Superior from which to judge the possibilities for increased exploitation.

MATERIALS AND METHODS

This study is based on 1,173 round whitefish collected at various localities in the Apostle Islands (fig. 1) area and 103 specimens captured off the southwestern end of Isle Royale during the operations of the U.S. Bureau of Commercial

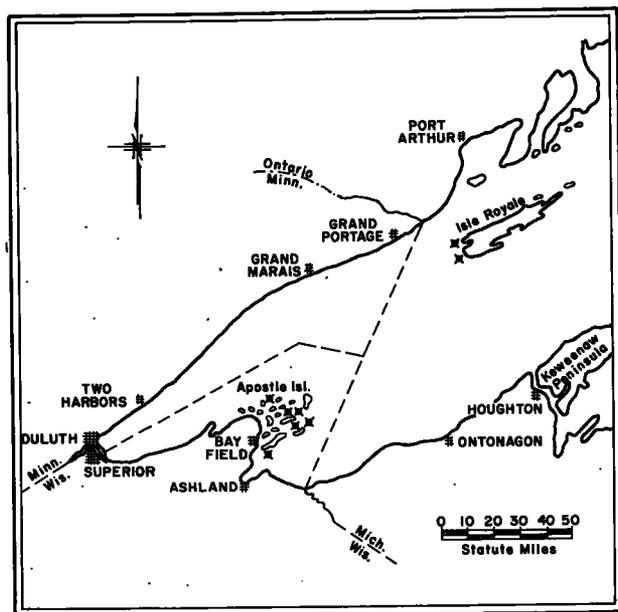


FIGURE 1.—Western Lake Superior. Dots with crosses represent sampling stations:

¹ The statistics for 1929-40 were taken from Gallagher and Van Oosten (1943); U.S. statistics after 1940 appeared in Lake Fisheries, issued by the U.S. Bureau of Commercial Fisheries. Canadian statistics were obtained from records of the Ontario Department of Lands and Forests.

Fisheries research vessel *Siscowet* (fig. 1). The study is based mainly on the Apostle Islands collections; the small samples from Isle Royale, taken coincidentally to the major work of the *Siscowet* in that area, were collected to obtain information on the possibility of local differences of growth rate. The majority of fish were taken in nylon gill nets 300 feet long and 6 feet deep (table 1). Nine nets of graded mesh sizes (1 to 5 inches; stretched measure, by ½-inch intervals) were joined end to end and fished on the bottom as a standard gang, usually overnight. The remaining gill net samples were collected in shorter gangs of 2- to 3-inch mesh nets.

The sample of April 30, 1959, includes 36 fish of age-group I taken by a semiballoon otter trawl, 30 feet wide at the mouth, with mesh sizes of 2½ inches in the wings and body and ½-inch mesh in the cod end. Tows were made on the bottom in 5-15 fathoms.

The total length of each fish (tip of head to tip of tail, lobes compressed) was determined to the nearest 0.1 inch. Weights of fish 18 ounces or less were recorded to the nearest 0.1 ounce from a spring balance calibrated in 0.2-ounce intervals. Fish heavier than 18 ounces were weighed on a

TABLE 1.—Collections of round whitefish from the Apostle Islands and Isle Royale

Locality and date	Gear			Total
	Gill net		Trawl	
	Standard gang ¹	Other ²		
Apostle Islands:				
1958:				
June 5.....	73			73
July 9.....		32		32
July 23.....	180			180
Aug. 10-12.....		157		157
Oct. 24.....	79			79
Oct. 31.....	40			40
1959:				
Apr. 30.....	221		36	257
June 4.....	4			4
June 9.....	54			54
July 29.....	6			6
Oct. 19.....	40			40
Nov. 10.....	73			73
1960:				
Dec. 1.....	178			178
Isle Royale:				
1958:				
Aug. 20.....	65			65
1960:				
Aug. 9.....		38		38
Total:				
Apostle Islands.....	948	189	36	1,173
Isle Royale.....	65	38		103
Grand total.....	1,013	227	36	1,276

¹ Mesh sizes, 1 to 5 inches by ½-inch intervals.

² Various combinations of mesh sizes, 2 to 3 inches.

³ Used only in determination of the length-weight relation (table 5).

similar balance calibrated to 0.1 pound. All weights obtained by this balance were later converted to ounces.

Sex and state of maturity were determined by gross examination of the gonads. A mature fish was one judged to be ready to spawn in the fall of that same year, regardless of whether it had spawned previously.

Scales were removed from the left side of the fish midway between the lateral line and the base of the dorsal fin. The scales were impressed in cellulose-acetate strips by a roller press (Smith, 1954) and were examined at the magnification X43. The diameters and growth fields within annuli of the projected scales were measured in millimeters along the longitudinal axis on a line passing through the focus. Lengths at time of formation of each annulus were determined nomographically from an empirically determined body-scale relation.

Ages were assessed by counting the number of annuli and are expressed in Roman numerals. Fish were moved to the next higher age group on January 1 of each year. A virtual annulus accordingly was assigned to the edge of the scale from that date until growth actually started. Some difficulty was encountered in reading scales of the older fish where the later annuli were indistinct and close together. These annuli were particularly hard to distinguish in the posterior field of the scale. Only a few scales (less than 1 percent) were discarded, however, as totally unreadable.

TIME OF ANNULUS FORMATION

Annulus formation for round whitefish in the Apostle Islands differed slightly in 1958 and 1959. Annulus formation was complete in 1958 for 32 percent of the fish collected on June 5. All fish examined had completed an annulus at the time of next collection on July 9. Fish captured on June 9, 1959, showed no evidence of annulus formation, but all of six fish captured on July 29 had completed the annulus. The period of annulus formation for this stock appears, then, to fall mostly in June but possibly may extend into early July.

With the exception of two individuals caught near Thompson Island on August 9, 1960, both samples from Isle Royale were taken at Rainbow Cove, on the southern shore, one on August 20,

1958, and the other on August 9, 1960. All fish of the 1958 collection but only 32 percent of the fish caught in 1960 had completed the annulus. An annual difference of surface water temperatures (73.4° F. in 1958 but only 62.0° F. in 1960) could explain the difference.² Another possible factor could have been the greater proportion of older fish in the 1960 sample. It has been demonstrated (Hile, 1941) that younger fish form annuli earlier than do the older ones. Difficulty in deciding whether or not an individual fish had completed the annulus for the current season did not interfere with age determination.

AGE COMPOSITION

Round whitefish from the Apostle Islands and Isle Royale exhibited pronounced differences in age distribution and average age (table 2). Age-group IV was dominant at both localities, but Isle Royale had much the stronger representation of fish older than the VII group, and, conversely lacked entirely members of age-groups I and II. In the Apostle Islands the fish of age-groups I and II together made up more than 16 percent of the sample. As a result of these differences the mean age at Isle Royale (6.0 years) was 1.8 years greater than the average of 4.2 years for the fish from the Apostle Islands. The oldest fish taken belonged to age-group IX in the Apostle Islands and to age-group XII at Isle Royale.

An under representation of the younger round whitefish was to be expected at Isle Royale in 1960 since the gill nets fished that year had meshes too large to take numbers of age-groups I and II and may have sampled age-group III inefficiently. The standard gangs (mesh sizes 1 to 5 inches by ½-inch intervals) fished in 1958, however, failed to capture any I- or II-group individuals. It is clear, then, that the younger round whitefish were not on the grounds fished at Isle Royale in 1958. This situation could represent a summer segregation by age within round whitefish stocks generally, but more probable, it is peculiar to the Isle Royale locality. A standard gang lifted in the Apostle Islands on July 23, 1958, took 32 II-group individuals—17.8 percent of a total sample of 180. The only sizable August collection from the Apostle Islands—157 fish on August

² Temperature data taken during the 1958 and 1960 operations of the U.S. Bureau of Commercial Fisheries vessel *Sicowet*.

10-12, 1958—lacked young fish because of the larger mesh sizes, the same as those fished at Isle Royale in 1960. This collection included a single II-group fish. Each of these two summer collections from the Apostle Islands contained representatives of age-groups II-IX, inclusive. The gill nets were fully capable of taking older fish at both the Apostle Islands and Isle Royale.

It is concluded that the difference between the two stocks is real. Even if age-groups I and II were excluded from the Apostle Islands samples, the average age would be increased only to 4.6 years—still 1.4 years below the mean for Isle Royale. No definite explanation is offered for the differences in age distribution and average age of round whitefish in the Apostle Islands and at Isle Royale. Differences in natural mortality and in fishing mortality both may have been factors.

TABLE 2.—Age composition of round whitefish taken in gill nets in the Apostle Islands and at Isle Royale

Age group	Apostle Islands		Isle Royale	
	Number	Percentage	Number	Percentage
I.....	13	0.3		
II.....	152	15.8		
III.....	190	19.8	12	11.7
IV.....	270	28.2	24	23.3
V.....	190	19.6	13	12.6
VI.....	111	11.6	16	15.5
VII.....	66	6.9	9	8.7
VIII.....	27	2.8	10	9.7
IX.....	10	1.0	11	10.7
X.....			6	5.8
XI.....			1	1.0
XII.....			1	1.0
Total.....	959		103	
Average age.....	4.2		6.0	

¹ Fish taken in trawls included 36 additional members of age-group I.

The records of age composition for individual years at the two locations (not given here) offered no indication of the occurrence of exceptionally strong or weak year classes.

LENGTH DISTRIBUTION AND AVERAGE LENGTH OF AGE GROUPS

To avoid bias from the capture of fish at various times in the growing season, the data on the length distributions of the age groups (tables 3 and 4) are based on the calculated lengths at the time of formation of the last annulus. All samples for which age was determined have been used in the tables.

The distributions of I- and II-group round whitefish from the Apostle Islands did not over-

lap, but those of all other successive age groups overlapped from 2 to 4 inches. The range of length in the well-represented age groups was fairly large for fish that do not attain a great size. Among age-groups II-VIII it fell within the limits of 3 to 5 inches. The shortest range (2.5 inches) in age-groups I and IX can be attributed partly to the small numbers of fish.

Because of the overlap of the length distributions of age groups in the Apostle Islands, most of the 0.5-inch length intervals included fish of several ages. Every length between 7.0 and 15.9 inches was represented by at least two age groups, and five groups were included at 14.0-14.4 inches.

The length distributions of age groups of round whitefish from Isle Royale were similar to those of the Apostle Islands fish, except that the ranges were generally smaller and the overlap correspondingly less extensive. The difference in range can be explained by the small numbers of fish in the Isle Royale collections.

The average lengths of the age groups require little comment since more extensive data on

TABLE 3.—Length distribution of age groups of round whitefish from the Apostle Islands

[Based on calculated lengths at last annulus]

Total length (inches)	Age group									Total
	I	II	III	IV	V	VI	VII	VIII	IX	
3.0-3.4.....	1									4
3.5-3.9.....	4									19
4.0-4.4.....	19									13
4.5-4.9.....	13									2
5.0-5.4.....	2									6
5.5-5.9.....		6								33
6.0-6.4.....		33								82
6.5-6.9.....		79	3							34
7.0-7.4.....		29	5							46
7.5-7.9.....		4	42							49
8.0-8.4.....		1	46	2						54
8.5-8.9.....			41	13						52
9.0-9.4.....			22	30						86
9.5-9.9.....			21	65						74
10.0-10.4.....			6	54	13	1				67
10.5-10.9.....			4	40	22	1				76
11.0-11.4.....				38	35	3				67
11.5-11.9.....				21	33	13				62
12.0-12.4.....				6	18	36	2			43
12.5-12.9.....				1	5	29	8			53
13.0-13.4.....					3	20	30			29
13.5-13.9.....					1	3	18	5	2	19
14.0-14.4.....						3	6	10		12
14.5-14.9.....						2	1	7	2	7
15.0-15.4.....							1	4	2	4
15.5-15.9.....									4	1
16.0-16.4.....								1		
16.5-16.9.....										
Total number of fish.....	39	152	190	270	130	111	66	27	10	995
Average length (inches).....	4.3	7.1	9.0	10.7	12.0	13.0	14.0	15.0	15.5	10.4

¹ Grand average length.

TABLE 4.—Length distribution of age groups of round whitefish from Isle Royale

[Based on calculated lengths at last annulus]

Total length (inches)	Age group										Total
	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
7.5-7.9	4										4
8.0-8.4	2										2
8.5-8.9	5										5
9.0-9.4	1	3									4
9.5-9.9		5									5
10.0-10.4		5									5
10.5-10.9		7									7
11.0-11.4		4	1								5
11.5-11.9			4								4
12.0-12.4			3								3
12.5-12.9			3	1							4
13.0-13.4				3	1						4
13.5-13.9				2	8	3					13
14.0-14.4					3	4					7
14.5-14.9				1	1	6	1				9
15.0-15.4						3	1	1			5
15.5-15.9						1	2	2	2		5
16.0-16.4							7	1			9
16.5-16.9								1			1
17.0-17.4										1	1
17.5-17.9									1		1
Total number of fish	12	24	13	16	9	10	11	6	1	1	103
Average length (inches)	8.3	10.4	12.3	13.7	14.0	15.0	15.9	16.0	17.8	17.3	12.7

¹ Grand average length.

growth are offered in the later section on calculated growth. Attention is called, however, to the relatively slow growth in both stocks. Nearly or fully 5 years were required at each locality for the fish to reach an average length of 1 foot, and the highest average length for any age group was not great (15.5 inches, IX group in the Apostle Islands; 17.8 inches, XI group at Isle Royale). Apostle Islands fish were the longer in age-groups III and IV, but at the higher ages (V-IX) the mean lengths of the Isle Royale stock equalled or exceeded those of fish of corresponding age in the Apostle Islands.

LENGTH-WEIGHT RELATION

The general parabola $W=cL^n$, where W = weight, L =length, and c and n are empirically determined constants, was used to describe the general length-weight relation of round whitefish (table 5). Determination of the length-weight relation was based on data from 755 fish, captured in the Apostle Islands during the 1958-60 collecting seasons, combined without regard to sex, state of maturity, or time of collection. Lengths and empirical weights are averages for 0.5-inch intervals of length. Since some 0.5-inch intervals had large numbers of individuals, not all of the 1,173 Apostle Islands fish were used. The 178 fish captured in the Apostle Islands in December 1, 1960, were included to strengthen the data at the higher length intervals. These fish were not used elsewhere in this study. Limited comparisons accord-

ing to sex, state of maturity, and date of capture revealed two significant differences. Ripe fish of both sexes were slightly heavier than spent individuals, and fish taken during July and August were generally heavier than those captured in April or November.

TABLE 5.—Length-weight relation of round whitefish from the Apostle Islands

[The lengths and empirical weights are averages by 0.5-inch intervals of length. The calculated weights were computed from the equation given in the text]

Number of fish	Total length (inches)	Weight (ounces)		Number of fish	Total length (inches)	Weight (ounces)	
		Empirical	Calculated			Empirical	Calculated
1	4.2	0.3	0.3	37	11.7	6.7	7.0
2	4.8	.4	.4	37	12.2	7.7	8.1
2	5.2	.6	.5	37	12.7	8.8	9.2
3	5.7	.8	.7	37	13.2	10.4	10.4
5	6.3	.9	1.0	37	13.7	11.8	11.7
33	6.8	1.1	1.2	37	14.2	13.3	13.1
37	7.2	1.3	1.5	37	14.7	14.8	14.7
25	7.7	1.7	1.8	37	15.1	17.1	16.0
27	8.2	2.2	2.2	31	15.7	19.6	18.2
37	8.7	2.6	2.7	19	16.1	22.0	19.7
37	9.2	3.0	3.2	21	16.7	22.8	22.2
37	9.7	3.6	3.9	15	17.1	25.6	23.9
37	10.1	4.2	4.4	9	17.7	27.6	26.7
37	10.7	4.9	5.3	7	18.1	29.0	28.7
37	11.2	5.9	6.1				

The length-weight equation, determined by fitting a straight line to the logarithms of the length and weight was:

$$\log W = -3.40468 + 3.2231 \log L,$$

where
and

W =weight in ounces,
 L =total length in inches.

This equation may also be written in the form,

$$W = 3.9384 \times 10^{-4} L^{3.2231}$$

The weights computed for the mean lengths of fish in each length interval are the basis of the curve in figure 2.

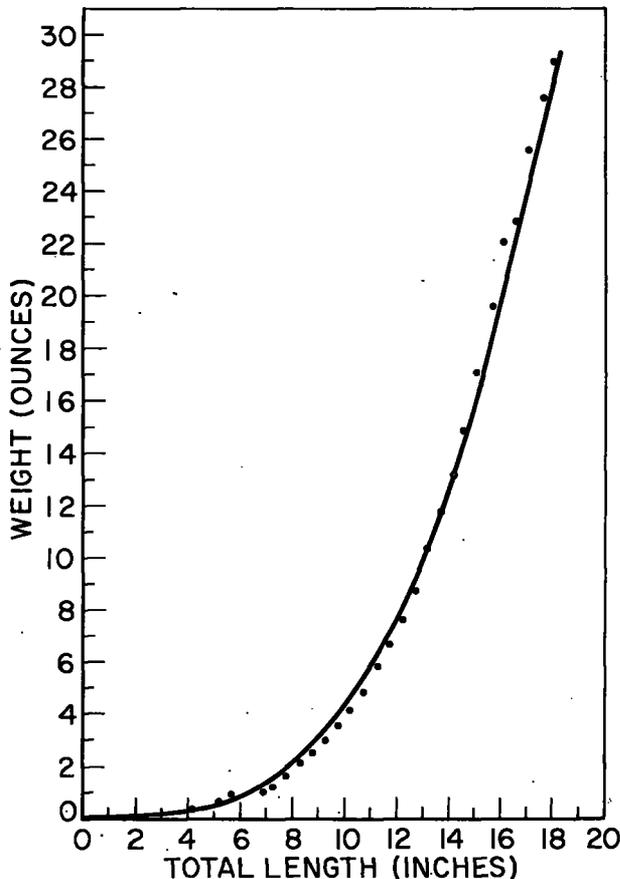


FIGURE 2.—Length-weight relation of round whitefish from the Apostle Islands. The curve represents the calculated weights and the dots, the empirical weights.

A direct comparison of empirical weights of Isle Royale and Apostle Islands round whitefish captured in August (details not given here) demonstrated almost no differences. It is suspected that the condition of the species is at its peak in August, as has been established for other coregonids—*Leucichthys kiyi* (Deason and Hile, 1947) and *Coregonus clupeaformis* (Van Oosten and Hile, 1949). The agreement between Apostle Islands and Isle Royale fish caught in the same month suggests that the length-weight equation derived for Apostle Islands fish may hold reason-

ably well for both stocks. The equation based on Apostle Islands fish caught in various months may be more suitable for the Isle Royale stock than one based on limited data for a single month in the latter area. The equation is accordingly applied to calculated lengths of both stocks in a later section on calculated growth in weight.

CALCULATED GROWTH

BODY-SCALE RELATION

The body-scale relation for round whitefish of the Apostle Islands area was determined from 429 specimens collected in 1958 and 1959 (table 6). Scale diameters were recorded only from the scale used in age determination. Care was taken, however, to read and measure a scale of average size after all scales on the slide were examined. A plot of the average fish lengths for 0.5-inch groupings, against the average scale diameters, indicated that a straight line best fitted the data (fig. 3).

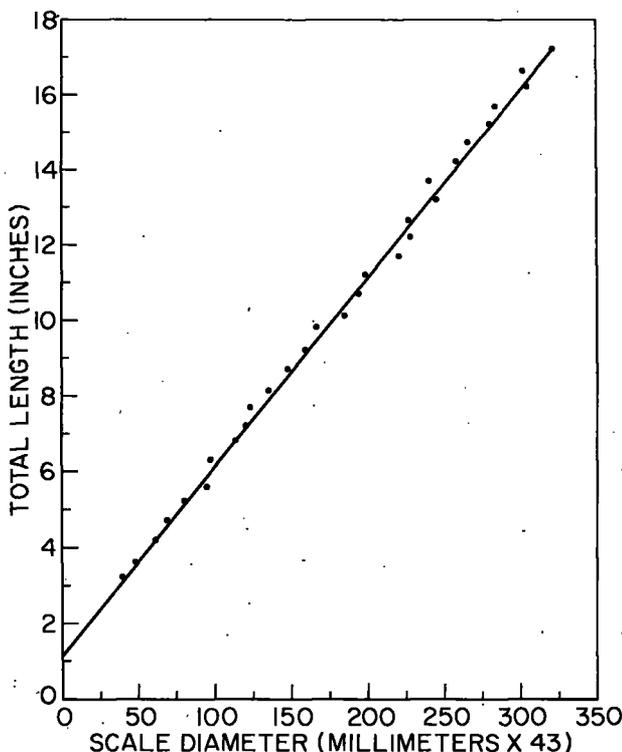


FIGURE 3.—Relation between total length of fish and magnified (X43) scale diameter for round whitefish from the Apostle Islands. [The dots represent the empirical data; the line is a graph of the equation given in the text.]

The equation for the line, fitted by least squares, is:

$$L = 1.1049 + 0.050 S,$$

where L = total length of the fish (inches),
and S = scale diameter (X43, in millimeters).

For practical purposes the intercept was taken to be 1.1 inches. Lengths at formation of each annulus were calculated nomographically.

GROWTH IN LENGTH

The average calculated lengths of round whitefish gave no evidence of differences according to sex or date of capture. Consequently all collections were combined at each locality in the preparation of tables 7 and 8.

The calculated growth histories of the age groups reveal both random and systematic discrepancies. Some of the randomly distributed discrepancies may reflect true differences of growth, but many

TABLE 6.—Relation between total length of fish and magnified (X43) scale diameter for round whitefish from the Apostle Islands

Number of fish	Average length ¹ (inches)	Average scale diameter (millimeters)	Number of fish	Average length ¹ (inches)	Average scale diameter (millimeters)
1	3.2	39	19	11.2	198
5	3.6	45	19	11.7	232
19	4.2	61	19	12.2	228
12	4.7	69	19	12.6	228
4	5.2	81	19	13.2	245
4	5.6	95	19	13.7	241
6	6.3	98	19	14.2	259
19	6.8	114	19	14.7	266
19	7.2	121	19	15.2	281
19	7.7	124	15	15.7	284
15	8.1	136	8	16.2	305
19	8.7	149	8	16.6	302
19	9.2	160	3	17.2	321
19	9.8	167	1	17.6	290
19	10.1	185	3	18.1	320
19	10.7	194	2	18.6	303

¹ Mean for fish within a 0.5-inch length interval.

TABLE 7.—Calculated total length at end of each year of life of each age group of round whitefish from the Apostle Islands and average growth for the combined age groups

[Collections of 1958 and 1959 combined]

Age group	Number of fish	Length (inches) at end of year								
		1	2	3	4	5	6	7	8	9
I	39	4.3								
II	152	4.8	7.2							
III	190	4.8	7.3	9.1						
IV	270	4.8	7.4	9.3	10.8					
V	130	4.4	7.2	9.2	10.9	12.1				
VI	111	4.2	6.8	8.9	10.8	12.2	13.1			
VII	66	4.0	6.5	8.6	10.6	12.0	13.2	14.0		
VIII	27	4.4	6.7	8.8	10.6	12.1	13.3	14.2	15.0	
IX	10	3.7	6.1	8.2	10.2	11.9	12.9	14.0	14.8	15.5
Grand average calculated length		4.6	7.2	9.1	10.8	12.1	13.1	14.1	14.9	15.5
Increment of average		4.6	2.6	1.9	1.7	1.3	1.0	1.0	0.8	0.6
Grand average increment of length		4.6	2.6	1.9	1.7	1.3	1.0	0.9	0.8	0.7
Sum of average increment		4.6	7.2	9.1	10.8	12.1	13.1	14.0	14.8	15.6

of them can be attributed to the small numbers of fish in certain age groups, especially at Isle Royale. The systematic discrepancies are in the form of a progressive decrease of calculated lengths with increase in the age of the fish on which the calculations were based.

In the Apostle Islands samples (table 7) it is difficult to find a trend in the first-year calculated lengths. True, the oldest fish (IX group) had the shortest calculated length (3.7 inches) but this average was based on only 10 fish. The first-year length of the better-represented VIII group (4.4 inches; 27 fish) exceeded that of the younger age-groups I, VI, and VII, and equaled the value for age-group V. Only age-groups II, III, and IV had higher first-year lengths (all 4.8 inches). The second- and third-year calculated lengths, on the other hand, showed pronounced, though irregular downward trends with increase of age. All second-year lengths, for example, were above 7.0 inches (7.2 to 7.4 in age-groups II-V) but were under 7.0 inches (6.1 to 6.8) in age-groups VI-IX. Similarly, third-year lengths exceeded 9.0 inches (9.1 to 9.3) in age-groups III-V, but were lower (8.2 to 8.9 inches) in age-groups VI-IX. Beyond the third year of life no clear trends of calculated length with increase of age can be established.

The tendency for calculated lengths to decline with increase in the age of the fish on which the calculations were based is much clearer in the records for round whitefish from Isle Royale and extends to a greater number of years of life (table 8). As was true for Apostle Islands fish, no clear trend is apparent in the first-year calculated lengths. The calculated lengths for years 2-7, on the contrary, exhibited a clear, though frequently

TABLE 8.—Calculated total length at end of each year of life of each age group of round whitefish from Isle Royale and average growth for the combined age groups

[Collections of 1958 and 1960 combined]

Age group	Number of fish	Length (inches) at end of year											
		1	2	3	4	5	6	7	8	9	10	11	12
III	12	3.6	6.1	8.4									
IV	24	3.4	6.3	8.7	10.5								
V	13	3.6	6.3	8.7	10.7	12.3							
VI	16	3.3	6.0	8.6	10.8	12.7	13.8						
VII	9	3.3	6.0	8.1	9.9	11.7	12.9	14.0					
VIII	10	3.3	5.5	7.8	9.9	12.0	13.4	14.3	15.1				
IX	11	3.5	6.0	8.2	10.3	12.0	13.4	14.3	15.2	15.9			
X	6	3.0	5.3	7.5	9.2	11.2	12.7	13.8	14.7	15.3	16.0		
XI	1	3.3	5.1	7.3	9.0	11.1	12.7	13.9	15.4	16.5	17.3	17.8	
XII	1	3.5	5.6	7.3	9.0	10.4	11.6	12.6	13.9	14.8	16.1	16.6	17.3
Grand average calculated length		3.4	6.0	8.4	10.3	12.1	13.3	14.1	15.0	15.7	16.2	17.2	17.3
Increment of average		3.4	2.6	2.4	1.9	1.8	1.2	0.8	0.9	0.7	0.5	1.0	0.1
Grand average increment of length		3.4	2.6	2.3	2.0	1.8	1.3	1.0	0.9	0.7	0.8	0.5	0.7
Sum of average increment		3.4	6.0	8.3	10.3	12.1	13.4	14.4	15.3	16.0	16.8	17.3	18.0

interrupted, tendency to decrease with increase of age. Beyond the seventh year, trends cannot be established—partly, perhaps, because of the small numbers of fish in the older age groups.

Systematic discrepancies in the calculated growth histories of different age groups are common in data on growth of fish. The most likely contributing factors for these discrepancies for Apostle Islands and Isle Royale round whitefish are: biased samples from gear selection; selective destruction of the faster growing fish in the fishery; higher natural mortality for fish with rapid growth than for those with slow growth.

Certain samples almost surely were biased from gear selection. As was recorded in table 1: 189 fish from the Apostle Islands and 38 from Isle Royale were taken in gangs of gill nets that included no mesh sizes under 2 inches. This gear would select only the larger, faster growing fish of the younger age groups. The higher calculated lengths of these selected fish may account for much of the disagreement in calculated lengths for the first few years. Again, these gangs of nets that had meshes only between 2 and 3 inches possibly took the smaller fish of the older age groups. The selection may explain their slow calculated growth during their early years of life.

The selective destruction of the faster growing fish in the fishery probably contributed little, if at all, to the systematic discrepancies in calculated length of round whitefish at either the Apostle Islands or Isle Royale. Commercial exploitation of the species in Lake Superior (see Introduction) is extremely limited.

Higher natural mortality rate among fast growing fish than among slow growing was demon-

strated by Hile (1936) in the cisco population of Silver Lake, Wis., but he found no evidence of similar mortality in three other cisco stocks. The possibility that differential natural mortality accounted for some of the discrepancies in the calculated growth of round whitefish does exist, but materials for verifying or disproving this possibility are not available.

The estimates of the general growth in length have been based on all age groups because of insufficient evidence of bias to exclude any one of them. Although some younger age groups may give overestimates of calculated growth, due to gear selection, their inclusion tends to compensate any underestimates from the older age groups, which, too, may have suffered gear selection or may have lost their faster growing members either to the fishery or through higher natural mortality.

Two basically valid approaches to the estimation of general growth are given—the grand average calculated lengths and the summation of the grand average annual increments of length (bottom sections, tables 7 and 8). Apostle Islands round whitefish gave closely similar results by both methods, but at Isle Royale the sums of the increments yielded the higher calculated lengths in the later years of life. The summation of increments has been used for the preparation of table 9 and figure 4 since it avoids the irregularities caused by successive dropping out of age groups.

The trends in growth of round whitefish were noticeably different in the Apostle Islands and at Isle Royale. The calculated length at the end of the first year at Isle Royale (3.4 inches) was 1.2 inches shorter than that of round whitefish from the Apostle Islands (4.6 inches). The second-

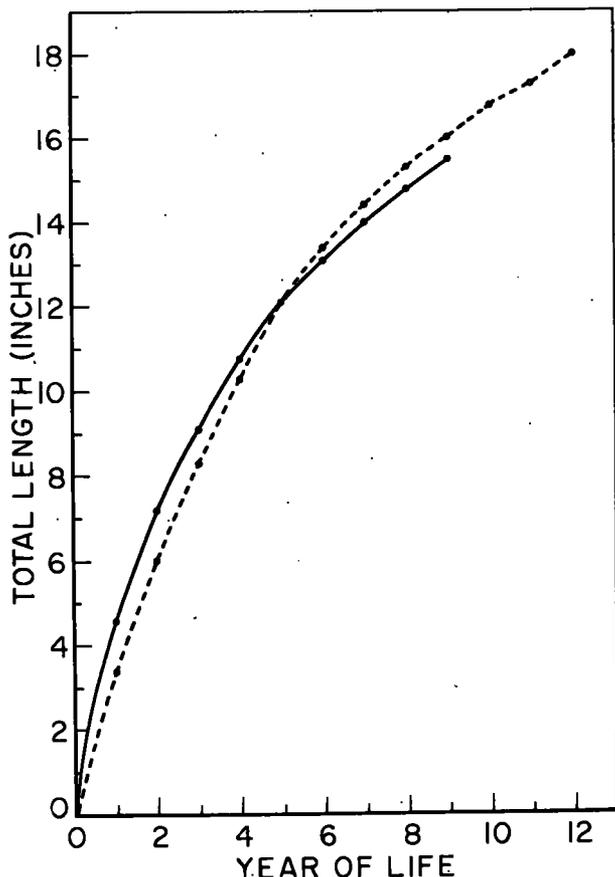


FIGURE 4.—Calculated growth in length of round whitefish from the Apostle Islands (solid line) and Isle Royale (broken line).

year increment was the same in both populations (2.6 inches), but in the third through eighth years, Isle Royale fish grew the faster. (The increments were the same in the ninth year.) The two populations had the same calculated length (12.1 inches) by the end of the fifth year, but thereafter Isle Royale fish were the longer each year through the ninth where further comparisons became impossible. The major difference between the two stocks, then, was the more rapid growth in the Apostle Islands in the first year and equal or better growth at Isle Royale from the second through the ninth years of life.

It is conceivable that the differences in growth rate of round whitefish of the Apostle Islands and Isle Royale, may not be exactly as indicated in table 9. An accurate body-scale relation could not be determined at Isle Royale because no small fish were captured. In consequence, lengths of Isle Royale fish were computed from the body-

TABLE 9.—Calculated growth in length of round whitefish from the Apostle Islands and at Isle Royale as estimated from the data for the combined age groups

[Based on summation of grand average annual increments; data from bottom of tables 7 and 8]

Year of life	Apostle Islands		Isle Royale	
	Length (inches)	Increment	Length (inches)	Increment
1.....	4.6	4.6	3.4	3.4
2.....	7.2	2.6	6.0	2.6
3.....	9.1	1.9	8.3	2.3
4.....	10.8	1.7	10.3	2.0
5.....	12.1	1.3	12.1	1.8
6.....	13.1	1.0	13.4	1.3
7.....	14.0	0.9	14.4	1.0
8.....	14.8	0.8	15.3	0.9
9.....	15.5	0.7	16.0	0.7
10.....	-----	-----	16.8	0.8
11.....	-----	-----	17.3	0.5
12.....	-----	-----	18.0	0.7

scale relation determined for round whitefish of the Apostle Islands. Should the body-scale relation actually differ materially between the two stocks apparent differences in growth rate would appear even though the true differences were small.

Both stocks of round whitefish made their best growth in length in the first year of life; thereafter the annual increments decreased with few exceptions. The increments beyond the second year were low, and beyond the sixth year were 1 inch or less.

At the present time there is no legal commercial size limit on the round whitefish in any of the Great Lakes. The only factor governing sale is acceptability on the commercial market. Prospects for increased exploitation are dimmed by the fact that nearly or fully 7 years are required for the species to reach a practical commercial size of about 14 inches.

GROWTH IN WEIGHT

Calculated growth in weight of round whitefish from the Apostle Islands and Isle Royale (table 10) was determined by applying calculated lengths (sum of the average increments) of table 9 to the length-weight equation given earlier. The estimates of growth in weight at Isle Royale are subject to possible error since calculated weights were computed from the length-weight equation derived for the Apostle Islands stock. As was explained in the section on the length-weight relation, however, the equation based on Apostle Islands fish, caught in various months, may be more satisfactory for the Isle Royale stock than

one based on limited collections made in a single month in the latter area. In the Apostle Islands the annual increments of calculated weight increased from 0.4 ounce in the first year to 2.5 ounces in the fifth year of life. The weight increments for subsequent years all fell within the range of 2.2 to 2.5 ounces. At Isle Royale yearly weight increments increased progressively from 0.1 ounce in the first year to 3.2 ounces in the fifth year of life. Thereafter the increments

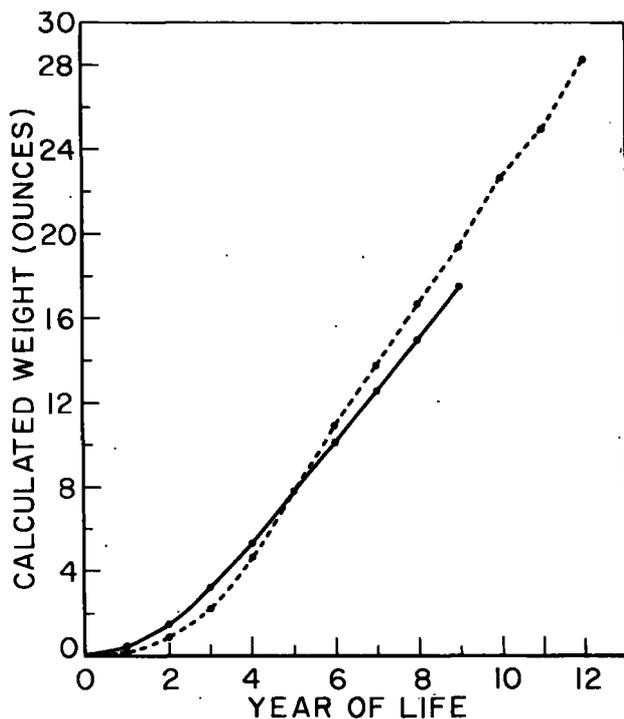


FIGURE 5.—Calculated growth in weight of round whitefish from the Apostle Islands (solid line) and at Isle Royale (broken line).

TABLE 10.—Calculated growth in weight of round whitefish from the Apostle Islands and at Isle Royale

[Weights were computed from the general length-weight relation and correspond to the lengths in table 9]

Year of life	Apostle Islands		Isle Royale	
	Weight (ounces)	Increment	Weight (ounces)	Increment
1	0.4	0.4	0.1	0.1
2	1.5	1.1	0.8	0.7
3	3.1	1.6	2.3	1.5
4	5.4	2.3	4.7	2.4
5	7.9	2.5	7.9	3.2
6	10.1	2.2	10.9	3.0
7	12.6	2.5	13.8	2.9
8	15.0	2.4	16.7	2.9
9	17.4	2.4	19.3	2.6
10			22.6	3.3
11			24.8	2.2
12			28.2	3.4

fluctuated without trend but all fell within the range of 2.2 to 3.4 ounces. Annual increments of weight for Isle Royale round whitefish were significantly higher than those of the Apostle Islands from the fifth year through the ninth year of life (fig. 5). Conversely, Apostle Islands fish revealed better weight increments in the first 3 years. Relatively slow growth in weight is evident in both populations. Nearly 7 years are required to reach a weight of $\frac{3}{4}$ pound.

SIZE AND AGE AT MATURITY SEX RATIO

No collections made near or during the spawning runs were included in determining the size and age at maturity or sex ratios of round whitefish from the Apostle Islands since segregation by sex and maturity can bias samples obtained at this period.

The shortest mature males were 7.0–7.4 inches long (table 11) and 100-percent maturity was reached at 13.0–13.4 inches. This range of 6 inches seems to be large, particularly for a species of relatively slow growth. One immature male was found at 14.0–14.4 inches, but it is highly probable that the gonads of this fish were undeveloped for other physiological reasons. The shortest mature female was at 6.5–6.9 inches. The suspicion that the single mature specimen at this length may be exceptional is supported by the fact that the next mature female was found at 8.5–8.9 inches. By the 10.0- to 10.4-inch interval, 60 percent of the females were mature, and all were mature at 12.5 inches. Male round whitefish apparently mature at a slightly smaller size than females, but 100-percent maturity is reached by both sexes at about the same length.

The youngest mature fish of both sexes belonged to age-group II (table 12). The single mature female in this age group, however, was the same fish found at 6.5–6.9 inches (see table 11). All males were mature at age-group V (one was immature in the VII group) and all females at age-group VI. In the younger age groups the higher percentage of maturity for males than for females is in agreement with findings for other species.

A commercial fishery for the round whitefish in the Apostle Islands region, based on the acceptable minimum length of about 14 inches (age-group VII), would take few, if any, immature fish.

FECUNDITY

Male round whitefish outnumbered females in the Apostle Islands (table 13) in the younger age group. The ratio was near 50-50 in age-groups IV and V, and females became progressively more plentiful in age-groups VI through IX. Males constituted only 20 percent of age-group IX.

TABLE 11.—*Relation between length and sexual maturity of round whitefish from the Apostle Islands*

[All fish shorter than 6.5 inches were immature; all fish longer than 14.4 inches were mature]

Total length (inches)	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Percentage mature
6.5-6.9	11	0	0.0	11	1	8.3
7.0-7.4	41	4	8.9	14	0	0.0
7.5-7.9	9	2	18.2	15	0	0.0
8.0-8.4	10	2	16.7	10	0	0.0
8.5-8.9	21	1	4.5	18	1	5.3
9.0-9.4	21	1	4.5	22	1	4.3
9.5-9.9	11	4	26.7	14	5	26.3
10.0-10.4	5	11	68.8	10	15	60.0
10.5-10.9	8	28	75.7	4	17	81.0
11.0-11.4	9	22	78.6	4	22	84.6
11.5-11.9	2	31	93.9	8	32	80.0
12.0-12.4	1	30	96.8	3	22	88.0
12.5-12.9	1	32	97.0	0	49	100.0
13.0-13.4	0	28	100.0	0	28	100.0
13.5-13.9	0	24	100.0	0	25	100.0
14.0-14.4	1	23	95.8	0	21	100.0

TABLE 12.—*Relation between age and sexual maturity of round whitefish from the Apostle Islands*

[All fish younger than age-group II were immature; all fish older than age-group VII were mature]

Age group	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Percentage mature
II	72	9	11.1	65	1	1.5
III	66	23	25.8	61	13	17.6
IV	10	78	88.6	6	107	94.7
V	0	67	100.0	3	47	94.0
VI	0	47	100.0	0	54	100.0
VII	1	26	96.3	0	36	100.0

TABLE 13.—*Sex composition of age groups of round whitefish from the Apostle Islands*

[No sex record for 47 fish]

Age group	Number of males	Number of females	Percentage males
I	1	1	50.0
II	82	66	55.4
III	110	78	58.5
IV	135	134	50.2
V	64	66	49.2
VI	51	58	46.8
VII	28	37	43.1
VIII	11	16	40.7
IX	2	8	20.0
Total	484	464	51.1

The number of eggs was estimated for 37 round whitefish collected in the Apostle Islands area between September 15 and October 20, 1960. Before estimates of egg numbers were undertaken, a test was made to determine the relative dependability of overnight drying at room temperatures and oven drying as described by Smith (1956).

The testing procedure was first to break up thoroughly the alcohol-preserved ovaries and separate and remove connective tissue and other foreign matter. Eleven random samples of 500 eggs each, all from the same ovary, were dried at room temperature and weighed on a milligram balance. The samples were then further dried in an oven at 60° C. and reweighed. Since further weight loss was found to be nearly constant for all samples after oven drying, this additional step was judged to be unnecessary.

For each of the 37 fish, a random sample of either 500 or 1,000 dried eggs (depending upon the ovary size) was removed from each ovary and weighed. The remainder of the eggs were also weighed and the total number estimated by direct proportion. The accuracy of this method was tested by actually counting the eggs in six ovaries. The errors (all slight overestimates) ranged from 0.02 to 4.9 percent and averaged 1.3 percent.

The average number of eggs for fish grouped by 0.5-inch intervals increased irregularly with increased fish length (table 14 and fig. 6). The single specimen at 10.5-10.9 inches had 1,076 eggs in its ovary, and the fish at 17.0-17.4 inches

TABLE 14.—*Relation between the length of round whitefish from the Apostle Islands and the number of eggs in the ovaries*

Total length (inches)	Number of fish	Number of eggs per fish		Number of eggs per ounce of fish
		Average	Range	
10.5-10.9	1	1,076	-----	199
11.5-11.9	1	2,888	-----	395
12.0-12.4	3	2,461	1,906-3,022	300
12.5-12.9	4	2,970	2,211-4,695	323
13.5-13.9	3	3,623	2,986-3,951	335
14.0-14.4	2	3,947	3,656-4,237	290
14.5-14.9	4	4,458	3,381-5,170	312
15.0-15.4	8	5,438	4,014-6,601	340
15.5-15.9	2	7,086	6,920-7,251	369
16.0-16.4	5	7,673	6,020-9,254	364
16.5-16.9	3	10,459	8,053-11,888	436
17.0-17.4	1	10,187	-----	398
All lengths	37	5,330	1,076-11,888	341

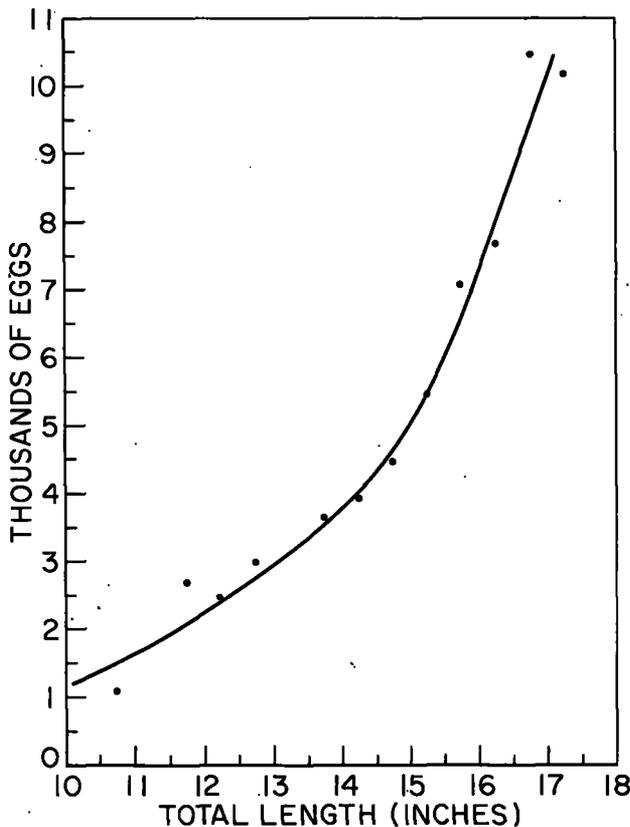


FIGURE 6.—Relation between length of round whitefish from the Apostle Islands and number of eggs per ovary. The dots represent the empirical data for 0.5-inch length groups; the curve was sketched by inspection.

contained 10,187 eggs. The mean number of eggs for all fish was 5,330.

The number of eggs per ounce of fish varied irregularly with length but tended to be higher among the longer than among the shorter fish. The number per ounce was low for the single female at 10.5–10.9 inches (199). The highest number (436) was for fish 16.5–16.9 inches long. The mean number of eggs per ounce of fish for all individuals was 341.

Only one publication could be located that included egg counts for round whitefish. Brice (1898) listed an average of 3,500 eggs per female; a 1.75-pound female produced 12,000 eggs.

SUMMARY

1. The round whitefish is found in all the Great Lakes but Lake Erie. It occurs northward to the Arctic and is common in the streams and lakes of eastern Canada and in the St. Lawrence River and Hudson River drainages.

2. The investigation of round whitefish from Lake Superior was based on data from 1,173 specimens collected in the Apostle Islands area and 103 captured at Isle Royale. This study is the first on the age and growth of the species in the Great Lakes.

3. Round whitefish production for the U.S. waters of Lake Superior generally has been small and averaged only 26,600 pounds in 1929–59. Canadian (Ontario) production averaged 11,000 pounds in 1952–59.

4. Slight year-to-year differences in time of annulus formation were found at both the Apostle Islands and Isle Royale. The period of annulus formation for the Apostle Islands stock appears to fall mostly in June, but 1960 Isle Royale samples suggest a later annulus formation date at this location.

5. The average age of 6.0 years at Isle Royale was concluded to be significantly higher than the mean of 4.2 years in the Apostle Islands. Age-group IV was dominant at both localities and the oldest fish taken belonged to age-group IX in the Apostle Islands and to age-group XII at Isle Royale.

6. Length distributions of the well-represented age groups demonstrate a fairly large range in length at both the Apostle Islands and Isle Royale. The distributions of I- and II-group round whitefish from the Apostle Islands did not overlap, but those of other successive age groups overlapped from 2 to 4 inches.

7. The general length-weight relation of round whitefish from the Apostle Islands is described by the equation: $\log W = -3.40468 + 3.2231 \log L$, where W is weight in ounces, and L is total length in inches. Weight varied according to state of maturity and date of capture. The length-weight equation derived for Apostle Islands fish was accepted for the Isle Royale stock since a comparison of empirical weights of fish captured in August from both areas revealed little difference.

8. The relation between the total body length in inches (L) and the magnified ($\times 43$) scale diameter in millimeters (S) is described by the equation, $L = 1.1049 + 0.050 S$. The intercept was taken to be 1.1 inches on the length axis and lengths at formation of each annulus were calculated nomographically.

9. The different age groups of both the Apostle Islands and Isle Royale stocks exhibited systematic discrepancies in the form of a progressive

decrease of calculated lengths with increase in the age of the fish on which calculations were based.

10. The most likely contributing factors for the systematic discrepancies are: biased samples from gear selection; selective destruction of the faster growing fish in the fishery; higher natural mortality for fish with rapid growth than for those with slow growth.

11. First-year growth in length in the Apostle Islands (4.6 inches) was greater than at Isle Royale (3.4 inches), but in subsequent years of life growth at Isle Royale exceeded or equaled that in the Apostle Islands. The Apostle Islands fish had the greater calculated lengths (by 1.2 to 0.5 inches) through the first 4 years, the lengths for the two stocks were equal at 12.1 inches in 5 years, and the Isle Royale fish were the longer (by 0.3 to 0.5 inch) in years 6-9. Both stocks required nearly or fully 7 years to reach an acceptable market length of 14 inches.

12. Differences between the two stocks in growth in weight resembled those of growth in length. Both required nearly 7 years to reach three-quarters of a pound.

13. The slow growth of round whitefish from the Apostle Islands and at Isle Royale suggests that possibilities for greatly increased commercial exploitation are small.

14. The percentage of maturity of male round whitefish from the Apostle Islands was higher than that of females at the shorter lengths and younger ages but 100-percent maturity was reached by both sexes at about the same length and age. All fish shorter than 6.5 inches were immature and all longer than 14.4 inches were mature. Youngest immature fish of both sexes belonged to age-group II. Only one male (possibly aberrant) older than the IV group and no females older than the V group were immature.

15. Male round whitefish from the Apostle Islands outnumbered females in the younger age groups (II and III) but females became progressively more plentiful as age increased and dominated the higher ages.

16. Estimates of the number of eggs in 37 round whitefish ovaries ranged from 1,076 to 10,187 and averaged 5,330 eggs for fish 10.5-17.4 inches long. The average numbers of eggs for fish grouped by 0.5-inch intervals increased irregularly with increased fish length. The mean number of eggs per ounce of fish was 341.

LITURATURE CITED

- BRICE, JOHN J.
1898. A manual of fish-culture based on the methods of the United States Commission of Fish and Fisheries [with notes on the cultivation of oysters and frogs]. Report of the U.S. Commissioner of Fisheries for 1897, pp. 1-340.
- COOPER, GERALD P., and JOHN L. FULLER.
1945. A biological survey of Moosehead Lake and Haymook Lake, Maine. Maine Department of Inland Fisheries and Game, Fish Survey Report No. 6, 160 pp.
- DEASON, HILARY J., and RALPH HILE.
1947. Age and growth of the kiyi, *Leucichthys kiyi* (Koeiz), in Lake Michigan. Transactions of the American Fisheries Society, vol. 74 (1944), pp. 88-142.
- ESCHMEYER, PAUL H., and REEVE M. BAILEY.
1955. The pygmy whitefish, *Coregonus coulteri*, in Lake Superior. Transactions of the American Fisheries Society, vol. 84 (1954), pp. 161-199.
- GALLAGHER, HUBERT R., and JOHN VAN OOSTEN.
1943. Supplemental report of the United States members of the International Board of Inquiry for the Great Lakes Fisheries. International Board of Inquiry for the Great Lakes Fisheries—Report and Supplement, pp. 25-213.
- HILE, RALPH.
1936. Age and growth of the cisco, *Leucichthys artedii* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. U.S. Bureau of Fisheries, Bulletin 19, vol. 48, pp. 211-317.
1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wis. Transactions of the Wisconsin Academy of Science, Arts, and Letters, vol. 33, pp. 189-337.
- HUBBS, CARL L., and KARL F. LAGLER.
1947. Fishes of the Great Lakes Region. The Cranbrook Institute of Science, Bloomfield Hills, Mich., Bulletin 26, 186 pp.
- KENNEDY, W. A.
1949. Some observations on the coregonine fish of Great Bear Lake, N.W.T. Fisheries Research Board of Canada, Bulletin 82, 10 pp.
- RAWSON, D. C.
1951. Studies of the fish of Great Slave Lake. Journal of the Fisheries Research Board of Canada, vol. 8, pp. 207-240.
- SMITH, STANFORD H.
1954. A method of producing plastic impressions of fish scales without the use of heat. Progressive Fish-Culturist, vol. 16, no. 2, pp. 75-78.
1956. Life history of lake herring of Green Bay, Lake Michigan. U.S. Fish and Wildlife Service, Fishery Bulletin 109, vol. 57, pp. 87-138.
- VAN OOSTEN, JOHN, and RALPH HILE.
1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77 (1947), pp. 178-249.

AGE AND GROWTH OF THE WHITEFISH IN LAKE SUPERIOR

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ABSTRACT

The average annual commercial production of whitefish in the U.S. waters of Lake Superior dropped from 2,194,000 pounds in 1879-1908 to 504,000 pounds in 1911-59. The modern production, though far below the earlier, has accounted for more than 10 percent of the total value of the fishery in all but one of the last 20 years.

Data are given on growth rate, age and year-class composition, size distribution, and length-weight relation of 1,800 fish collected in 1957-59 at Bayfield, Wis., and Marquette, Whitefish Point, and Dollar Settlement, Mich. Studies of the body-scale relation, sex ratio, and age and size at maturity were limited to fish collected at Bayfield.

The age composition and mean age varied widely by port and year of capture. Oldest fish were those of the 1957 Bayfield samples which were dominated by age-group VII and averaged 5.5 years old. The youngest were from Whitefish Point in 1959; age-group III was dominant, and the mean age was 3.2 years. The evidence on the strength of year classes was not clear-cut, but it was obvious that fluctuations in stocks of different areas were largely independent.

The percentage of legal-size fish (17 inches or longer) in age groups ranged widely; only 8.6 percent of the V

group were legal in the 1957 Bayfield collections, whereas 100 percent of fish of the same age were legal in the 1957-59 collections from Whitefish Point. The weight of whitefish in the combined samples increased as the 3.2408 power of the length.

The growth rate from the fastest to the slowest growing stocks ranked as follows: Whitefish Point; Dollar Settlement and Marquette (fish from the two ports reversed ranks after 3 years); Bayfield. The major differences in growth in length among the various stocks occurred during the first years of life. Beyond the fifth year the annual increments were nearly the same in all stocks. The whitefish from Whitefish Point, Dollar Settlement, and Marquette are among the fastest growing in the Great Lakes.

The differences among the Lake Superior stocks in age and year-class composition, and in growth rate offer convincing evidence that populations of different areas are entirely independent.

The sexes were almost equally represented (51.5 percent males) in the combined Bayfield samples, but males were scarce in age groups older than VIII. Whitefish from Bayfield shorter than 14.5 inches were immature and those larger than 17.4 inches were mature. The youngest mature fish belonged to age-group V, and all older than the VII group were mature.

The whitefish, *Coregonus clupeaformis* (Mitchell), is the largest and the most widely known coregonine in the Great Lakes; it occurs in all five lakes. It was the principal species sought in the early Great Lakes fisheries: for the period 1941-54, the whitefish comprised more than 10 percent of

the total value of the U.S. catch in the Great Lakes (only exception in 1943 when the value was 9 percent); for the years 1947-50 it ranked first in money value among all Great Lakes species. The 1948 production of whitefish in U.S. waters amounted to 12¼ million pounds, with a value of 3¾ million dollars, which represents 30 percent of the total value of the Great Lakes catch.

NOTE.—Approved for publication March 8, 1962.

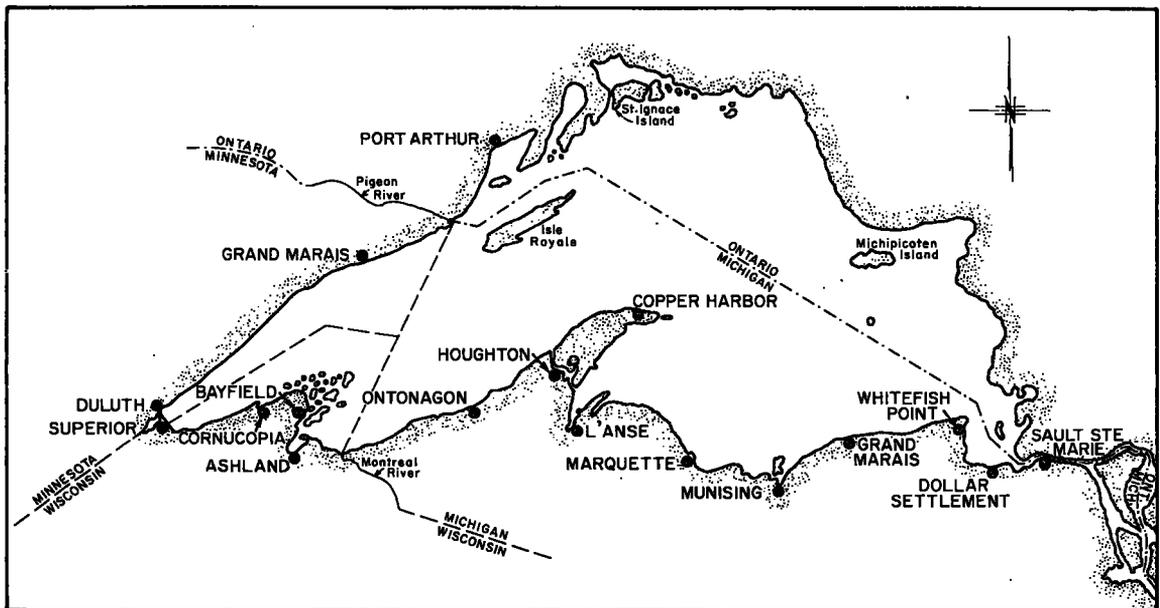


FIGURE 1.—Map of Lake Superior.

The recent production of whitefish in Lake Superior, though far below that of the earlier years, still has been of great economic importance. The species has accounted for more than 10 percent of the total value of the U.S. catch in this lake for the period 1941–59 (exception in 1952 when the whitefish accounted for only 7 percent), and the production in 1956 represented over 26 percent of the value of the U.S. catch. The progressive decline of the lake trout (*Salvelinus namaycush*) makes the high-priced whitefish relatively even more valuable, and greater exploitation of it is to be expected to supplement income from the lower-priced lake herring (*Coregonus artedii*) and chubs (*Coregonus* spp.). Sound management and rational exploitation require knowledge of the species, such as average size composition, growth rate, and maturity. The present paper is a contribution to that knowledge.

Relatively little is known of the whitefish in Lake Superior. The only published study on growth is that of Edsall (1960) on the unexploited stock of dwarf whitefish in Munising Bay.

MATERIALS AND METHODS

The present study is based on 1,800 whitefish captured off four Lake Superior ports (fig. 1) from 1957 through 1959. The number of fish collected at each port (table 1) was: Bayfield, 748; Mar-

quette, 458; Whitefish Point, 340; Dollar Settlement, 254.

More than one-half of the whitefish taken at Bayfield were from commercial pound nets. Most pound nets at Bayfield are 50 to 70 feet deep and have a 4¼-inch-mesh pot. The whitefish collections from the other ports were all from commercial trap nets with a 4½-inch-mesh pot. Net-run samples were taken from commercial pound nets and trap nets by dipping out 150–200 fish without regard to size. When the total number was less than 150–200 fish, the sample included the entire catch.

The remainder of the Bayfield samples came from commercial gill nets of 4½-inch mesh and from experimental gill nets and trawls fished from the Bureau's research vessel *Siscowet*.

All of the fish listed for the *Siscowet* at Bayfield were used in some phase of this study, but they were not employed as part of the materials on age composition and growth since they are not comparable to samples from commercial gear. The small individuals taken with trawls were of particular value in studies of the body-scale regression and length-weight relation. Helpful also were records of calculated lengths that illustrated the effects of gear selection of commercial nets.

The listings in table 1 exclude individuals not used in age and growth analyses because of scale

TABLE 1.—Locality, gear, and date of capture of Lake Superior whitefish used for the study of age and growth

Port	Date	Number of fish, by gear				Total
		Trap net ²	Pound net ²	Gill nets ¹	Siscowet experimental gear ³	
	1957					
Bayfield, Wis.	June 13.		135			135
	July 22.		138			138
	Aug. 15.		99			99
Marquette, Mich.	June 20.	20				20
	July 16.	51				51
	Sept. 30.	117				117
Whitefish Point, Mich.	June 19.	123				123
	Sept. 20.	61				61
Dollar Settlement, Mich.	July 24.	96				96
	Aug. 13.	24				24
	1958					
Bayfield, Wis.	June-Nov.				93	93
Marquette, Mich.	Oct. 2.	141				141
Whitefish Point, Mich.	Sept. 30.	108				108
	1959					
Bayfield, Wis.	June-Nov.				138	138
	June 1.		106			106
	Dec. 18.			39		39
Marquette, Mich.	Sept. 28.	129				129
Whitefish Point, Mich.	Sept. 24.	48				48
Dollar Settlement, Mich.	Sept. 24.	134				134
	1957-59					
Bayfield, Wis.	All months.		478	39	231	748
Marquette, Mich.	do.	468				468
Whitefish Point, Mich.	do.	340				340
Dollar Settlement, Mich.	do.	254				254
	1957					
All ports.	All months.	492	372			864
	1958					
Do.	do.	249			93	342
	1959					
Do.	do.	311	106	39	138	594
Grand total.		1,052	478	39	231	1,800

¹ 4½-inch mesh.

² 4¾-inch mesh.

³ Gill nets 1- to 5-inch mesh by ½-inch intervals and 31-foot semiballoon trawls.

regeneration or extreme difficulty in identifying annuli. The number of fish excluded from the total sample was less than 2 percent.

Total lengths (from the tip of the head to the tip of the tail, with the lobes compressed to give the maximum measurement) were read from a measuring board calibrated in 0.1-inch intervals. Weights were determined with a spring balance and were recorded either to the nearest 0.1 ounce or 0.1 pound. All weights given in this paper are in pounds.

The sex and state of gonads were determined for fish from all the *Siscowet* collections and about 75 percent of the Bayfield pound net collections. The remaining 25 percent of the Bayfield pound net collections were omitted from the sex-ratio and maturity studies because of uncertainty as to the sex. Most of these fish were from a single sample

collected in June 1957. Data on sex and state of gonads are lacking for samples from commercial gill nets at Bayfield and for collections from all the other ports. The whitefish captured at Marquette, Whitefish Point, and Dollar Settlement were marketed in the round and hence could not be opened. The fish from the commercial gill nets at Bayfield had been dressed before they were examined. A whitefish was considered mature if it would have spawned in the fall of the year of capture.

Scales were removed from the left side of the fish at a point midway between the lateral line and the middle of the base of the dorsal fin.

Scale impressions were made in cellulose acetate (Smith, 1954) and were magnified 42 diameters by means of a microprojector (Moffett, 1952). Diameters of scales and of growth fields within scales were measured through the focus along a line that roughly bisected the anterior field and were recorded to the nearest millimeter.

Age groups are designated by Roman numerals corresponding to the number of completed annuli. All the fish were considered to have passed into the next higher age group on January 1. A virtual annulus was credited, therefore, at the edge of the scale on all fish collected between January 1 and the time an annulus was actually completed.

Among the whitefish collected during the period of annulus formation in mid-June, no difficulties were experienced in separating individuals with a new annulus from those in which the year-mark had not yet been completed. Most of the scale samples were collected before or well after growth had started; for them the interpretation of marginal growth outside the last visible annulus obviously offered no problem.

Statistics on commercial production were obtained from various sources as given in the next section.

PRODUCTION OF WHITEFISH IN LAKE SUPERIOR

The Lake Superior fisheries were the last to be developed in the Great Lakes. As in the other Great Lakes, the whitefish was the principal species sought in the early years of fishing. Seines were the first gear fished along the south shore of Lake Superior, but because of the rough, rocky bottom their usefulness was limited. Gill nets were soon employed; and the pound net,

introduced in this country from Scotland in 1836, was established in Whitefish Bay about 1860. The pound net was first fished in the Apostle Islands area in 1871, and by 1885 about 125 were in use. Only 40 pound nets were fished in the Apostle Islands in 1960. The trap net, which was invented by Lake Ontario fishermen in 1865, was introduced in Lake Superior during the early 1900's. This net was not adapted for taking whitefish until the 1930's and since then has been important only in Michigan. The use of trap nets is prohibited in Wisconsin and Minnesota waters. The first steamer was introduced in 1871, and the first motor boat appeared at Marquette, Mich., in 1899.

Up to 1890 whitefish were the principal species in the commercial production in United States waters of Lake Superior (Koelz, 1926). Between 1891 and 1899 the lake trout occupied first place, and in the early 1900's large-scale production of lake herring placed them in first rank. The whitefish has held third position behind the lake herring and lake trout up to the recent collapse of the lake trout fishery.

The statistical records of whitefish production in Lake Superior (table 2) came from various sources. The figures through 1940 are from Gallagher and Van Oosten (1943). The U.S. data for 1941-59 are from Lake Fisheries issued by the Bureau of Commercial Fisheries. The later records for Ontario were issued by the Province.

The first published record of whitefish production in Lake Superior is for 1867 in Ontario. The first record of whitefish production in the U.S. waters of Lake Superior is for 1879 (fig. 2).

The catch of whitefish in U.S. Waters of Lake Superior was 2¼ million pounds in 1879 and exceeded 4½ million pounds in 1885—the highest production recorded. Landings fell off drastically during the following 30 years, and by 1913 the catch reached an all-time low of 113,000 pounds.

Koelz (1926) stated pessimistically that from a commercial point of view the whitefish was practically extinct along the United States shore of Lake Superior in 1922 when the total catch in U.S. waters was 319,000 pounds. The production of 144,000 pounds in 1923 marked a still further decline. It was not until the early 1930's that whitefish production in U.S. waters began to improve. An erratic increase in the catch con-

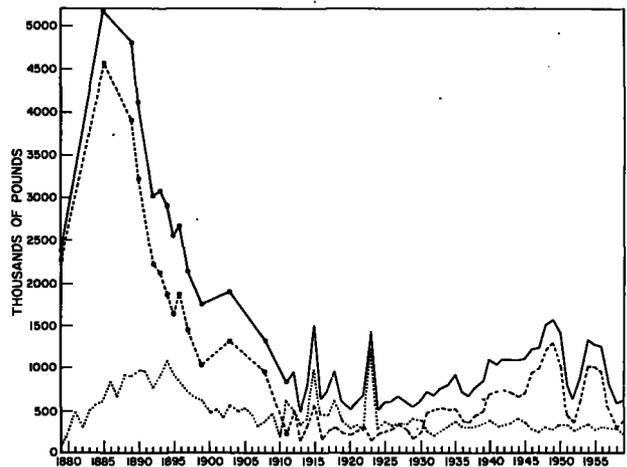


FIGURE 2.—Production of whitefish in Lake Superior, 1879-1959. United States, short dashes; Ontario, dotted lines; entire lake, solid line. Because of the numerous interruptions in the records for U.S. waters, the points for individual years prior to 1912 are shown by dots on the lines for the catch in U.S. waters and in the entire lake.

tinued for about 20 years, and in 1949 the take reached 1,284,000 pounds, the highest since 1903. Since 1949 the catch of whitefish in U.S. waters has fluctuated widely between 1,040,000 pounds in 1950 and 309,000 in 1958. The 1911-59 average production of 508,000 pounds was only 23.2 percent of the 1879-1908 mean of 2,194,000.

The distribution of the yield of whitefish from the different States has not changed greatly during the period for which statistics are available. With the exception of 10 years when Wisconsin had the largest catch (1885, 1925, 1946-50, and 1955-57) Michigan has dominated the yield of whitefish (table 3). For the period 1885-1908 Michigan contributed 70.3 percent of the total U.S. production, Wisconsin 23.8 percent, and Minnesota 5.9 percent. In 1911-59 Michigan continued to occupy first place but with a slightly lower percentage (62.8 percent). Wisconsin's contribution increased to 35.9 percent, and Minnesota's dropped from 5.9 to 1.3 percent.

The production of whitefish in Canadian waters of Lake Superior has not shown the wide fluctuations experienced in U.S. waters. Production exceeded 1,000,000 pounds only in 1894 (1,056,000 pounds) and in 1923 (1,268,000 pounds¹). On-

¹ A possibility exists that the 1923 statistic may be erroneous. The figure 268,000 pounds would be in better agreement with the production from Ontario in neighboring years. There are no records, however, from which to check this figure.

TABLE 2.—Production (thousands of pounds) of whitefish in Lake Superior, 1879–1959

[Totals are given for U.S. waters in all years with records for both Wisconsin and Michigan]

Year	United States				Canada	Grand total
	Minnesota	Wisconsin	Michigan	U.S. total	Ontario	
1879				2,287	99	2,386
1880					245	
1881					466	
1882					320	
1883					508	
1884					563	
1885					606	
1886	628	2,243	1,701	4,572	847	5,178
1887					657	
1888					932	
1889					896	4,785
1890	211	951	2,736	3,899	896	4,795
1891	40	1,109	2,084	3,213	978	4,192
1892			3,848		967	
1893			2,015	2,221	784	3,004
1894		206	1,919	2,170	899	3,068
1895		301	1,554	1,855	1,056	2,911
1896		301	1,325	1,626	911	2,538
1897		700	1,162	1,862	796	2,658
1898	31	162	1,246	1,438	688	2,124
1899			1,088		659	
1900	13	62	1,058	1,132	623	1,756
1901			829		462	
1902			794		483	
1903			1,513		417	
1904	8	129	1,200	1,336	564	1,900
1905			630		478	
1906			684		524	
1907	7		587		452	
1908	4	174	764	942	301	1,305
1909		24			363	
1910		9			470	
1911		13	202	214	202	834
1912		32	456	488	459	947
1913	(1)	20	93	113	357	470
1914	1	18	335	355	397	752
1915	2	43	522	567	955	1,523
1916	1	44	131	175	462	637
1917	1	36	220	257	452	708
1918	3	66	258	327	628	955
1919	4	62	174	240	366	606
1920	7	16	198	231	303	524
1921	8	56	192	255	329	585
1922	7	52	260	319	287	606
1923	5	60	79	144	1,263	1,412
1924	5	89	142	236	383	519
1925	5	143	99	247	347	594
1926	4	90	185	280	317	597
1927	5	74	249	328	337	665
1928	3	54	229	286	327	613
1929	3	62	101	166	389	555
1930	5	85	161	252	372	623
1931	12	52	410	474	256	730
1932	11	57	417	484	193	678
1933	6	72	442	520	245	765
1934	10	91	388	488	295	784
1935	11	73	429	512	377	890
1936	7	137	230	374	320	694
1937	7	99	258	364	301	665
1938	6	123	327	455	312	767
1939	6	106	385	497	340	837
1940	9	152	532	692	385	1,077
1941	9	273	446	728	315	1,042
1942	9	253	489	751	320	1,071
1943	6	265	461	732	336	1,068
1944	15	263	386	663	403	1,066
1945	11	338	368	717	359	1,076
1946	13	481	421	915	275	1,190
1947	11	619	321	951	246	1,197
1948	11	713	477	1,201	306	1,506
1949	13	767	504	1,284	277	1,561
1950	9	523	508	1,040	341	1,381
1951	14	183	244	442	341	782
1952	13	140	198	351	268	618
1953	5	171	431	607	282	889
1954	8	332	665	1,005	328	1,333
1955	2	501	497	1,000	254	1,255
1956	3	544	374	921	303	1,223
1957	(1)	288	236	525	285	809
1958	(1)	88	221	309	287	596
1959	1	121	260	383	210	593

¹ Less than 500 pounds.

TABLE 3.—Average annual production (pounds) of whitefish in different States and percentage contribution of each State to the total U.S. catch in Lake Superior in 1885–1908 and 1911–59

Period and item	Minnesota	Wisconsin	Michigan	Total ¹
1885–1908:				
Average production.....	117,695	472,899	1,394,964	1,985,558
Percentage.....	5.9	23.8	70.3	
Number of years of record.....	8	14	21	
1911–59:				
Average production.....	6,510	182,449	318,591	507,550
Percentage.....	1.3	35.9	62.8	
Number of years of record.....	47	49	49	

¹ Sum of the average annual contribution of the States.

tario's average annual production for the period 1879–1908 was 618,000 pounds which was 22.0 percent of the total for Lake Superior. Ontario's average annual production dropped to 368,000 pounds in 1911–59; yet this figure represented 42.0 percent of the mean annual take for the entire lake.

Little or no correlation exists between annual fluctuations in production of whitefish in U.S. and Ontario waters. The lack of correlation suggests that U.S. and Canadian fishermen are exploiting different stocks and that conditions controlling fluctuations of the take are not the same over the entire lake.

AGE AND SIZE AT CAPTURE

AGE AND YEAR-CLASS COMPOSITION

The age and year-class composition of Lake Superior whitefish in net-run samples (table 4) varied considerably from port to port and year to year. Although the data are not sufficient for a dependable ranking, certain year classes clearly were of greater or less than average strength.

The interpretation of data on age composition for judging the strength of year classes can be made uncertain by a variety of disturbing factors. Port-to-port differences or annual fluctuations of cropping rate and differences of natural mortality have a strong influence on the representation of age groups. The age at which a year class appears in the sample also must affect judgment as to the original strength. For example, a year class that makes up 20 percent of the sample as age-group VIII must have been originally much stronger than one that contributes 20 percent as age-group IV.

The 1957 Bayfield samples included 10 age groups (I–X). The percentage representation

TABLE 4.—Age and year-class composition of whitefish caught in commercial trap nets, pound nets, and gill nets

[Asterisks indicate dominant year classes in different collections]

Port, year of capture, and item	Age group										Total or average ¹	
	I	II	III	IV	V	VI	VII	VIII	IX	X		
Bayfield, 1957:												
Year class	1956	1955	1954	1953	1952	1951	*1950	1949	1948	1947		
Number	2	22	73	6	70	55	81	59	3	1		372
Percentage	0.5	5.9	19.5	1.6	18.8	14.8	21.8	15.9	0.8	0.3		5.6
Bayfield, 1959:												
Year class			1956	*1955	1954							
Number			6	117	22							145
Percentage			4.1	80.7	15.2							4.1
Marquette, 1957:												
Year class			1954	1953	*1952	1951	1950	1949	1948	1947		
Number			15	63	74	20	7	4	1	1		188
Percentage			9.1	33.9	39.9	10.7	3.2	2.2	0.5	0.5		4.8
Marquette, 1958:												
Year class		1956	*1955	1954	1953	1952	1951	1950		1948		
Number		3	78	29	17	9	3	1		1		141
Percentage		2.1	55.3	20.6	12.1	6.4	2.1	0.7		0.7		3.8
Marquette, 1959:												
Year class		1957	1956	*1955	1954	1953	1952			1949		
Number		13	19	61	24	9	2			1		129
Percentage		10.1	14.7	47.3	18.6	7.0	1.6			0.8		4.1
Whitefish Point, 1957:												
Year class		1955	*1954	1953	1952	1951	1950					
Number		5	92	61	20	5	1					184
Percentage		2.7	50.0	33.2	10.9	2.7	0.5					3.6
Whitefish Point, 1958:												
Year class		1956	*1955	1954	1953	1952						
Number		13	62	21	11	1						108
Percentage		12.0	57.4	19.4	10.2	0.9						3.3
Whitefish Point, 1959:												
Year class	1958	1957	*1956	1955		1953	1952					
Number	1	9	24	12		1	1					48
Percentage	2.1	18.8	50.0	25.0		2.1	2.1					3.2
Dollar Settlement, 1957:												
Year class			1954	1953	*1952	1951	1950	1949		1947		
Number			14	38	54	9	3	1		1		120
Percentage			11.4	31.7	45.0	7.5	2.5	0.8		0.8		4.6
Dollar Settlement, 1959:												
Year class	1958	1957	*1956	1955	1954	1953	1952					
Number	1	40	81	9	1	1	1					134
Percentage	0.7	29.9	60.4	7.3	0.7	0.7	0.7					2.8

¹ Average number of annuli.

was 14.8 percent or higher for age-groups III and V–VIII. The high representation (21.8 percent) of age-group VII and the substantial representation of age-group VIII (15.9 percent) indicate that the 1950 and the 1949 year classes were originally strong. The 1953 year class, represented as age-group IV, was obviously weak since it contributed only 1.6 percent to the catch. The average age of 5.5 for the 1957 Bayfield fish was the highest at any port in any year.

Only three age groups (III–V) were represented in the 1959 samples from Bayfield. The 1955 year class as age-group IV was overwhelmingly dominant (80.7 percent). The absence of age groups above V is difficult to explain. The strong 1949 and 1950 year class probably had largely disappeared by reason of advanced age and continued exposure to exploitation, but some representation of the moderately good 1951 and 1952 year classes (age-groups V and VI in 1957; VII and VIII in 1959) should have been expected. The mean age of 4.1 for the whitefish in the 1959

Bayfield samples was 1.4 years younger than that of the 1957 collections.

The age composition of the Marquette samples also varied with year of collection. The 1952 year class as age-group V was dominant (39.9 percent) in 1957 but failed to show strength in 1958 and 1959. The clear dominance of the 1955 year class as age-group III in 1958 (55.3 percent) and as age-group IV in 1959 (47.3 percent) gives good evidence of strength. The 1954 class, in contrast, was moderately weak. Even though it contributed 20.6 percent to the catch in 1958 its percentage representation was the lowest recorded for both age-groups III and IV and the next to lowest as age-group V. The average ages of the Marquette samples were 4.8 in 1957, 3.8 in 1958 (this low value reflected the strong 1955 year class as age-group III), and 4.1 in 1959 (also dominated by the 1955 year class).

The Whitefish Point collections were unique in that they were persistently dominated by age-group III (50.0 to 57.4 percent) in each year. This situation well may be the result of small

fluctuations in year-class strength and a high mortality rate due to the intensive trap net fishery in the area. Most of the whitefish at Whitefish Point attain legal size during their fourth year of growth (age-group III) and consequently become vulnerable to the fishery. Few individuals may survive to represent the older age groups in subsequent years. Large percentages of the fish in age groups younger than III undoubtedly escape from the 4½-inch-mesh trap nets. Because of persistent dominance by a single age group, judgments of year-class strength at Whitefish Point are not considered possible. The mean age of the Whitefish Point samples varied little from year to year—3.6 in 1957, 3.3 in 1958, and 3.2 in 1959.

The 1952 year class dominated (45.0 percent) the trap net samples at Dollar Settlement as age-group V in 1957. No samples were collected in 1958, but in 1959 the 1956 year class dominated strongly (60.4 percent) as age-group III. Undoubtedly both the 1952 and 1956 year classes were strong, but lack of data from 1958 makes evaluation of relative strength difficult. The 1954 and 1955 year classes appear to have been weak at Dollar Settlement. The mean age of the Dollar Settlement whitefish was 4.6 in 1957 and 2.8 in 1959.

Little evidence exists for lakewide similarity of fluctuations of year-class strength. The 1955 year class was strong at Bayfield and Marquette

but weak at Dollar Settlement. The 1952 year class was strong at Marquette and Dollar Settlement but only moderate at Bayfield. The 1949 and 1950 year classes, which were strong at Bayfield, seemingly were too old to be represented in catches at the other ports. The 1956 year class exhibited strength at Dollar Settlement only. No two ports agreed in the appearance of a weak year class.

LENGTH AND WEIGHT OF THE AGE GROUPS

Comments on the sizes of age groups in samples from commercial gear are kept brief since more discriminating data on growth are offered in later sections. The records of table 5 serve, nevertheless, to establish roughly the differences among the several stocks and provide a general idea of the relation between size and age in catches of commercial gear.

The average lengths and weights of the age groups at capture were determined from the combined samples for each locality with the exception of Bayfield where records for the 1957 and 1959 collections were tabulated separately; the 1958 and 1959 *Siscowet* samples were omitted for reasons made clear in the section on calculated growth. Whitefish collected from the commercial fishery at Bayfield in 1959 showed more rapid growth than those in the 1957 samples. Annual differences at other ports were small and erratically distributed; they can be ascribed to the small numbers of fish

TABLE 5.—Total length (inches) and weight (pounds) of the age groups of Lake Superior whitefish and percentage of legal fish (17 inches or longer) in each age group
[Net-run samples from commercial gear]

Port, year and item	Age group									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Bayfield, 1957:										
Total length.....	7.5	11.0	13.3	16.6	15.5	16.7	17.4	17.9	19.7	18.6
Weight.....	0.1	0.4	0.7	1.5	1.2	1.5	1.8	1.9	2.6	2.2
Number of fish.....	2	23	73	6	70	55	81	59	3	1
Percentage legal.....	0.0	0.0	0.0	50.0	8.6	25.5	61.7	83.1	100.0	100.0
Bayfield, 1959:										
Total length.....			16.4	16.8	17.5					
Weight.....			1.4	1.6	1.8					
Number of fish.....			6	117	22					
Percentage legal.....			33.3	34.2	59.1					
Marquette, 1957-59:										
Total length.....		14.7	17.1	19.2	20.7	21.8	23.5	24.8	24.2	26.0
Weight.....		1.0	1.7	2.4	3.0	3.6	4.6	5.5	5.0	6.4
Number of fish.....		16	115	153	115	38	12	5	1	3
Percentage legal.....		6.3	58.3	92.8	99.1	100.0	100.0	100.0	100.0	100.0
Whitefish Point, 1957-59:										
Total length.....	10.5	15.1	17.1	18.8	21.7	22.9	21.9			
Weight.....	0.4	1.1	1.7	2.3	3.6	4.3	3.7			
Number of fish.....	1	27	178	94	31	7	2			
Percentage legal.....	0.0	0.0	53.4	86.2	100.0	100.0	100.0			
Dollar Settlement, 1957, 1959:										
Total length.....	10.8	14.7	16.6	17.3	18.0	19.9	21.2	19.7		26.1
Weight.....	0.4	1.0	1.5	1.7	2.0	2.7	3.3	2.6		6.5
Number of fish.....	1	40	95	47	55	10	4	1		1
Percentage legal.....	0.0	0.0	37.9	48.9	78.2	90.0	100.0	100.0		100.0

in some age groups. The sexes were also combined in these data. Sex differences in the average lengths and weights at capture were not appreciable in samples for which records of sex were available.

Some of the differences in the average lengths and weights of whitefish of the same age groups from different localities were striking. The 1957 Bayfield whitefish were the smallest fish, age for age, of all the collections. The average size of the V-group fish, for example, was 6.2 inches shorter and 2.4 pounds lighter than V-group fish from Whitefish Point. Indeed, the weight of the Whitefish Point fish at this age was 3 times that of Bayfield fish. Age-group VII was the youngest at Bayfield in which the average length exceeded the minimum legal size of 17 inches. The mean weight of the 1957 Bayfield whitefish increased less than one-half pound from their fourth to their eighth growing season (from 1.5 to 1.9 pounds).

The 1959 Bayfield whitefish averaged smaller than whitefish from the other ports, but were larger than those in the 1957 Bayfield collections. The average length of the V-group fish, for example, was 17.5 inches, 0.5 inch above the legal minimum and 2 inches longer than the V group in 1957. The weight advantage of the 1959 V group amounted to 0.6 pound.

The available evidence suggests that a temporary improvement in the growth rate of whitefish accounted for the greater size of the age groups in the 1959 samples. Details are not given here since the materials were not suitable for a thorough study of annual fluctuations of growth. They left little doubt, nevertheless, that growth in 1954-57 was substantially more rapid than in the preceding 5 or 6 years (the growth rate dropped sharply in 1958). Since whitefish normally grow much more rapidly in the early than in the late years of life, the relatively young fish of the 1959 samples were in good position to benefit from the 1954-57 period of heightened growth rate. The whitefish caught in 1957 had also lived during most of the period of exceptional growth, but they were of such advanced age that this improved growth did not add materially to their size.

Differences among the average sizes of the fish from other areas of the lake were small at some ages and substantial at others. Among age groups represented by 16 or more fish at each locality, the differences between the largest and smallest fish

increased from 0.4 inch and 0.1 pound in age-group II to 3.7 inches and 1.6 pounds in age-group V. Somewhat puzzling is the consistency with which the age groups in samples from Whitefish Point were larger than those from Dollar Settlement. The two collecting localities are barely 30 miles apart (Whitefish Point is at the northwestern entrance to Whitefish Bay and Dollar Settlement at the southern end). The difference appears almost surely to be real, but the true extent of the separation of the two stocks remains to be learned.

The percentage of legal-size whitefish in the age groups was influenced strongly by differences in the growth of fish taken at the various ports (table 5). Not one whitefish in any sample was legal as age-group I, and only one was legal size as age-group II (a 17.1-inch fish captured at Marquette in 1959). At Bayfield in 1957 the first whitefish reached legal size as age-group IV, and age-group IX was the first in which all of the fish were legal size. In 1959 at Bayfield, 33.3 percent of the III-group fish were legal size and 59.1 percent had reached legal size as age-group V.

Much larger percentages of fish reached legal size in the younger age groups at the ports east of Bayfield. More than 50 percent of the III-group fish were legal size at Marquette and Whitefish Point, and all were legal at age-group V at Whitefish Point and at age-group VI at Marquette. It was not until age-group VII was reached that all the fish were legal size at Dollar Settlement.

LENGTH DISTRIBUTION

Data on the length-frequency distribution of the age groups (tables 6, 7, and 8) provide comparisons by age group between the stocks with the slowest and fastest growth and show the length distributions of the combined age groups for the 1957 and 1959 Bayfield samples and the combined collections at Marquette, Whitefish Point, and Dollar Settlement.

The overlap of length distributions of the age groups is influenced strongly by the rate of growth. The range in length of age groups represented by 20 or more fish in the 1957 Bayfield samples (table 6) was 7.9 inches for all age groups except VII where it was 8.9 inches. This wide range in combination with slow growth caused such extensive overlap as to make length an extremely poor index of age. The length interval of 15.0 to 15.9 inches, for example, was represented by seven age

TABLE 6.—Length distribution of whitefish taken off Bayfield, 1957

Total length (inches)	Age group									
	I	II	III	IV	V	VI	VII	VIII	IX	X
7.0-7.9	2									
8.0-8.9		1								
9.0-9.9		2	1							
10.0-10.9		9	4							
11.0-11.9		9	4							
12.0-12.9			17		1					
13.0-13.9			21		2	1	1			
14.0-14.9			18		19	4	1			
15.0-15.9		1	6	2	25	13	5	1		
16.0-16.9				1	17	23	24	9		
17.0-17.9			2	2	3	7	24	24		
18.0-18.9				1	2	5	16	13		1
19.0-19.9					1	1	5	9	2	
20.0-20.9						1	3	2	1	
21.0-21.9							2			
22.0-22.9								1		
Total number	2	22	73	6	70	55	81	59	3	1
Average length	7.5	11.0	13.3	16.6	15.5	16.7	17.4	17.9	19.7	18.6

groups (II-VIII). The span of ages was six at 16.0-16.9 inches and several other 1-inch intervals had spans of five age groups. Slow growth and broad length ranges also caused the distributions of five age groups to lie across the legal size limit of 17 inches.

The range in length of the age groups in the 1957-59 Whitefish Point samples (table 7) was also large (9.9 inches at age-group IV and 4.9 to 7.9 inches in other age groups represented by more than 20 fish) but overlapping was reduced by more rapid growth. Because of the good growth and a scarcity of older fish, overlap did not exceed four age groups at any 1-inch interval. The length distributions of only three groups (III-V) fell across the minimum legal size of 17 inches.

The lengths of the 1957 Bayfield samples, age groups combined, ranged from 7.0 to 22.9 inches

TABLE 7.—Length distribution of whitefish taken off Whitefish Point, 1957-1959

Total length (inches)	Age group						
	I	II	III	IV	V	VI	VII
10.0-10.9	1						
11.0-11.9							
12.0-12.9							
13.0-13.9		5					
14.0-14.9		4	5	2			
15.0-15.9		9	25	2			
16.0-16.9		8	53	9			
17.0-17.9			51	19	1		
18.0-18.9			30	20	3		
19.0-19.9			7	21	1	1	
20.0-20.9			7	9	5	1	
21.0-21.9				8	7	1	1
22.0-22.9				2	6		1
23.0-23.9				2		4	
24.0-24.9					4		
25.0-25.9						1	
Total number	1	27	178	94	31	7	2
Average length	10.5	15.1	17.1	18.8	21.7	22.9	21.9

TABLE 8.—Length distribution of whitefish caught in commercial pound nets, trap nets, and gill nets

Total length (inches)	Bayfield		Marquette	Whitefish Point	Dollar Settlement
	1957	1959	1957-59	1957-59	1957, 1959
7.0-7.9	2				
8.0-8.9	1				
9.0-9.9	3				
10.0-10.9	13			1	1
11.0-11.9	13		1		
12.0-12.9	18			1	2
13.0-13.9	25		1	5	5
14.0-14.9	42	3	9	11	24
15.0-15.9	53	23	12	36	65
16.0-16.9	76	64	52	70	40
17.0-17.9	60	36	36	71	59
18.0-18.9	38	11	61	53	31
19.0-19.9	18	5	56	29	11
20.0-20.9	7	3	53	22	5
21.0-21.9	2		53	17	4
22.0-22.9	1		41	9	2
23.0-23.9			14	10	4
24.0-24.9			10	4	
25.0-25.9			4	1	
26.0-26.9			4		1
27.0-27.9			1		
Total number	372	145	458	340	254
Average length	15.8	16.9	19.3	18.0	17.0
Percentage legal	33.9	37.9	83.6	63.5	46.1

and had a mean of only 15.8 inches (table 8). Only 33.9 percent of the fish were legal size. In contrast, the 1959 Bayfield whitefish had a range of only 6.9 inches, from 14.0 to 20.9 inches. The mean length in 1959 was 16.9 inches, and 37.9 percent of the fish were legal size.

The length distributions of the fish from Marquette, Whitefish Point, and Dollar Settlement were similar. The range from the shortest to the longest fish was 15.9 inches at Whitefish Point and 16.9 inches at Marquette and Dollar Settlement. The average lengths of the whitefish from these ports ranged from 17.0 inches at Dollar Settlement to 19.3 inches at Marquette. The percentage of

legal-size fish in the total catches varied considerably—36.1 percent at Dollar Settlement, 63.5 percent at Whitefish Point, and 83.6 percent at Marquette.

LENGTH-WEIGHT RELATION

The general length-weight relation of the Lake Superior whitefish (table 9) was based on the combination of materials regardless of locality, year and season of capture, type of gear, sex, or state of maturity. Undoubtedly the length-weight relation varies during the year and between ripe and recently spent females, as was demonstrated for Lake Erie whitefish by Van Oosten and Hile (1949). The data for this study were not affected by the presence of spawning fish as all fish used were collected in the summer, none later than September 30. Differences among samples from different ports were slight. The lack of small fish from ports east of Bayfield prevented construction of length-weight curves for comparison of localities.

TABLE 9.—Length-weight relation of Lake Superior whitefish of the combined collections of 1967-69

Number of fish	Total length ¹ (inches)	Weight (pounds)		Number of fish	Total length ¹ (inches)	Weight (pounds)	
		Empirical	Calculated			Empirical	Calculated
1	5.9	0.06	0.05	156	17.3	1.69	1.70
20	6.2	0.06	0.06	142	17.8	1.81	1.86
10	6.7	0.06	0.08	118	18.2	2.01	2.02
4	7.1	0.11	0.10	82	18.7	2.21	2.20
2	7.7	0.15	0.12	68	19.2	2.41	2.40
4	8.2	0.18	0.15	52	19.7	2.54	2.61
14	8.7	0.20	0.19	44	20.2	2.80	2.83
19	9.3	0.25	0.22	38	20.7	3.05	3.06
22	9.7	0.26	0.26	28	21.2	3.42	3.31
13	10.2	0.30	0.31	43	21.7	3.62	3.56
35	10.7	0.38	0.36	21	22.3	3.83	3.87
12	11.2	0.40	0.42	21	22.7	4.18	4.12
15	11.7	0.47	0.48	12	23.1	4.34	4.38
14	12.2	0.54	0.56	16	23.7	4.95	4.75
18	12.7	0.60	0.63	7	24.3	5.14	5.12
19	13.2	0.71	0.72	9	24.7	5.88	5.45
23	13.7	0.80	0.81	2	25.2	6.15	5.79
37	14.2	0.89	0.91	3	25.6	6.80	6.08
55	14.7	1.00	1.01	2	26.2	6.13	6.53
87	15.2	1.12	1.13	1	26.5	5.90	6.82
103	15.8	1.31	1.26	1	27.5	8.00	7.69
120	16.2	1.43	1.39	1	29.2	8.90	9.34
170	16.7	1.53	1.62				

¹ Actual averages for fish grouped by ½-inch intervals.

The empirical weights of whitefish at different lengths are shown graphically by dots in figure 3. The curve is a graph of the following equation obtained by fitting a straight line by least squares to the logarithms of the average lengths and weights:

$$W = 1.6643 \times 10^{-4} L^{3.2408}$$

where W = weight in pounds,
and L = total length in inches.

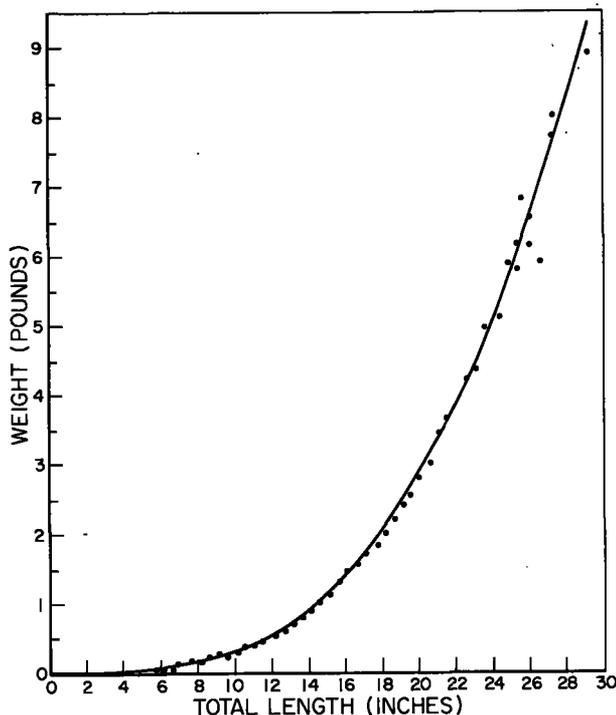


FIGURE 3.—Length-weight relation of Lake Superior whitefish. The curve represents the calculated weights and the dots the empirical weights.

The length of the Lake Superior whitefish increases as the 3.2408 power of the length. The substantial departure of this power above 3 indicates a considerable increase of plumpness with increase of length.

The agreement between the calculated and empirical weights was generally good. The greatest discrepancies were among the larger fish where the numbers of individuals were small. The largest disagreement occurred at 26.5 inches where the empirical weight (5.90 pounds) was 0.92 pound below the calculated weight (6.82 pounds). Other disagreements between the calculated and empirical weights were without trend and did not exceed 0.72 pound among fish above 21.2 inches and 0.07 pound for fish less than 21.2 inches long.

CALCULATED GROWTH BODY-SCALE RELATION

The body-scale relation of Lake Superior whitefish taken at Bayfield supports the earlier finding of Van Oosten (1923) that direct-proportion calculations of the length of whitefish based on diameter measurements of the scales are satis-

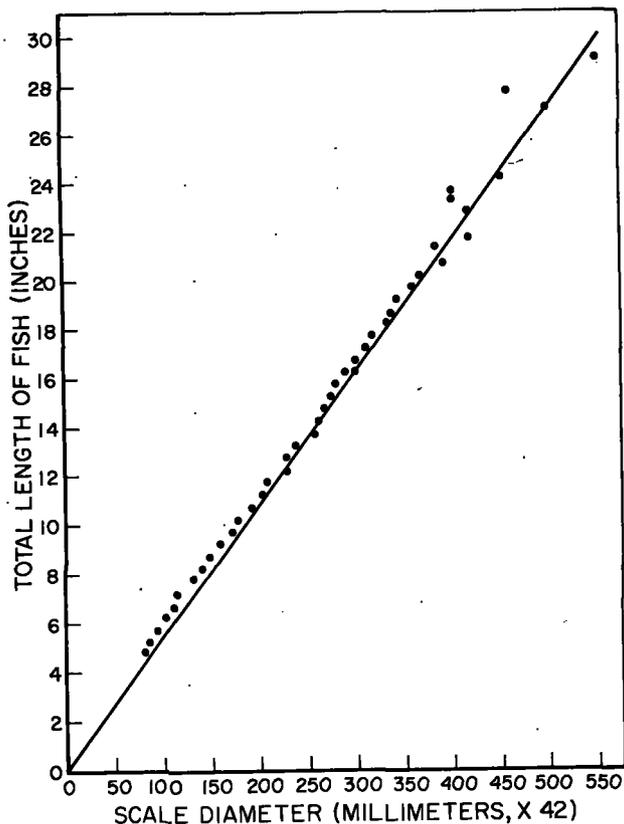


FIGURE 4.—Relation between body length and scale diameter of Lake Superior whitefish taken at Bayfield, 1957-59. The line is a graph of the equation given in the text. The dots show the empirical averages by 0.5-inch intervals of total length.

factory. Key scales, taken from an exactly defined location, were not available, but scale samples removed from the same area of all fish are believed to be reliable for the determination of a body-scale regression.

The body-scale relation (table 10, fig. 4) constructed from records for 694 whitefish collected at Bayfield is obviously linear. A straight line fitted by least squares to the means of scale diameters and lengths of fish had the equation:

$$L = 0.04443 + 0.5401 S,$$

where L = total length in inches,

and S = scale diameter ($\times 42$) in millimeters.

The intercept of 0.04 inch on the length axis is so small it can be ignored; growth, accordingly, may be calculated by direct proportion. This procedure was further justified by the fact that

TABLE 10.—Relation between body length (L) and the diameter measurement of scales (S) of Bayfield whitefish

[Scale samples from 54 additional fish were not removed from the key area; these fish were not included in the study of the body-scale relation]

Number of fish	Total length ¹ (inches)	Scale diameter (millimeters $\times 42$)	Body-scale ratio ² ($\times 100$)	Number of fish	Total length ¹ (inches)	Scale diameter (millimeters $\times 42$)	Body-scale ratio ² ($\times 100$)
1	4.8	85	5.64	32	15.2	276	5.52
4	5.2	87	5.95	46	15.7	281	5.59
3	5.7	95	5.97	75	16.2	294	5.49
20	6.2	103	6.04	70	16.7	301	5.55
10	6.6	113	5.87	43	17.2	313	5.44
6	7.2	115	6.25	45	17.7	318	5.56
3	7.8	133	5.87	23	18.2	336	5.42
5	8.2	141	5.79	17	18.7	338	5.53
17	8.7	148	5.91	15	19.2	345	5.56
20	9.2	160	5.77	11	19.7	360	5.55
23	9.7	174	5.59	6	20.1	368	5.46
14	10.2	177	5.78	5	20.7	382	5.45
22	10.7	192	5.58	5	21.3	369	5.78
12	11.2	205	5.48	4	21.7	418	5.20
13	11.7	208	5.64	2	22.8	418	5.50
12	12.2	228	5.35	1	23.3	401	5.81
18	12.7	230	5.52	1	23.7	401	5.91
23	13.2	241	5.50	1	24.2	453	5.34
13	13.7	258	5.31	1	27.8	460	6.04
28	14.2	263	5.41	1	29.1	553	5.26
21	14.7	270	5.44				

¹ Means for fish within a 0.5-inch interval of total length.

² Means of the body-scale ratio computed for individual fish.

the values of the body-scale ratio remained nearly constant regardless of the length of the fish.

Body-scale data were inadequate for whitefish from other parts of Lake Superior because small fish were lacking in the samples. Preliminary observations suggest the possibility of slight differences between the body-scale relation of these fish and those from Bayfield. Because data were insufficient to test this possibility, calculations for all of the samples, regardless of locality, were made by direct proportion. Edsall (1960) described the body-scale relation of Munising Bay whitefish with a straight line that had an intercept of 1.486 inches on the length axis.

GROWTH IN LENGTH OF THE AGE GROUPS

The sexes have been combined for calculated growth of whitefish from the various ports. Sex records were lacking for most collections, but the comparison of the calculated growth of males and females, age group by age group, at Bayfield where sex data were available for most fish, disclosed no differences.

The major difficulties in the estimation of growth lay in the systematic decline in growth rate with increase of age at capture in collections from all four ports (tables 11, 12, 13, and 14). For example, first-year calculated lengths of whitefish taken at Bayfield in 1957 (table 11) decreased from 7.5 inches for age-group I to 4.2

TABLE 11.—Calculated total length (inches) of whitefish taken at Bayfield in 1957 and 1959 and average calculated lengths for each year's collections and for the combined collections

[In the bottom section the numbers of fish are in parentheses]

Age and year of capture	Number of fish	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	10
I 1957	2	7.5									
II 1957	22	5.8	10.3								
III 1957	73	5.4	8.8	12.6							
1959	6	5.3	9.9	14.2							
IV 1957	6	5.2	8.4	11.4	15.3						
1959	117	5.6	8.9	12.4	16.1						
V 1957	70	4.2	6.9	9.6	12.2	14.8					
1959	22	5.3	8.2	11.2	14.4	17.0					
VI 1957	55	4.2	6.7	8.9	11.1	13.6	15.9				
VII 1957	81	4.6	6.5	8.3	10.1	12.4	14.8	16.8			
VIII 1957	59	4.6	6.1	7.9	9.6	11.7	13.8	15.8	17.5		
IX 1957	3	4.8	6.9	8.0	9.7	11.8	14.0	16.1	18.3	19.7	
X 1957	1	4.4	6.3	8.2	9.8	11.2	13.2	14.8	16.6	17.9	18.6
Average:											
1957 ¹		4.7 (372)	7.3 (370)	9.5 (348)	10.8 (275)	13.1 (269)	14.8 (199)	16.4 (144)	18.1 (63)	19.5 (4)	20.2 (1)
1959		5.5 (145)	8.8 (145)	12.3 (145)	15.8 (139)	17.0 (22)					
1957, 1959 ²		5.1	8.0	10.9	13.3	15.0	16.7	18.3	20.0	21.4	22.1

¹ Based on successive addition of grand average increments beyond the seventh year of life.

² Unweighted mean average lengths for the 1957 and 1959 samples through

the first 5 years of life; lengths for later years obtained by successive addition of annual increments for the fish of the 1957 sample.

inches for age-group V. Second-year calculated lengths decreased from 10.3 inches for the II group to 6.1 inches for VIII group. Similar discrepancies occurred in the data for all of the collections. Second-year calculated lengths, for example, decreased from 11.6 inches for the II group to 7.9 inches for the VI group at Marquette (table 12), from 12.2 inches for the II group to 8.4 inches for the VII group at Whitefish Point (table 13), and from 11.7 inches for the II group to 8.0 inches for the V group at Dollar Settlement (table 14).

The high calculated lengths of the younger age groups and the low values for the older fish can be traced to two major sources: gear selection of the larger fish in the younger age groups, and the progressive destruction of the faster growing

fish of a year class as they attain the legal length of 17 inches. Gear selection leads to over-estimates of growth of the younger age groups, and the selective destruction of the faster growing fish modifies progressively the growth characteristics of the survivors, and thus leads to successively more severe underestimates of the growth that would occur if the stock were not subjected to this type of exploitation. The selective destruction can end only when the smallest members of the year class reach legal length.

A comparison of calculated lengths of whitefish taken by the *Siscowet* with those taken from commercial gear at Bayfield in 1959 (table 15) illustrates bias through gear selection. The calculated lengths of fish from the commercial samples were nearly always higher than the

TABLE 12.—Calculated total length (inches) of whitefish taken off Marquette, 1957-59

[In the bottom section the numbers of fish are in parentheses]

Age group	Number of fish	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	10
II	16	6.0	11.6								
III	115	5.9	9.7	13.9							
IV	153	5.6	9.0	12.6	16.7						
V	115	5.3	8.5	11.5	15.2	18.9					
VI	38	5.2	7.9	10.6	13.7	17.3	20.5				
VII	12	5.6	8.1	10.5	13.2	16.1	19.4	21.8			
VIII	5	5.3	8.0	11.1	14.2	17.8	20.9	23.0	24.3		
IX	1	4.5	6.6	8.6	10.1	11.2	13.2	17.0	18.9	23.1	
X	3	5.5	8.0	9.4	11.9	14.0	16.8	19.2	21.8	23.4	25.0
Grand average ¹		5.6 (458)	9.0 (458)	12.4 (442)	15.6 (327)	18.2 (174)	20.0 (59)	21.5 (21)	22.9 (9)	25.2 (4)	26.8 (3)

¹ Based on successive addition of mean increments in the 9th and 10th years of life.

TABLE 13.—Calculated total length (inches) of whitefish taken off Whitefish Point, 1957-59

[In the bottom section the numbers of fish are in parentheses]

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	
I.....	1	6.8	-----	-----	-----	-----	-----	-----	
II.....	27	6.8	12.2	-----	-----	-----	-----	-----	
III.....	178	6.7	11.7	15.1	-----	-----	-----	-----	
IV.....	94	6.7	10.6	14.3	17.8	-----	-----	-----	
V.....	31	6.4	10.5	14.2	17.8	20.9	-----	-----	
VI.....	7	5.5	8.7	12.8	15.9	19.0	22.3	-----	
VII.....	2	5.1	8.4	11.8	14.9	17.5	19.8	21.4	
Grand average ¹	-----	6.6 (340)	11.2 (339)	14.7 (312)	17.6 (134)	20.4 (40)	21.7 (9)	23.3 (2)	-----

¹ Based on addition of the increments in the seventh year of life.

calculated lengths from the *Siscowet* samples. The differences were particularly great for age-groups III and V but were limited in age-group IV. Whitefish collected by the *Siscowet* were taken from small-mesh trawls (2½-inch-mesh body; ½-inch-mesh cod end) and experimental gill nets with mesh sizes ranging from 1 to 5 inches by ½-inch intervals. The commercial samples were taken from 4¾-inch-mesh pound nets and 4½-inch-mesh gill nets. Undoubtedly only the larger members of the younger age groups were retained by the large meshes of the commercial gear, whereas most sizes were retained by the *Siscowet* gear.

The effect of the progressive destruction of the faster growing fish is illustrated by records for whitefish samples collected in 1957 at Bayfield in June, July, and August (table 16). The growth of members of the same age group taken in successive months differed widely. With few exceptions, whitefish at age-groups V to VIII taken earlier in the season had greater lengths at capture and higher calculated lengths than did

those taken later. The shift was progressive; the lengths of fish taken in June were greater than for those taken in July; the lengths of fish taken in July were greater than for those taken in August. The length distributions of the age groups (table 17) also show a systematic decrease in size as the summer progressed. With only one exception (August V-group sample) the percentage of legal fish in each of the age groups decreased as the season advanced.

The pound net fishery for whitefish begins at Bayfield about mid-June, and legal-size fish are selected immediately from the population. As the season progresses the number of legal-size whitefish in the commercial catch, despite summer growth, declines until middle and late August when operations cease because production levels make it economically impossible to continue. In 1957, 44.7 percent of the whitefish in the entire June sample were legal size. In July, 37.9 percent were legal, and by August only 16.3 were legal, a reduction of 28.4 in the percentage since June.

Since the growth rate of the Bayfield whitefish is so slow, the number of legal-size fish taken from the fishery far exceeds the number of undersized fish growing to legal size during the early-summer fishing season.

Records on the progress of the season's growth (table 18) suggest that one-third or more of the total growth occurs after August 15 which is about the time that the heavy pound netting ends. This growth, though less than 1 inch, is sufficient to bring a good number of whitefish into legal-size range by the following spring when pound netting is resumed.

TABLE 14.—Calculated total length (inches) of whitefish taken off Dollar Settlement, 1957-59

[In the bottom section the numbers of fish are in parentheses]

Age group	Number of fish	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	10
I.....	1	7.0	-----	-----	-----	-----	-----	-----	-----	-----	-----
II.....	40	6.3	11.7	-----	-----	-----	-----	-----	-----	-----	-----
III.....	95	6.3	9.9	14.2	-----	-----	-----	-----	-----	-----	-----
IV.....	47	6.0	9.1	12.5	16.1	-----	-----	-----	-----	-----	-----
V.....	55	5.1	8.0	10.6	14.1	17.2	-----	-----	-----	-----	-----
VI.....	10	5.3	8.6	11.3	13.4	16.5	19.1	-----	-----	-----	-----
VII.....	4	5.4	8.1	10.4	12.3	14.8	17.7	20.2	-----	-----	-----
VIII.....	1	5.5	9.5	11.5	13.1	15.7	17.1	18.7	20.2	19.4	-----
X.....	1	5.0	8.1	9.9	11.4	14.7	18.1	22.1	23.4	24.4	25.8
Grand average ¹	-----	5.9 (254)	9.5 (253)	12.7 (213)	14.8 (118)	16.9 (71)	18.6 (16)	20.3 (6)	21.4 (2)	22.4 (1)	23.8 (1)

¹ Based on successive addition of the mean increments in the 9th and 10th years of life.

TABLE 15.—Calculated total lengths (inches) of three age groups of whitefish taken by the M/V Siscowet and from Commercial gear at Bayfield, 1959

Age group and source of sample	Number of fish	Calculated length at end of year of life				
		1	2	3	4	5
III Siscowet.....	14	4.8	8.5	11.5	-----	-----
Commercial.....	6	5.3	9.9	14.2	-----	-----
IV Siscowet.....	21	5.5	9.0	12.3	15.4	-----
Commercial.....	117	5.6	8.9	12.4	16.1	-----
V Siscowet.....	18	5.3	7.7	10.4	13.0	15.4
Commercial.....	22	5.3	8.2	11.2	14.4	17.0

Discrepancies of calculated length of the type shown by Lake Superior whitefish have been observed repeatedly among fish sorted about a size limit or taken by highly selective gear. Numerous explanations of discrepancies in calculated lengths can be found in the literature. Some have been traced to the use of incorrect formulas for growth calculation, but where the body-scale relation has been determined accurately, investigators generally have agreed that gear selectivity and destruction of the more rapidly growing individuals by the fishery are the two major sources of bias. Discussions of this problem may

be found in Deason and Hile (1947) and El-Zarka (1959).

GENERAL GROWTH IN LENGTH

The information on gear selectivity and selective destruction of the rapidly growing fish given in the previous section makes it obvious that any estimate of general growth is of necessity an approximation. Since the two major sources of bias are to an unknown degree compensating, the estimate of general growth for each locality is based on all available fish. The Siscowet samples have been omitted from the general growth studies in order to permit comparisons among the net-run collections from commercial gear at the various ports.

The 1957 and 1959 Bayfield samples have been combined even though differences were wide between the sizes at capture and the calculated lengths of the two collections. As was explained in the section on age and size at capture, the differences most probably can be attributed to a period of exceptionally good growth in 1954-57.

TABLE 16.—Size at capture and calculated total lengths (inches) of four age groups in samples of whitefish collected at Bayfield in different months, 1957

Age and Date of collection	Number of fish	Average length at capture	Calculated length at end of year of life							
			1	2	3	4	5	6	7	8
V June 13.....	21	16.4	4.4	7.0	10.0	13.0	16.4	-----	-----	-----
July 22.....	32	15.2	4.3	7.0	9.3	12.2	14.4	-----	-----	-----
Aug. 15.....	16	15.1	4.2	6.5	8.9	11.1	13.7	-----	-----	-----
VI June 13.....	12	17.9	4.6	7.1	9.6	12.5	15.3	17.9	-----	-----
July 22.....	28	16.6	4.4	6.9	9.0	11.1	13.6	15.7	-----	-----
Aug. 15.....	14	16.0	4.2	6.4	8.1	9.9	12.1	14.7	-----	-----
VII June 13.....	24	18.4	4.6	6.7	8.7	10.9	13.4	15.8	18.4	-----
July 22.....	41	17.3	4.7	6.6	8.4	10.3	12.3	14.6	16.4	-----
Aug. 15.....	16	16.4	4.6	6.1	7.7	9.4	11.4	13.5	15.3	-----
VIII June 13.....	21	18.9	4.5	6.3	8.3	10.1	12.3	14.6	16.8	18.9
July 22.....	27	17.5	4.6	6.1	7.9	9.6	11.6	13.7	15.5	16.9
Aug. 15.....	11	17.4	4.5	5.9	7.3	9.0	10.7	12.5	14.5	16.4

TABLE 17.—Length distribution of the age groups of samples of whitefish collected at Bayfield in different months, 1957

Total length (inches)	V-group			VI-group			VII-group			VIII-group		
	June	July	August	June	July	August	June	July	August	June	July	August
12.0-12.9.....	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----
13.0-13.9.....	-----	-----	2	-----	-----	-----	-----	-----	1	-----	-----	-----
14.0-14.9.....	-----	13	4	-----	1	1	-----	1	2	-----	-----	-----
15.0-15.9.....	5	14	5	-----	4	6	-----	3	8	-----	-----	-----
16.0-16.9.....	9	5	3	-----	3	5	-----	2	5	-----	-----	-----
17.0-17.9.....	2	-----	1	3	7	1	2	10	-----	4	15	4
18.0-18.9.....	2	-----	-----	4	2	1	-----	11	-----	7	5	1
19.0-19.9.....	1	-----	-----	1	-----	-----	-----	5	-----	7	1	1
20.0-20.9.....	-----	-----	-----	1	-----	-----	-----	2	-----	2	-----	-----
21.0-21.9.....	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
22.0-22.9.....	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Total number.....	21	32	16	12	28	14	24	41	16	21	27	11
Average length.....	16.4	15.2	15.1	17.9	16.6	16.0	18.4	17.3	16.4	18.9	17.5	17.4
Percentage, legal size.....	23.8	0.0	6.3	75.0	32.1	14.3	91.7	56.1	18.8	100.0	77.8	63.6

TABLE 18.—Amount of season's growth in length (inches) of four age groups of Bayfield whitefish up to and following August 15, 1957

Age group	Growth to Aug. 15	Full season's growth ¹	Growth after Aug. 15	Percent-age of total growth
V.....	1.4	2.3	0.9	39
VI.....	1.3	2.0	.7	35
VII.....	1.1	1.7	.6	35
VIII.....	1.0	1.4	.4	29

¹ Determined from the next higher age group in the same collection.

Growth in length of Lake Superior whitefish varied considerably according to port (table 19, fig. 5). Bayfield whitefish were by far the slowest growing. The first-year calculated length was 5.1 inches. The annual increments decreased from 2.9 inches in the second and third years to 0.7 inch in the tenth, at which time the fish were 22.1 inches long.

The whitefish from Marquette were considerably faster growing. These fish attained an average length of 5.6 inches in the first year, and fairly rapid growth continued through the fifth year of life when their average calculated length was 18.2 inches. Marquette whitefish were 26.8 inches long at the end of their tenth growing season.

The Whitefish Point whitefish were by far the fastest growing in the four areas studied. At the end of the first year the fish averaged 6.6 inches long. The annual increments decreased slowly from 4.6 inches in the second year to 2.8 inches

in the fifth at which time the fish averaged 20.4 inches (compared to 15.0 inches at Bayfield). By the end of the seven growing seasons, the Whitefish Point whitefish were 23.3 inches long. The samples included no fish older than age-group VII.

TABLE 19.—Calculated total length (inches) of Lake Superior whitefish according to port

[The collections from the different years have been combined]

Year of life	Bayfield		Marquette		Whitefish Point		Dollar Settlement	
	Length	Increment	Length	Increment	Length	Increment	Length	Increment
1.....	5.1	5.1	5.6	5.6	6.6	6.6	5.9	5.9
2.....	8.0	2.9	9.0	3.4	11.2	4.6	9.5	3.6
3.....	10.9	2.9	12.4	3.4	14.7	3.5	12.7	3.2
4.....	13.3	2.4	15.6	3.2	17.6	2.9	14.8	2.1
5.....	15.0	1.7	18.2	2.6	20.4	2.8	16.9	2.1
6.....	16.7	1.7	20.0	1.8	21.7	2.9	18.6	1.6
7.....	18.3	1.6	21.5	1.5	*23.3	1.6	20.3	1.7
8.....	*20.0	1.7	22.9	1.4	-----	-----	21.4	1.1
9.....	*21.4	1.4	*25.2	2.3	-----	-----	*22.4	1.0
10.....	*22.1	0.7	*26.8	1.6	-----	-----	*23.8	1.4

Asterisks indicate lengths based on the successive addition of grand average increments.

Dollar Settlement whitefish were longer than the Marquette stocks for the first 3 years, but were the shorter in the subsequent 7 years. Dollar Settlement whitefish attained an average length of 5.9 inches in the first year of life, and 16.9 inches by the end of the fifth year. Their calculated length after 10 growing seasons was 23.8 inches. The growth rate of the Dollar Settlement stock was clearly different from that of the Whitefish Point fish even though the grounds are barely 30 miles apart. Preliminary examination of scale samples collected in 1960 from Dollar Settlement and Whitefish Point further demonstrated faster growth of fish from Whitefish Point; the differences were not as pronounced, however, as in the 1957-59 samples.

The differences in the calculated growth of whitefish taken off different ports, along with the differences in age composition and size at capture of the commercial catch, were sufficiently great and consistent to suggest that a number of distinct stocks of whitefish inhabit Lake Superior. This belief is given further support by the findings of Edsall (1960) on the very slow growth of whitefish in Munising Bay, Lake Superior. The Munising Bay whitefish averaged 5.5 inches long after the first growing season, but second-year growth amounted to only 1.7 inches, and no annual increment exceeded 1.0 inch after the third year or

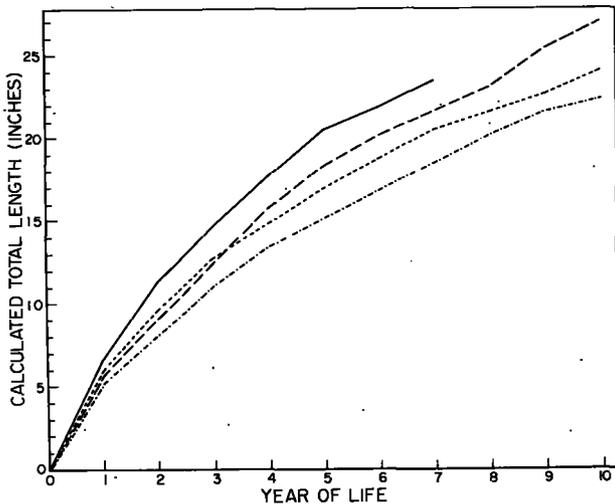


FIGURE 5.—Calculated length of Lake Superior whitefish according to port. Whitefish Point, solid line; Marquette, long dashes; Dollar Settlement, short dashes; Bayfield, dots and dashes.

0.5 inch after the twelfth. The highest calculated length attained was 16.7 inches in 16 years.

The major differences in growth among the four open-lake stocks of Lake Superior whitefish occur during the first few years of life. After the fifth year the annual increments of growth agree reasonably well. It would appear that the factors controlling growth rates are most effective during the first few years of life.

The order of the four stocks with respect to calculated length was the same for all years of life except in the samples from Marquette and Dollar Settlement (fig. 5). The Bayfield fish had the shortest and the Whitefish Point fish the longest calculated lengths in all possible comparisons, but the position of fish from Marquette and Dollar Settlement was reversed as growth proceeded. The differences in calculated lengths between whitefish from Bayfield and Whitefish Point were very large. At the end of 7 years, the calculated length of the Whitefish Point stock was 5.0 inches longer than that of the Bayfield whitefish.

GENERAL GROWTH IN WEIGHT

The weights of table 20 (see also fig. 6) were computed by means of the general length-weight equation given on p. 86 and correspond exactly with lengths of table 19. All questions relating to the reliability of the calculated lengths of table 19 apply, therefore, to the calculated weights.

The calculated weights differed little at the end of the first year, but in subsequent years wide differences developed among fish from the several ports. Since the calculated weights were computed from the calculated lengths, the Bayfield whitefish exhibited the slowest growth in weight.

TABLE 20.—*Calculated weight (pounds) at the end of each year of life of Lake Superior whitefish according to port*

[Weights were computed from the calculated lengths of table 19 by means of the general length-weight equation]

Year of life	Bayfield		Marquette		Whitefish Point		Dollar Settlement	
	Weight	Increment	Weight	Increment	Weight	Increment	Weight	Increment
1.....	0.04	0.04	0.05	0.05	0.07	0.07	0.05	0.05
2.....	.14	.10	.20	.15	.42	.35	.25	.20
3.....	.40	.26	.57	.37	1.01	.59	.63	.38
4.....	.72	.32	1.20	.63	1.80	.79	1.02	.39
5.....	1.05	.33	2.00	.80	2.90	1.10	1.57	.55
6.....	1.52	.47	2.70	.70	3.56	.66	2.13	.56
7.....	2.02	.50	3.40	.70	4.48	.92	2.88	.75
8.....	2.70	.68	4.20	.80	-----	-----	3.37	.49
9.....	3.40	.70	5.79	1.59	-----	-----	3.95	.58
10.....	3.85	.45	7.05	1.26	-----	-----	4.80	.85

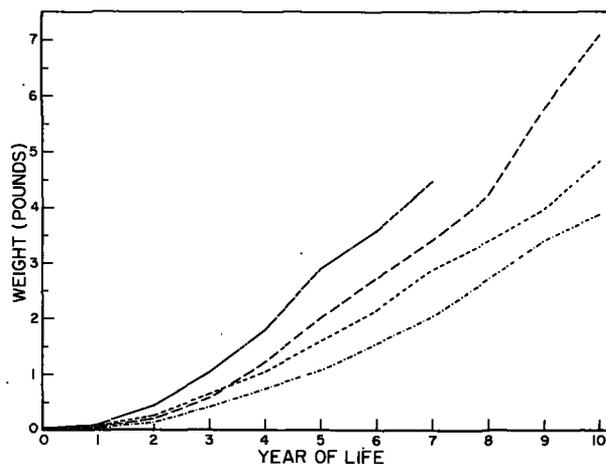


FIGURE 6.—Calculated growth in weight of Lake Superior whitefish according to port. Whitefish Point, solid line; Marquette, long dashes; Dollar Settlement, short dashes; Bayfield, dots and dashes.

Increments in individual years of life were small at Bayfield (0.04 pound the first year to 0.70 pound in the ninth). Bayfield stocks did not reach 1 pound until the fifth year of life and weighed only 3.85 pounds after 10 years.

The Marquette whitefish grew considerably faster in weight than the Bayfield stock. These fish reached 1 pound during the fourth growing season, and by the tenth they had reached 7.05 pounds. The annual increments of weight increased steadily from 0.05 pound in the first year to 0.80 pound in the fifth year. Between the fifth and eighth years the increments varied only from 0.70 to 0.80 pound. During the ninth year the increment was 1.59 pounds, and in the tenth it was 1.26 pounds.

Growth was faster at Whitefish Point, of course, than at any other port. The fish reached 1 pound at the end of the third growing season, and by the seventh year they weighed 4.48 pounds. Annual increments exceeded 0.5 pound in each year after the second.

The growth in weight of Dollar Settlement stocks was better than Bayfield fish but slower than the Marquette (after 3 years) and Whitefish Point stocks. Four years were required for the fish to reach 1 pound, and at the end of 10 years they weighed 4.80 pounds. The annual increments varied from 0.05 pound in the first year to 0.85 pound in the tenth year of life.

TABLE 21.—Growth in total length (inches) of whitefish in different parts of the Great Lakes

[Sources of data: Lake Ontario, Hart (1931); Lake Erie, Van Oosten and Hile (1949); Lake Huron, Van Oosten (1939); Lake Michigan, Roelofs (1958); Lake Superior, Munising Bay, Edsall (1960). Records are not carried beyond 10 years]

Area	Calculated length at end of year of life									
	1	2	3	4	5	6	7	8	9	10
Lake Ontario ¹			9.4	12.0	15.4	17.9	19.1	20.4	21.0	22.3
Lake Erie.....	6.9	12.7	16.1	18.1	19.6	20.7	21.4	22.1	22.8	23.2
Lake Huron.....	5.0	8.9	12.3	16.1	19.2	21.4	22.9	23.9	24.8	25.3
Lake Michigan:										
Big Bay de Noc.....	5.6	9.4	13.8	17.9						
South Fox Island.....	4.3	7.0	9.9	13.2						
Lake Superior:										
Bayfield.....	5.1	8.0	10.9	13.3	15.0	16.7	18.3	20.0	21.4	22.1
Marquette.....	5.6	9.0	12.4	15.6	18.2	20.0	21.5	22.9	25.2	26.8
Munising Bay.....	5.5	7.2	8.4	9.4	10.1	10.8	11.5	12.1	12.9	13.6
Whitefish Point.....	6.6	11.2	14.7	17.6	20.4	21.7	23.3			
Dollar Settlement.....	5.9	9.5	12.7	14.8	16.9	18.6	20.3	21.4	22.4	23.8

¹ Actual lengths at capture during growing season subsequent to indicated year.

GROWTH OF WHITEFISH IN LAKE SUPERIOR AND OTHER GREAT LAKES

The records of growth of whitefish in other Great Lakes localities were published originally with various measurements and units, and some presentations included no calculated lengths. Certain adaptations were required and some explanations are needed to permit an instructive study of the data of table 21. The lengths for the Lake Ontario whitefish represent actual lengths at capture for fish collected during the indicated year of life; they have been converted to total length from the standard lengths given by Hart (1931). The data for Lake Huron and Lake Erie are from a table in Van Oosten and Hile (1949).

The differences in growth among the various stocks of Great Lakes whitefish do not allow a clear ranking for individual populations. The relations among the stocks shifted according to age, and not one group was consistently the faster or slower growing population. The whitefish from South Fox Island grew only 4.3 inches during the first year of life but by the end of the fourth year they were 13.2 inches long. Munising Bay whitefish grew 5.5 inches the first year but did not reach 13.0 inches until the tenth year of life. The growth of whitefish from Whitefish Point, Marquette, and Dollar Settlement compared closely with the growth of Lake Erie, Lake Huron, and Big Bay de Noc stocks. Again, the relations shifted according to age, but all of these stocks were among the fastest growing whitefish in the Great Lakes. The growth of the Bayfield whitefish was similar to that of the Lake Ontario

stock; faster growing than Munising Bay and South Fox Island fish but slower than the other populations.

SEX RATIO AND MATURITY

SEX RATIO

Usable data on the sex ratio of Lake Superior whitefish are available only for part of the Bayfield samples of 1957 and 1959 (table 22). The data from the samples for the 2 years were so similar that the collections have been combined. Fish of age-group I were omitted from this study because of uncertainties in sex determination. With the exception of age-groups V and VII, the number of males exceeded the number of females in age-groups II–VIII. The advantage of the males over the females was small—not over 58.1 percent males (age-group III). Age-groups IX and X were represented by very small numbers of fish, but males were scarce at these ages—only one male in a total of seven fish. The percentage of male whitefish in samples from Lake Huron (Van Oosten, 1939) and Lake Erie (Van Oosten and Hile, 1949) decreased with increase of age.

In the entire Bayfield sample, all ages combined, the sexes were almost equally represented (51.5 percent males).

SIZE AND AGE AT MATURITY

All whitefish from Bayfield shorter than 14.5 inches were immature, and all fish longer than 17.4 inches were mature. The first mature male appeared in the 14.5- to 14.9-inch group (table 23). The percentage of mature males reached 57.1 percent at 16.0–16.4 inches, and all of the males were mature at lengths greater than 16.9 inches.

TABLE 22.—Sex ratio of whitefish taken at Bayfield
[Based on the combined collections of 1957 and 1959]

Age group	Number of males	Number of females	Percentage males
II.....	35	29	54.7
III.....	50	36	58.1
IV.....	54	47	53.5
V.....	46	47	49.5
VI.....	25	24	51.0
VII.....	38	46	45.2
VIII.....	32	30	51.6
IX.....		3	0
X.....	1	3	25.0
All ages.....	281	265	51.5

TABLE 23.—Relation of length to maturity of whitefish taken at Bayfield in July and August 1957

[Data on maturity were not recorded for all individuals. All fish shorter than 14.5 inches were immature, and all longer than 17.4 inches were mature]

Length (inches)	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Percentage mature
14.5-14.9.....	5	1	16.7	7	0	0
15.0-15.4.....	8	2	20.0	6	0	0
15.5-15.9.....	5	2	28.6	8	0	0
16.0-16.4.....	6	8	57.1	8	7	46.7
16.5-16.9.....	1	16	90.9	5	11	68.8
17.0-17.4.....	0	12	100.0	1	5	83.3

The first mature females appeared at 16.0-16.4 inches, and all females longer than 17.4 inches were mature. First maturity of males occurred at a length 1.0 inch shorter than in females, and 100-percent maturity of males occurred at a length 0.5 inch shorter than in females.

The youngest mature fish of each sex belonged to age-group V (table 24), and all whitefish older than age-group VII were mature. Among age-groups V-VII the percentage maturity of males was consistently higher than for females of corresponding age. The mature fish of each sex without exception were longer than the immature fish of the same age group.

The scanty data on sexual maturity from other ports are inadequate for detailed study, but they suggested that the faster growing whitefish mature at a greater length and a lower age. Alm (1959) held that fish which have particularly slow growth may mature at a higher age but at a length which is below that of faster growing specimens. Comparisons of length and age at maturity of Bayfield whitefish with those of whitefish from other localities support this argument. Munising Bay whitefish (Edsall, 1960), which grow much more slowly than the Bayfield stock, exhibit first maturity at 11.5 inches and 100-percent maturity

TABLE 24.—Length of mature and immature whitefish of three age groups taken off Bayfield in July and August 1957

[Number of fish in parentheses. All whitefish younger than age-group V were immature, and all older than age-group VII were mature]

Sex and state of gonads	Calculated length at last annulus		
	V	VI	VII
Male:			
Mature.....	15.4 (3)	17.0 (15)	17.3 (20)
Immature.....	15.0 (24)	15.2 (6)	16.4 (2)
Percentage mature.....	11.1	71.4	90.9
Female:			
Mature.....	17.2 (1)	16.6 (9)	17.7 (21)
Immature.....	15.1 (16)	16.0 (11)	15.8 (10)
Percentage mature.....	5.9	45.0	67.7

at 15.0 inches. All Munising Bay whitefish younger than age-group VII were immature, and some were still immature as age-group XI. In direct contrast, Van Oosten (1939) reported first maturity for males at 17.8 inches and for females at 18.3 inches in Lake Huron. All of the males were mature at 20.1 inches, and all of the females at 21.5 inches. All male whitefish younger than age-group III and females younger than age-group IV were immature, and all males older than age-group V and females older than VI were mature. It appears, then, that among fish of the same length, those from stocks with the slower growth are the more likely to be mature, and among fish of the same age those from stocks with the more rapid growth are the more likely to be mature.

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LITERATURE CITED

- ALM, GUNNAR.
1959. Connection between maturity, size and age in fishes. Report of the Institute of Freshwater Research, Drottningholm, vol. 40, pp. 5-145.
- DEASON, HILARY J., and RALPH HILE.
1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74, for the year 1944, pp. 88-141.
- EDSALL, THOMAS A.
1960. Age and growth of the whitefish, *Coregonus clupeaformis*, of Munising Bay, Lake Superior. Transactions of the American Fisheries Society, vol. 89, no. 4, pp. 323-332.

EL-ZARKA, SALAH EL-DIN.

1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay, Lake Huron. U.S. Fish and Wildlife Service, Fishery Bulletin 151, vol. 59, pp. 365-415.

GALLAGHER, HUBERT R., and JOHN VAN OOSTEN.

1943. Supplemental report of the United States members of the International Board of Inquiry for the Great Lakes Fisheries. International Board of Inquiry for the Great Lakes Fisheries—Report and Supplement, pp. 25-213.

HART, JOHN LAWSON.

1931. The growth of the whitefish, *Coregonus clupeaformis* (Mitchill). Contributions to Canadian Biology and Fisheries, N.S., vol. 6, no. 20, pp. 427-444.

KOELZ, WALTER N.

1926. Fishing industry of the Great Lakes. Department of Commerce, Report of U.S. Commissioner of Fisheries for 1925, Appendix II, pp. 553-617.

MOFFETT, JAMES W.

1952. The study and interpretation of fish scales. The Science Counselor, vol. 15, no. 2, pp. 40-42.

ROELOFS, EUGENE W.

1958. Age and growth of whitefish, *Coregonus*

clupeaformis (Mitchill), in Big Bay de Noc and northern Lake Michigan. Transactions of the American Fisheries Society, vol. 87, for the year 1957, pp. 190-199.

SMITH, STANFORD H.

1954. Method of producing impressions of fish scales without using heat. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 16, no. 2 (April), pp. 75-78.

VAN OOSTEN, JOHN.

1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. Zoologica, Scientific Contributions of the New York Zoological Society, vol. 2, no. 17, pp. 380-412.

VAN OOSTEN, JOHN.

1939. The age, growth, sexual maturity, and sex ratio of the common whitefish, *Coregonus clupeaformis* (Mitchill), of Lake Huron. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 24, for the year 1938, part 2, pp. 195-221.

VAN OOSTEN, JOHN, and RALPH HILE.

1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77, for the year 1947, pp. 178-249.

INFLUENCE OF WATER VELOCITY UPON ORIENTATION AND PERFORMANCE OF ADULT MIGRATING SALMONIDS

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ABSTRACT

During the months of August and September 1957 a series of experiments were conducted at Bonneville Dam, to determine (1) how adult migrating salmonids respond to differences in flow velocity, (2) how they perform in two relatively high-velocity flows, and (3) how the velocity of flow influences their rate of movement.

Given a choice of entering either of two parallel channels carrying flows of different velocities, steelhead trout (*Salmo gairdneri*), chinook salmon (*Oncorhynchus tshawytscha*), and silver salmon (*O. kisutch*) generally demonstrated a preference for the channel with the higher velocity flow. The magnitude of the response varied between species and with velocities of the choice condition.

The performances of steelhead trout and chinook salmon were examined in flow velocities of 13.4 and 15.8

feet per second by determining the distance they could achieve in an 85-foot channel. Although there was considerable variation in the distances attained by individual fish at each velocity, steelhead trout were generally more successful in negotiating these velocities than chinook salmon. Larger fish of both species were more successful in negotiating the two flows than smaller fish. Both species performed better in the 13.4 feet per second flow than in the 15.8 f.p.s. flow.

Rates of movement of steelhead trout, chinook salmon, and silver salmon were measured in velocities ranging from 2 to 15.8 f.p.s. Rates of movement varied with species, size of fish, and velocity. Maximum observed swimming speeds are given for each species and various factors affecting rate of movement are discussed.

The increasing demand for greater utilization of water resources in the Pacific Northwest has resulted in plans for the construction of many new dams on the Columbia River and its tributaries. One of the major problems arising from these dams is that of preserving the valuable anadromous fish populations indigenous to these waters. Although there are several important aspects to the problem, one which is of primary concern is ensuring that the adult fish, migrating from the ocean to their fresh-water spawning grounds, are provided safe passage over these obstacles. In view of the number of dams which these fish will eventually have to surmount before reaching their destinations, it is extremely important to ensure that the passage facilities provided at each dam (including temporary passage during construction) are designed to operate as efficiently as possible. The cumulative effect of even minor losses or delays at each dam could seriously jeopardize

the perpetuation of this valuable fishery resource. The material reported upon in this paper represents one phase of a research program being conducted by the Bureau of Commercial Fisheries (reviewed by Collins and Elling, 1961) under contract to the U.S. Army Corps of Engineers,¹ to gain more precise knowledge of the principles involved in adult fish passage.

Although fish passage requirements may vary with the nature of the obstacle to be bypassed, the basic problems entailed in achieving efficient passage are: (1) attracting the migrating fish into the fishway entrance without delay and (2) providing conditions which will promote a normal rate of movement through the facility without taxing the physical capacities of the fish. The

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¹ Research financed by the U.S. Army Corps of Engineers as part of a broad program of research to provide design criteria for more economical and more efficient fish-passage facilities at Corps projects on the Columbia River.

purpose of these experiments was to acquire a better understanding of how the velocities of fishway flows may be related to these problems. The following three types of experiments were conducted: velocity-preference, high-velocity, and rate-of-movement. The objectives were (1) to examine the orientative influence of water velocity upon adult migrating salmonids to determine how the relative attractiveness of fishway entrances may be influenced by the velocities of adjacent flows, (2) to examine the performance of these fish at two relatively high-velocity flows to gain a better idea of the maximum water velocities which might be tolerated in fishways or passage channels, and (3) to measure the rate of movement of the fish in flows of various velocities to determine which velocities might be more conducive to a uniform rate of passage through fishway channels.

The work was conducted at the Fisheries-Engineering Research Laboratory at Bonneville

Dam on the Columbia River during the months of August and September 1957. Steelhead trout (*Salmo gairdneri*), fall chinook salmon (*Oncorhynchus tshawytscha*), and silver salmon (*O. kisutch*) were the salmonids used in the experiments.

RESEARCH LABORATORY

The laboratory is located immediately below the north end of the spillway section of Bonneville Dam adjacent to the Washington shore fishway (fig. 1). The laboratory and its entrance and exit fishways form a bypass around a short section of the main fishway (fig. 2). This unique feature permits fish to be collected, subjected to various types of experiments within the laboratory, and returned to the main fishway without being handled at any time.

The laboratory is composed of a collection pool where fish are collected prior to testing, an ex-

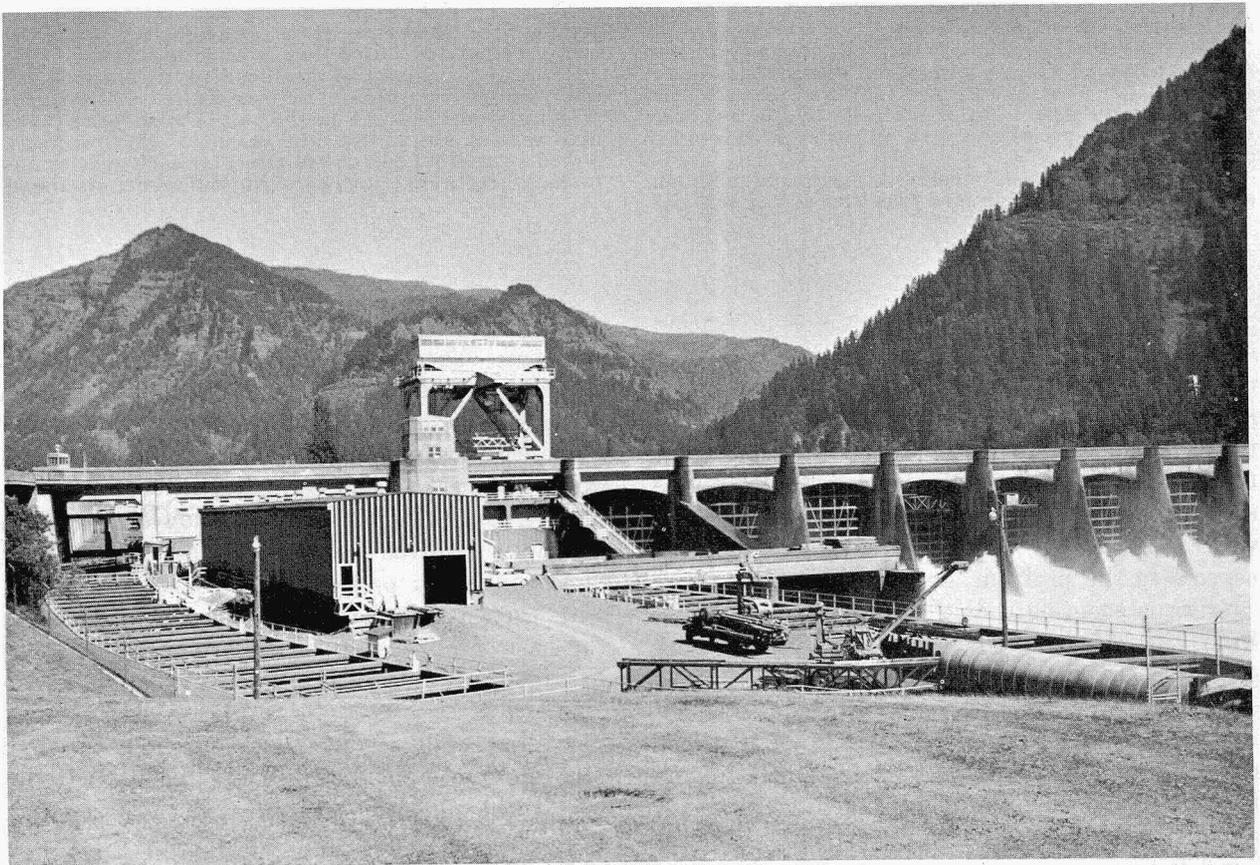


FIGURE 1.—Research laboratory showing Washington shore fishway in the foreground and section of main dam in background.

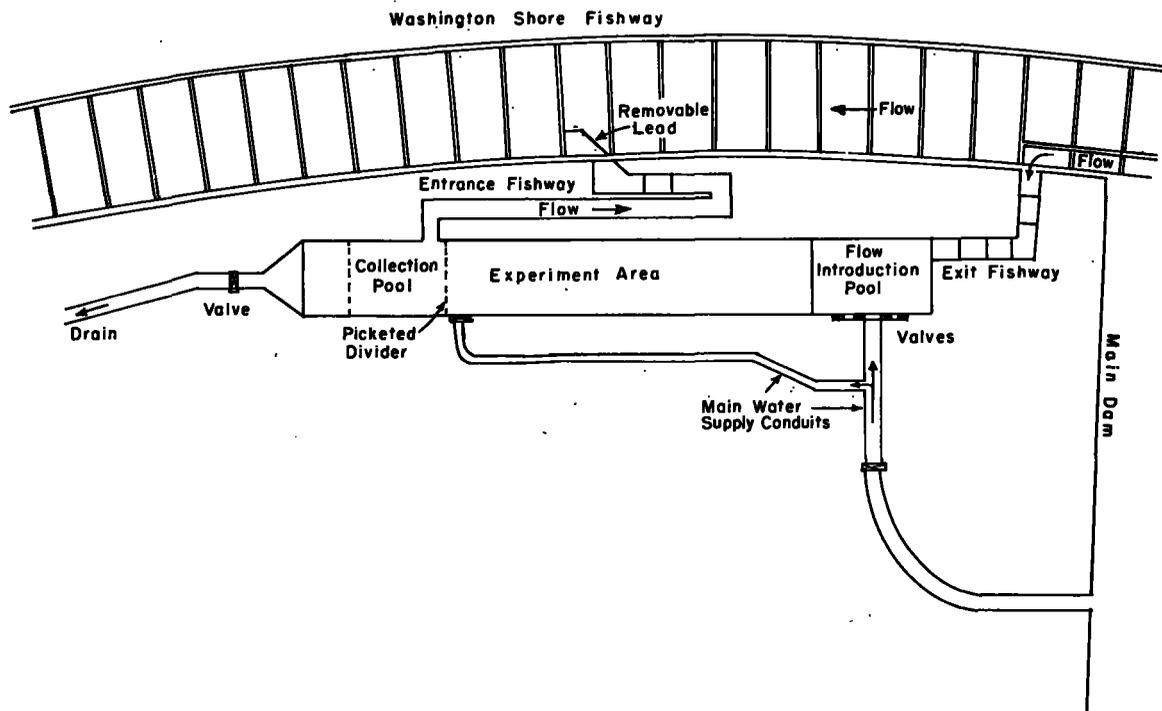


FIGURE 2.—Plan of research laboratory showing the basic components.

perimental area which can be modified to provide a variety of experimental conditions, and a flow-introduction pool where water is introduced into the laboratory. Water is supplied from two sources. The main source, capable of supplying approximately 200 cubic feet per second, comes directly from the forebay of the dam through a large conduit. The secondary source, approximately 20 c.f.s., is drawn from the Washington shore fishway to supply the facility exit fishway. The main water supply is distributed through smaller conduits to the flow-introduction pool, the collection pool, and other portions of the facility by manipulation of appropriate valves.

Water is discharged from the laboratory through a 48-inch drain conduit at the downstream end of the laboratory and through the entrance fishway. Discharge through the drain conduit is controlled by an electrically operated drain valve. Any desired water level can be maintained in the laboratory by proper adjustment of valves.

VELOCITY-PREFERENCE EXPERIMENTS

METHODS AND MATERIALS

The method employed in these experiments was patterned after the one used by Collins (1952)

in his studies of factors influencing the orientation of alewives (*Alosa pseudoharengus*) and glut herring (*A. aestivalis*). As the migrating fish passed through the laboratory they were presented with a choice of entering either of two channels. During control experiments the velocities of the flows in the two channels were equal; in test experiments the velocity of the flow in one channel was always greater than the other. The responses of the fish to the various test and control conditions were measured by the number of fish entering each channel.

Experimental Area

The basic experimental area of the facility was modified for these experiments to provide a choice or introductory area, 25 feet long and 11 feet wide, joining two parallel channels each 85 feet long and 5 feet wide (figs. 3 and 4). The channels, which will be referred to hereafter as the north and south channels, were centered in the experimental area and were separated by a common center wall 1 foot thick. The downstream end of the center wall was provided with a tapered hydrofoil to converge the two channel flows smoothly as they entered the choice area.

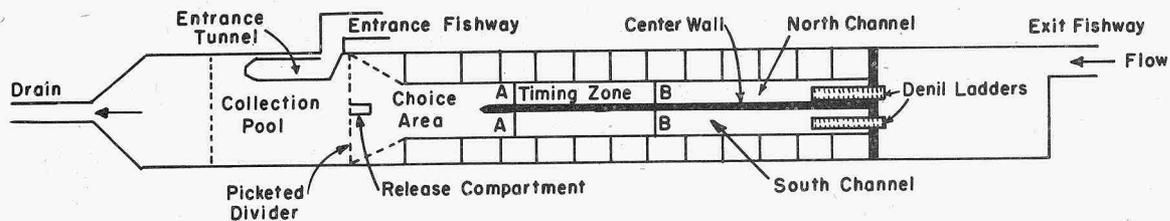


FIGURE 3.—Sketch of laboratory showing experimental area modified for the velocity-preference experiments.

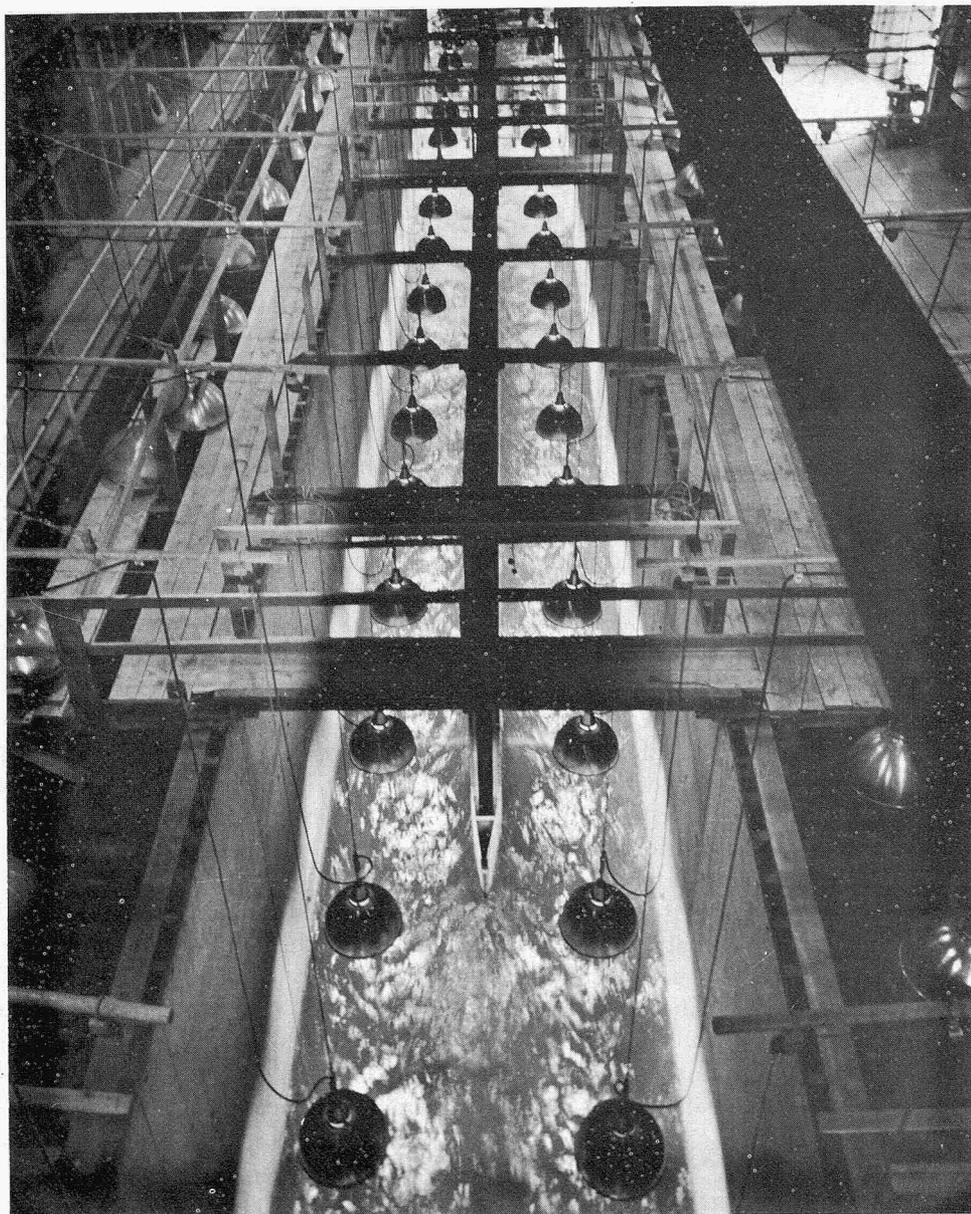


FIGURE 4.—View of the two channels and choice area during a control test. The velocity of flow in each channel is 4 f.p.s.

Stoplogs at the upstream end blocked the flow through the two areas outside of the channels (fig. 3). The downstream ends of these areas were open, allowing them to backfill when water was introduced into the area. Screens prevented fish from entering these areas.

The walls and floors of the channels and choice area were painted light brown to provide a uniform background throughout the experimental area.

Hydraulic Conditions

Water velocities in the two channels were controlled independently by regulating the quantity of water admitted to them from the flow introduction pool. This was accomplished by employing a prescribed arrangement of stoplogs at the upstream ends of the channels and maintaining the proper water level in the flow-introduction pool. Since the channel floors were level (zero slope) and the water at the downstream end of the two channels was maintained at nearly the same depth by regulation of the collection pool level, the ratio of the velocities of the two channels was equal to the ratio of the quantities of water flowing through the two channels. That is to say, if the velocity (f.p.s.) of one channel was twice as great as the other, then the quantity of water flowing through the channel (c.f.s.) would also be twice as great.

Velocities approximating 2, 4, 6, and 8 f.p.s. were utilized in these experiments. Table 1 lists the various combinations of these velocities which

were tested and gives the actual mean water velocities and depths as they were measured at the downstream end of the channels.

Hydraulic conditions within the channels and choice area varied with the velocity of the flow. At velocities of 2 and 4 f.p.s. uniform flow was maintained throughout the channels and choice area. At 6 and 8 f.p.s. velocities, standing waves were created within the channels and choice area (fig. 5). The position of these waves in relation to the channel and choice area walls remained fixed once the flows had become established. The structure shown at the upstream end of each channel in figure 5 are adjustable Denil-type ladders, which were provided to ensure that the fish would have no difficulty in negotiating the turbulent overfall created by the stoplogs.

Figure 6 illustrates the velocity gradients occurring in the choice area during the various tests at a point approximately 8 feet upstream from the release compartment. Velocities were measured with a Price current meter. Mean velocities were determined from measurements taken vertically at 4-inch intervals.

Release Compartment

Fish were introduced into the choice area through a release compartment 18 inches wide by 48 inches long by 18 inches deep. The compartment was mounted on the upstream face of the picketed divider in line with the center of the choice area (fig. 3). Fish entered the compartment through a sliding gate in the picketed divider and were released into the choice area by means of a second sliding gate at the upstream end of the compartment. The compartment was equipped with a false bottom or brail which could be raised to bring the fish near the water surface to facilitate the identification of species and estimation of length.

Efforts were made to achieve as near perfect symmetry as possible in the components of the release compartment and in the surrounding choice area to ensure that the fish would not perceive any visual stimuli which might bias their responses to the velocity test condition. The release compartment gate was operated from above and to the side to avoid frightening the fish by the motion of opening the gate, and wood panels were installed on each side of the compartment to shield the release compartment operator from the fish.

TABLE 1.—List of six test conditions and four control conditions utilized in the velocity-preference experiments

Condition	Desired velocity		Actual velocity ¹		Depth of water ¹	
	High-velocity channel	Low-velocity channel	High-velocity channel	Low-velocity channel	High-velocity channel	Low-velocity channel
Test	<i>F.p.s.</i>	<i>F.p.s.</i>	<i>F.p.s.</i>	<i>F.p.s.</i>	<i>Feet</i>	<i>Feet</i>
	8	2	8.14	1.91	1.7	1.9
	8	4	8.03	3.96	1.7	1.8
	8	6	8.09	5.91	1.7	1.7
	6	2	6.00	1.95	1.8	1.9
	6	4	6.02	3.96	1.7	1.9
	4	2	3.98	2.00	1.9	1.9
		North channel	South channel	North channel	South channel	North channel
Control	2	2	2.03	2.01	1.9	1.9
	4	4	3.93	3.96	1.9	1.9
	6	6	5.97	6.04	1.7	1.7
	8	8	8.36	8.19	1.7	1.7

¹ Mean velocities derived from measurements taken during individual trials of each condition. Both velocities and water depths were measured at the downstream ends of the channels (fig. 5).



FIGURE 5.—View of choice area and channels showing 6 f.p.s. flow on left and 8 f.p.s. flow on right. Note positions of standing waves. Platform above downstream end of channels was used to check water velocities and was removed during the tests.

Lighting

Uniform lighting was maintained within the channels and choice area by use of 1,000-watt mercury-vapor lamps mounted in polished reflectors. The lamps were suspended from horizontal wall brackets spaced 6 feet apart along the walls of the building and were adjusted to hang 8 feet above the level of the floor. This placed the lamps approximately 6 feet above the surface of the water (fig. 5).

Mean incident light intensities at the water surface in the choice area and within the channels were 604 foot-candles and 746 foot-candles, respectively. This light intensity was roughly comparable to that measured in daylight on a bright overcast day.

PROCEDURE

Experimental Design

The experiments were conducted in accordance with a balanced 4 by 4 lattice-square design in five replicates (Cochran and Cox, 1950). The high velocity for the 6 test conditions was alternated between north and south channels to provide a total of 12 different test treatments (table 2, section A). These, combined with the 4 control treatments provided a total of 16 different treatments for each replicate. The rows and columns of the design were randomized, and the treatments were assigned at random to the 16 treatment numbers in each replicate (table 2, section B). The order of testing proceeded from replicate I to V, and within each replicate from left to right

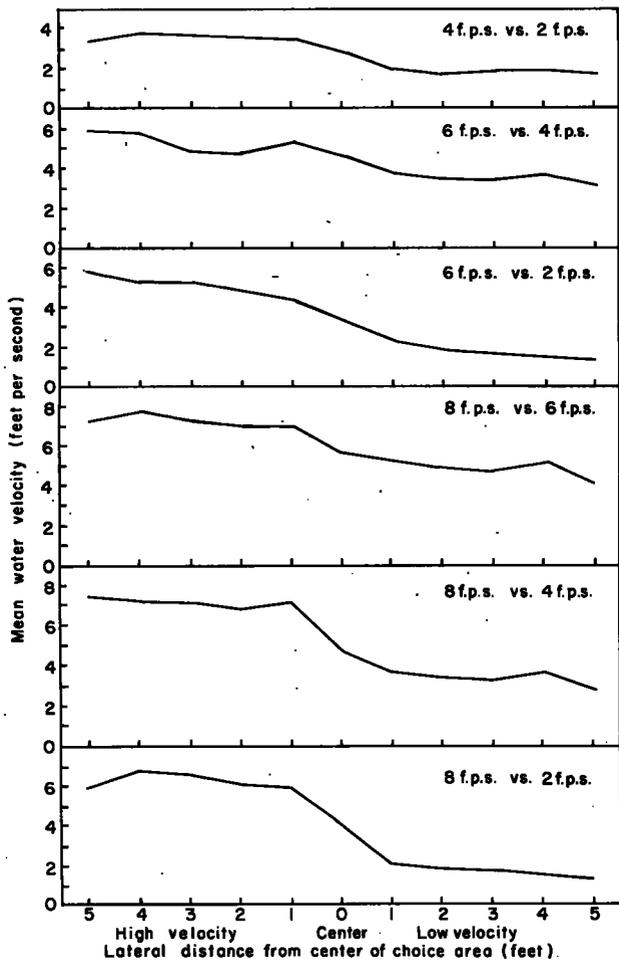


FIGURE 6.—Examples of velocity gradients occurring in cross section of choice area for each test condition.

along successive rows. The sample size for each test was set at 20 fish.

The original plan was to test both steelhead trout and chinook salmon simultaneously, continuing each test until the 20-fish sample of each species had been obtained. It became apparent, however, during several trial runs that chinook salmon were not sufficiently abundant to meet these requirements. The replicated tests, therefore, applied only to steelhead trout. Chinook salmon were tested as they presented themselves during the course of the experiments, but no effort was made to maintain consistency in the sample sizes with regard to these species. A few silver salmon were also tested during the course of the experiments.

To insure that the replicated tests would be as homogeneous as possible, the samples of 20 steel-

TABLE 2.—Outline of the 4 x 4 lattice-square design listing (A) the various test and control conditions and (B) the order of testing

A. EXPERIMENTAL CONDITIONS (TREATMENTS)

Channel	Water velocity (feet per second)															
	Test conditions												Control conditions			
South.....	8	2	8	4	8	6	6	2	6	4	4	2	2	4	6	8
North.....	2	8	4	8	6	8	2	6	4	6	2	4	2	4	6	8

B. EXPERIMENTAL CONDITIONS (TREATMENTS) RANDOMLY FITTED TO BASIC LATTICE SQUARE DESIGN

Replicate	Treatments ¹			
I.....	1. S ₂ N ₆	2. S ₂ N ₈	3. S ₂ N ₃	4. S ₂ N ₄
	5. S ₂ N ₂	6. S ₂ N ₄	7. S ₂ N ₈	8. S ₂ N ₆
	9. S ₂ N ₂	10. S ₂ N ₆	11. S ₂ N ₄	12. S ₂ N ₂
	13. S ₂ N ₆	14. S ₂ N ₈	15. S ₂ N ₂	16. S ₂ N ₄
II.....	17. S ₂ N ₆	18. S ₂ N ₄	19. S ₂ N ₂	20. S ₂ N ₈
	21. S ₂ N ₄	22. S ₂ N ₂	23. S ₂ N ₈	24. S ₂ N ₆
	25. S ₂ N ₂	26. S ₂ N ₈	27. S ₂ N ₆	28. S ₂ N ₄
	29. S ₂ N ₈	30. S ₂ N ₂	31. S ₂ N ₄	32. S ₂ N ₈
III.....	33. S ₂ N ₆	34. S ₂ N ₄	35. S ₂ N ₂	36. S ₂ N ₈
	37. S ₂ N ₂	38. S ₂ N ₈	39. S ₂ N ₆	40. S ₂ N ₄
	41. S ₂ N ₄	42. S ₂ N ₆	43. S ₂ N ₈	44. S ₂ N ₂
	45. S ₂ N ₈	46. S ₂ N ₂	47. S ₂ N ₄	48. S ₂ N ₆
IV.....	49. S ₂ N ₆	50. S ₂ N ₄	51. S ₂ N ₂	52. S ₂ N ₈
	53. S ₂ N ₈	54. S ₂ N ₂	55. S ₂ N ₄	56. S ₂ N ₆
	57. S ₂ N ₄	58. S ₂ N ₆	59. S ₂ N ₈	60. S ₂ N ₂
	61. S ₂ N ₂	62. S ₂ N ₈	63. S ₂ N ₆	64. S ₂ N ₄
V.....	65. S ₂ N ₆	66. S ₂ N ₄	67. S ₂ N ₂	68. S ₂ N ₈
	69. S ₂ N ₈	70. S ₂ N ₂	71. S ₂ N ₄	72. S ₂ N ₆
	73. S ₂ N ₄	74. S ₂ N ₆	75. S ₂ N ₈	76. S ₂ N ₂
	77. S ₂ N ₂	78. S ₂ N ₈	79. S ₂ N ₆	80. S ₂ N ₄

¹ Arabic numeral indicates order of testing, letter denotes channel, (S = south, N = north) and subscript denotes velocity (f.p.s.).

head were restricted to fish estimated to be from 22 to 26 inches in length. Smaller and larger steelhead were tested when available; however, they were not included in the 20-fish samples.

Conduct of Experiments

In preparing for a given test, the predetermined stoplog arrangement was inserted at the upstream end of each channel and the water levels of the flow-introduction and collection pools were adjusted to the proper heights. A brief period was allowed for the flows to become stabilized, then water velocities were measured with a current meter at the downstream end of each channel (fig. 5).

After the velocities of each channel had been measured and the observers had taken their respective stations, the release compartment operator was signaled to start the test. The sliding gate on the picketed divider was raised, and a single fish was allowed to enter the compartment. After determining the species and estimating the length of the fish, the operator raised the sliding gate at the upstream end of the release compartment, allowing the fish to enter the choice area. An

observer stationed on a walkway over the choice area followed the fish as it passed through the choice area and noted which channel was chosen. After the fish had passed through the channel a second fish was released and so on until the desired sample of 20 steelhead within the 22- to 26-inch size range had been tested.

Upon completion of a test, the main water supply entering the flow-introduction pool was shut off and the stoplog arrangement at the head of the channels was changed for the next test. The changeover could generally be accomplished within 15 minutes. However, usually several minutes elapsed before the fish would enter the release compartment after this change in hydraulic conditions.

During the course of the experiments every effort was made to keep the release technique and operation procedure as uniform as possible. The release compartment operator alternated his position in relation to the compartment after releasing each fish to minimize the chance of bias due to visual cues. If fish were noted in the upper reaches of the channels, tests were halted until these fish had moved on through the channel. This precaution was taken to ensure that the fish entering the choice area would not be affected by scent or visual perception of other fish in the channels. Rubber gloves were worn when changing the stoplogs at the head of channels to eliminate the chance of bias in response due to human scent.

An average of three to four tests were conducted each day, depending upon the availability of fish. Twenty-three days were required for the entire series of experiments.

RESULTS

A total of 80 individual tests were conducted: 60 involving a choice between a high and low velocity and 20 in which the velocities of the two flows were equal. Throughout the series of experiments a total of 2,064 steelhead trout (includes fish of all sizes), 750 chinook salmon, and 108 silver salmon were tested.

Response of Steelhead Trout

The analysis of the steelhead data was based upon the individual tests composed of 20 fish in the length range of 22 to 26 inches. The total sample consisted of 1,600 individuals, 1,200 in the

test, and 400 in the control experiments. The responses of these fish to the various individual control and test experiments are presented in tables 3 and 4. The data have been grouped according to experimental conditions to facilitate comparisons between individual trials and between test conditions.

The first step in the analysis of the data was to determine whether there were differences between the five replicates of the experimental design (table 2). If not, the results of individual test and control experiments could be combined to test for differences in response for the two channels in control tests, and differences in response for the different velocity combinations in test experiments.

Since the high velocity of each test condition occurred once in the north and once in the south channel within each replicate, the percentage of fish choosing the north channel should be the same for each replicate if the nature of the response did

TABLE 3.—Percentage of steelhead choosing north and south channels in each of the 20 control experiments

[Samples consist of 20 fish ranging from 22-26 inches in length (estimated)]

Replicate	Water velocity							
	2 f.p.s.		4 f.p.s.		6 f.p.s.		8 f.p.s.	
	North	South	North	South	North	South	North	South
I.....	40	60	60	40	30	70	55	45
II.....	30	70	70	30	65	35	65	35
III.....	55	45	50	50	50	50	75	25
IV.....	55	45	60	40	45	55	55	45
V.....	55	45	55	45	50	50	45	55
Mean....	47	53	59	41	48	52	59	41

TABLE 4.—Percentage of steelhead trout choosing high velocity channel in each of the 60 test experiments

[Each entry represents the response of 20 fish ranging from 22-26 inches in length (estimated)]

High velocity channel	Replicate	Test condition																												
		8 f.p.s. vs. 2 f.p.s.	8 f.p.s. vs. 4 f.p.s.	8 f.p.s. vs. 6 f.p.s.	6 f.p.s. vs. 2 f.p.s.	6 f.p.s. vs. 4 f.p.s.	4 f.p.s. vs. 2 f.p.s.																							
		North.....	I..... 75	65	65	70	60	60	II..... 90	65	55	80	50	65	III..... 90	55	25	60	60	85	IV..... 80	60	60	75	60	65	V..... 75	60	50	55
South.....	I..... 80	50	60	75	70	85	II..... 80	50	50	65	75	70	III..... 80	75	55	70	90	75	IV..... 95	75	60	70	60	55	V..... 90	75	35	90	40	65
Pooled percentage ¹ to higher velocity.		83.5	61.0	51.5	71.0	63.5	68.0																							

¹ Channels and replicates combined.

not differ between replicates. To test this hypothesis, data for each of the 80 trials given in table 2 were transformed to $\arcsin \sqrt{\text{percentage}}$ to north channel and subject to an analysis of variance test. The results illustrate that the differences between replicates, columns, and rows were not significant (table 5).

TABLE 5.—Analysis of variance for percentage of steelhead choosing north channel using the lattice-square design

[Original percentages were transformed to $\arcsin \sqrt{\text{percentage}}$ to north channel]

Source	Sum of squares	Degrees of freedom	Mean square	F value
Replications.....	139.498	4	34.87	.73 N.S.
Treatments.....	9025.443	15		
Rows (adjusted for treatments).....	597.438	15		
Rows (adjusted for treatments and columns).....	550.809	15	36.73	.76 N.S.
Columns (adjusted for treatments).....	1078.693	15		
Columns (adjusted for treatments and rows).....	1037.063	15	69.14	1.44 N.S.
Error.....	1441.367	30	48.05	
Total.....	12235.809	79		

N.S.—Not significant.

Response in control experiments.—Since no significant differences could be detected between the five replicates of the lattice-square design, the four control tests for each replicate were combined and subjected to chi-square tests to determine whether a preference was demonstrated for either the north or south channel when the flows were of equal velocity. The results of these tests show that the disparity between the observed response and the expected 1:1 ratio was not great enough to indicate that a preference had been demonstrated for either channel in any of the combined control tests (table 6).

TABLE 6.—Results of chi-square tests on number of steelhead choosing the north and south channels in control tests at each velocity

[Samples are composed of fish ranging from 22–26 inches in length]

Water velocity	Sample size	Observed response		Expected response		Degree of freedom	Chi-square
		Chose north channel	Chose south channel	To north channel	To south channel		
<i>F.p.s.</i>							
2.....	100	47	53	50	50	1	.36 N.S.
4.....	100	59	41	50	50	1	3.24 N.S.
6.....	100	48	52	50	50	1	.16 N.S.
8.....	100	59	41	50	50	1	3.24 N.S.
Sum of chi-squares.....						4	7.00 N.S.

N.S.—Not significant, $p > .05$.

Response in test experiments

As no preference was shown for either the north or south channel in control tests and no significant differences between replicates were apparent, the data in table 4 (transformed to $\arcsin \sqrt{\text{percentage}}$ to higher velocity) were subjected to a two-way analysis of variance to test the effects of channel and velocity differences in the 60 trials involving a choice between a high and low velocity. The results of the analysis of variance (table 7) illustrate that: (1) there were significant differences between the responses of the fish to the different test conditions, (2) these differences were independent of channel effects, i.e., they were evident when the higher velocity was in either the north or south channel and, (3) there was no preference indicated for either the north or south channels independent of velocity effects.

TABLE 7.—Analysis of variance of the responses of steelhead trout to differences in water velocity for the six test conditions

Variation due to—	Degrees of freedom	Mean square	Variance ratio
Differences between test conditions.....	5	482.956	**9.89
Differences between channels.....	1	156.558	3.21 N.S.
Interaction.....	5	6.937	.14 N.S.
Error.....	48	53.167	
Error (main effects).....	53	48.805	

** Significant at .01 level.
N.S.—Not significant.

Although the preceding analysis of variance demonstrated that the responses for the higher velocity differed between test conditions, it does not reveal whether each test condition differed from all the rest or whether some were undifferentiated. A test devised by Tukey (Snedecor 1956) was employed in examining these differences. The results of the test demonstrate that the response for the higher velocity in the 8 vs. 2 f.p.s. choice condition was significantly greater than that exhibited in any of the other five test conditions, and the responses in the 6 vs. 2 and 4 vs. 2 f.p.s. test conditions were significantly greater than that in the 8 vs. 6 f.p.s. condition (table 8). Other differences were not significant. The mean percentages to the higher velocity listed in this table are transformed data and should not be confused with the actual percentages to the higher velocity given in table 4.

TABLE 8.—Tests of differences between mean percentages of steelhead choosing the higher velocity

[Data are arcsin $\sqrt{\text{percentage to higher velocity}}$]

Test condition		Mean percentage choosing higher velocity	Differences between mean percentages to higher velocity				
High velocity	Low velocity		$\bar{X}-$ 45.80	$\bar{X}-$ 51.53	$\bar{X}-$ 53.24	$\bar{X}-$ 55.89	$\bar{X}-$ 57.77
<i>F.p.s.</i>	<i>F.p.s.</i>	\bar{X}					
8	2	66.55	*20.75	*15.02	*13.31	*10.66	*8.78
6	2	67.77	*11.97	6.24	4.53	1.88	
4	2	55.89	*10.09	4.36	2.65		
6	4	53.24	7.44	1.71			
8	4	51.53	5.73				
8	6	45.80					

* Differences greater than 7.89 are significant at .05 level.

Since there were no significant differences between replicates and no preference (independent of the effects of velocity) was shown for either channel during control or test experiments, all trials of each test condition were combined to determine whether there was a significant response to the higher velocity. The results of chi-square tests performed on these data illustrate that the proportion of steelhead selecting the higher velocity is significantly greater than that choosing the low velocity in all except the 8 vs. 6 f.p.s. choice condition (table 9).

Response in relation to fish size.—A thorough examination of the relationship between fish size and response was not possible as the steelhead tested during the course of the experiments were of nearly the same size, 80 percent ranging from 22 to 26 inches (fig. 7). Gross comparisons were made, however, by dividing all of the steelhead tested at each test condition into two size categories, small fish less than 25 inches and large fish 25 inches and greater in length, and comparing the percentages choosing the high velocity for each of

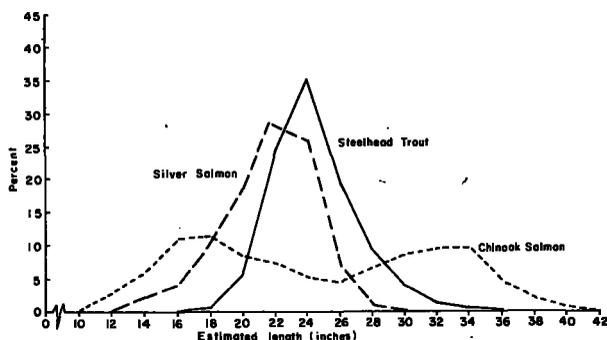


FIGURE 7.—Length composition of samples of steelhead trout, chinook salmon, and silver salmon tested in the velocity-preference experiments.

TABLE 9.—Chi-square tests on results of choice experiments [Data are for steelhead estimated to be 22-26 inches in length.]

Test condition		Sample size	Observed response		Expected response		Chi-square
High velocity	Low velocity		Chose high velocity	Chose low velocity	To high velocity	To low velocity	
<i>F.p.s.</i>	<i>F.p.s.</i>	<i>Number of fish</i>	<i>Number of fish</i>	<i>Number of fish</i>			
8	2	200	167	33	100	100	**89.78
8	4	200	122	78	100	100	**9.68
8	6	200	103	97	100	100	.18 N.S.
6	2	200	142	58	100	100	**35.28
6	4	200	127	73	100	100	**14.58
4	2	200	136	64	100	100	**25.92

**Significant at .01 level.
N.S.—Not significant.

TABLE 10.—Comparison between the responses of small (less than 25 inches) and large (25 inches and larger) steelhead for the high-velocity flow

[Entries are percentage choosing high-velocity flow]

Length group	Test condition					
	8 f.p.s. vs. 2 f.p.s.	8 f.p.s. vs. 4 f.p.s.	8 f.p.s. vs. 6 f.p.s.	6 f.p.s. vs. 4 f.p.s.	6 f.p.s. vs. 2 f.p.s.	4 f.p.s. vs. 2 f.p.s.
Small	81	58	50	66	72	67
Large	75	62	56	59	75	68

the 6 test conditions (table 10). No significant differences could be detected between the percentage of small and large fish choosing the high velocity.

Response of Chinook Salmon

It has been stated that testing of chinook and silver salmon was considered as an incidental phase of the experiments, each test being terminated when the desired sample of steelhead trout had been tested. Samples of chinook salmon in individual tests ranged from 0 to 27 fish.

Control experiments.—In order to provide sample sizes large enough to test the hypothesis of random choice of channels in control experiments, it was necessary to combine the data for the four control tests (2 vs. 2, 4 vs. 4, 6 vs. 6, and 8 vs. 8 f.p.s.) within each replicate. Results of chi-square tests on these data demonstrate that a random choice of channels was exhibited when the flows were of equal velocity (table 11).

Test experiments.—As in control tests the data for individual experiments were combined in order to examine the response of chinook salmon to the various test conditions. Since there was a pronounced variation in the sizes of fish tested during the experiments it was appropriate to examine first the response in relation to fish size.

TABLE 11.—Response of chinook salmon to control tests for each of the five replicates

[Responses in each replicate represent grouped data for four individual tests. Chi-square values test the hypothesis that equal numbers entered the two channels]

Replicate	Number of fish	Observed response		Expected response		Chi-square	Degrees of freedom
		Number of fish to—		Number of fish to—			
		North channel	South channel	North channel	South channel		
I.....	25	11	14	12.5	12.5	0.36 N.S.	1
II.....	34	19	15	17	17	47 N.S.	1
III.....	43	26	17	21.5	21.5	1.88 N.S.	1
IV.....	19	7	12	9.5	9.5	1.32 N.S.	1
V.....	51	21	30	25.5	25.5	1.59 N.S.	1
Pooled Sum of 5 chi-squares	172	84	88	86	86	09 N.S.	1
Heterogeneity (difference)						5.62 N.S.	4
						5.53 N.S.	3

N.S.—Not significant.

The length frequency curve was bimodal and the fish could be conveniently divided into two general size groups; one composed of fish less than 25 inches and the other composed of fish 25 inches and greater in length (fig. 7). Chi-square tests on these data indicate that there was a significant difference in the responses of small and large fish in only one out of the six test conditions (table 12). In the 8 vs. 4 f.p.s. test a significantly greater proportion of large fish chose the higher velocity.

Since the response of large and small fish did not differ significantly in the majority of the tests, sizes were combined to examine the group response of chinook to the different test conditions (table 13). Chi-square values illustrate that a significantly greater proportion of chinook chose the high velocity in all except the 6 vs. 8 f.p.s. test

TABLE 12.—Comparison between the responses of small (less than 25 inches) and large (25 inches and larger) chinook for each test condition

Test condition		Number of fish		Chose high velocity channel		Chi-square
High velocity	Low velocity	Small	Large	Small	Large	
F.p.s.	F.p.s.			Percent	Percent	
8.....	2	37	63	91.9	83.6	0.09 N.S.
8.....	4	38	42	52.6	50.9	**7.19
8.....	6	35	31	45.7	45.2	.08 N.S.
6.....	2	74	65	86.5	87.7	.70 N.S.
6.....	4	42	37	57.1	70.4	1.24 N.S.
4.....	2	64	60	71.9	75.0	.15 N.S.

**Significant difference between responses, $p < .01$.

N.S.—Not significant.

TABLE 13.—Chi-square tests on responses of chinook salmon to the higher velocity in the six different test conditions

Test condition		Number of fish	Observed response		Expected response		Chi-square
High velocity	Low velocity		Chose high velocity	Chose low velocity	To high velocity	To low velocity	
F.p.s.	F.p.s.						
8.....	2	100	93	7	50	50	***73.96
8.....	4	80	54	26	40	40	**9.80
8.....	6	66	30	36	33	33	.54 N.S.
6.....	2	139	121	18	69.5	69.5	***76.32
6.....	4	69	43	26	34.5	34.5	*4.19
4.....	2	124	91	33	62	62	***27.13

N.S.—Not significant.

*Significant difference, $p < .05$.

**Significant difference, $p < .01$.

***Significant difference, $p < .001$.

condition. In this instance a larger proportion (not significant) of the fish chose the 6 f.p.s. velocity.

Response of Silver Salmon

Comparatively few silver salmon were tested during the course of the experiments. The combined data in table 14 illustrate that silver salmon, like steelhead trout and chinook salmon, demonstrated a preference for the higher velocity in all except the 8 vs. 6 f.p.s. choice condition. Of the 18 fish tested during the control experiments, 8 chose the north channel and 10 chose the south channel.

TABLE 14.—Velocity preference of silver salmon in six test conditions

Water velocity		Number of fish	Chose high-velocity channel
High-velocity channel	Low-velocity channel		
F.p.s.	F.p.s.		Percent
8.....	2	12	83.3
8.....	4	14	85.7
8.....	6	13	46.1
6.....	2	24	83.3
6.....	4	22	68.2
4.....	2	5	100.0

Comparison Between Responses of Chinook Salmon and Steelhead Trout

Although a basic similarity in the response of steelhead trout and chinook salmon has been demonstrated, it is of interest to know whether the magnitude of the response varied between the two species. Chinook salmon demonstrated a stronger response for the higher velocity in four (8 vs. 2, 8 vs. 4, 6 vs. 2, and 4 vs. 2 f.p.s.) choice conditions (table 15). Chi-square values indicate that the response was significantly

stronger in the 6 vs. 2 and 8 vs. 2 f.p.s. choice conditions. In the 8 vs. 6 and 6 vs. 4 f.p.s. choice conditions, steelhead trout demonstrated a stronger response for the higher velocity; however, chi-square values were not significant in either case. The data in table 15 include all steelhead trout and chinook salmon tested regardless of fish size.

TABLE 15.—Comparison between the responses of steelhead trout and chinook salmon in the six test conditions

[Chi-square values test the hypothesis that there was no difference in the response of the two species]

Test condition		Number of fish ¹		Chose high-velocity channel		Chi-square
High-velocity channel	Low-velocity channel	Steelhead trout	Chinook salmon	Steelhead trout	Chinook salmon	
<i>F.p.s.</i>	<i>F.p.s.</i>			<i>Percent</i>	<i>Percent</i>	
8-----	2	258	100	79.4	63.0	*9.47
8-----	4	249	80	59.0	67.5	1.55
8-----	6	266	66	52.2	45.4	.63
6-----	2	264	139	78.1	37.1	*10.86
6-----	4	257	69	63.8	62.3	.09
4-----	2	263	124	67.2	73.4	1.98

¹ Includes all sizes.

*Significant difference $p < .01$.

Response of Steelhead Trout and Chinook Salmon to a 12.9 vs. 2.7 f.p.s. Choice Condition

Upon completion of the high-velocity tests, exploratory experiments were conducted to examine the response of steelhead and chinook when presented with a choice between flows averaging 12.9 and 2.7 f.p.s. Velocities were measured at the downstream ends of the two channels. Average water depths were 1.8 feet in the 12.9 f.p.s. channel and 3.4 feet in the 2.7 f.p.s. channel. Water temperature remained a constant 66° F. during these tests.

The two channels and a portion of the introductory area are shown in figure 8. Fish were released individually into the introductory area by means of a release compartment mounted on the entrance tunnel (fig. 9). Experiments were conducted for only 2 days, September 18-19, and observations were made on 41 steelhead trout and 57 chinook salmon.

Results of these tests were quite similar to the preceding choice experiments, for both steelhead trout and chinook salmon demonstrated a preference for the higher velocity. Choosing the higher velocity were 75.6 and 89.5 percent, respectively. Of the 51 chinook entering the 12.9 f.p.s. velocity channel only 26 were able to swim the entire dis-

tance (85 feet) to the flow-introduction pool. The remaining 25 fish negotiated varying distances up the channels but were eventually swept back downstream to the introductory area. There was evidence that some of these fish even made second attempts at the high-velocity channel. Steelhead trout demonstrated a superior performance: 29 out of the 31 fish choosing the high velocity were able to negotiate the entire length of the channel.

HIGH-VELOCITY EXPERIMENTS

METHODS AND MATERIALS

The method employed in measuring the performance or swimming ability of salmonids at relatively high velocities, like the choice experiments, relied entirely on the natural drives or instincts which motivate the fish to migrate upstream. These experiments differed from the choice experiments in that the migrating fish passing through the facility had no alternative but to pass through a channel carrying the test flow. The fish were permitted to enter the channel of their own volition, and if they failed to negotiate the entire channel and were swept back downstream they were allowed to remain in the introductory pool. Performance was measured by the distance which the fish could negotiate in the channel before becoming exhausted or discouraged. Velocities approximating 13 and 16 f.p.s. were tested. Tests were conducted during the period September 5-15. Water temperatures ranged from 66° to 67° F.

Experimental Area

The experimental area was modified for these experiments so that only the south channel was utilized (fig. 9). The north channel was blocked with stoplogs at the upstream end and screened at the downstream end to prevent fish from entering. Gray section markers painted on the channel floor at 5-foot intervals were used to measure the distance and fish were able to negotiate through the channel. Lighting was the same as was employed in the choice experiments.

Hydraulic Conditions

The two experimental flows were created by adjusting the slope of the channel floor and regulating the head (difference between the water level in flow-introduction pool and fish-intro-

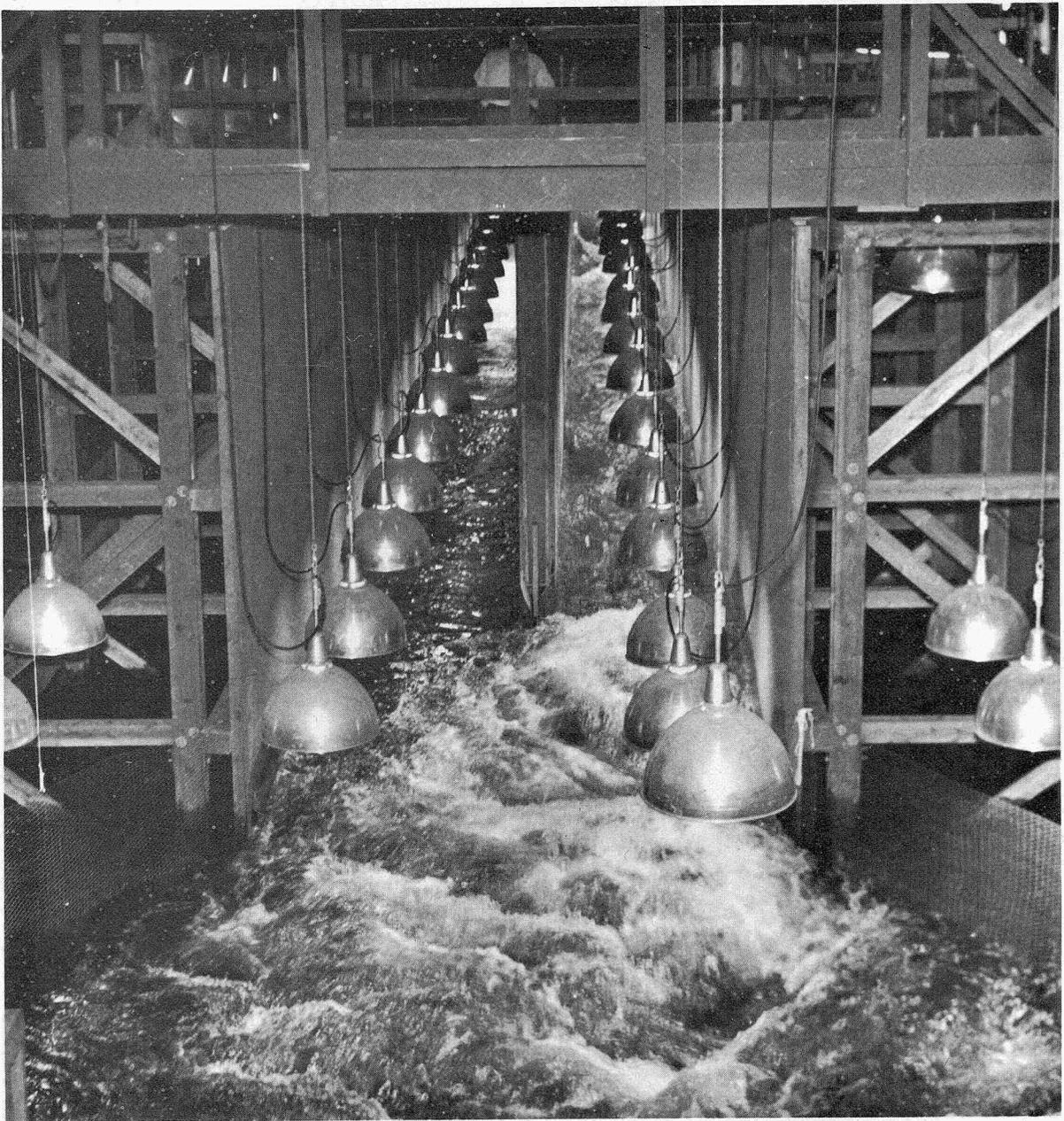


FIGURE 8.—View of two channels and introductory area during a choice experiment involving water velocities of 12.9 f.p.s. on the right and 2.7 f.p.s. on the left.

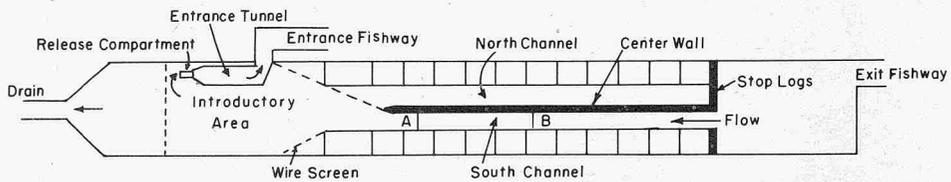


FIGURE 9.—Sketch of laboratory showing experimental area modified for the high-velocity experiments.

ductory pool) on the channel. The total rise in floor level from the downstream end to the upstream end of the channel ranged from 1.4 feet at 13 f.p.s. to 2.5 feet at 16 f.p.s. The head on the channel ranged from 2.5 feet to 5.3 feet, respectively.

The mean water velocity and depth of flow for the two test conditions determined from rather extensive measurements in the first 35 feet of the channel before the experiments were begun, were 13.4 f.p.s. and 1.8 feet, and 15.8 f.p.s. and 1.8 feet, respectively. Velocities were measured with a current meter vertically at 4-inch intervals from the floor and horizontally at 1-foot intervals from the center of the channel at five different stations within the 35-foot reach. Examples of the distribution of velocities within the channel derived

from these measurements are given in appendix figure 1 for each test condition. Velocities ranged from 11.8 to 14.4 f.p.s. in the 13.4 f.p.s. test condition and from 14.9 to 16.7 f.p.s. in the 15.8 f.p.s. test condition. The lowest velocities occurred near the floor next to the channel walls; the highest occurred just below the surface. During the course of the experiments velocities were checked only at the downstream end of the channel. Measurements at this point were made with a current meter at 1-foot intervals across the channel at 0.6 of the depth from the water surface.

With exception of the rather turbulent area at the upstream end, flows through the channel were nearly uniform for both test conditions. Although standing waves were created just below the channel entrance at both velocities, the

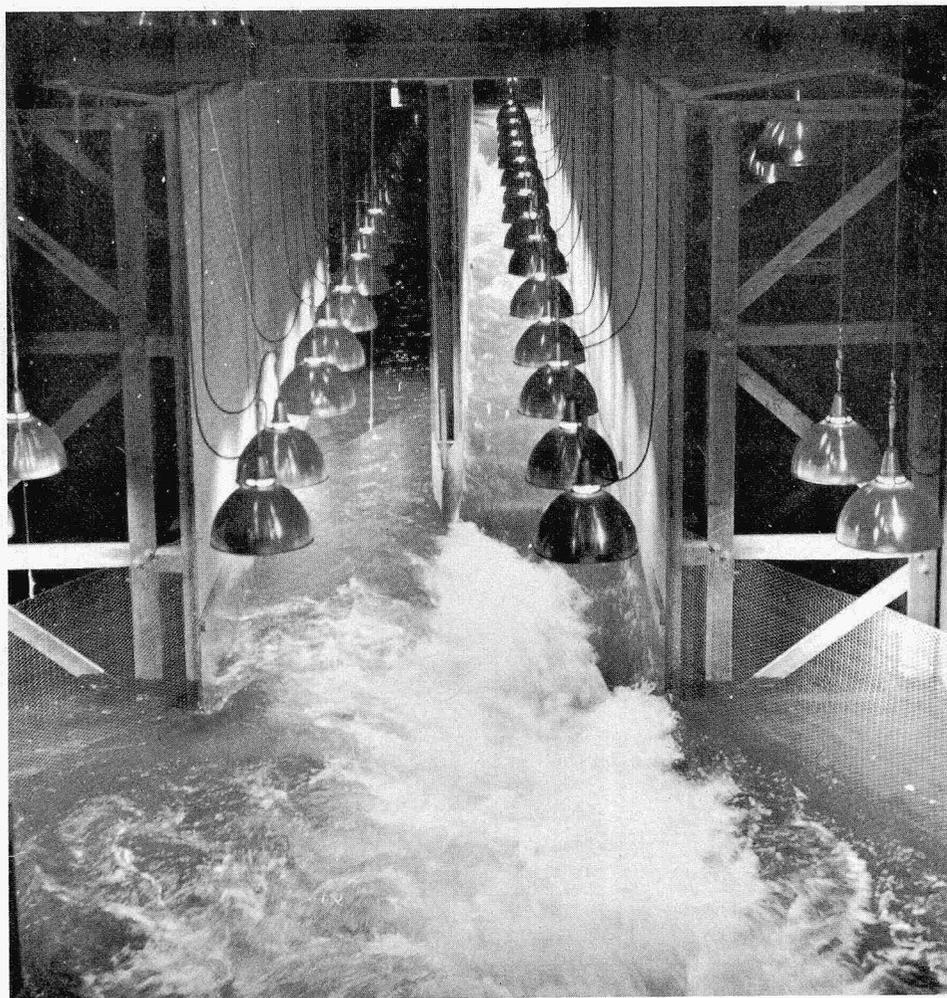


FIGURE 10.—View of south channel with 15.8 f.p.s. flow. A screen (barely visible) blocks entrance to north (left) channel.

PROCEDURE

position of the wave and its effect on the flow in the approach area were quite different at the two velocity levels. At 13.4 f.p.s. the wave was positioned at the end of the hydrofoil and at right angles to the channel flow (fig. 8). As a result, the water velocity within the approach area was greatly reduced. At 15.8 f.p.s. the standing wave extended diagonally across the entrance to approximately the center of the channel. In this instance a high-velocity jet was created along the south wall of the approach area (fig. 10). Velocities as high as 17.8 f.p.s. were measured at the end of the south wall. Although the flow through the introductory area was turbulent at both velocities, there were areas near both walls where fish could rest in relatively calm water.

The fish utilized in these experiments were collected daily from the Washington Shore fishway. They swam into the entrance fishway channel (fig. 2) where they were held until tested. They were released individually by means of a release compartment mounted on the end of the entrance tunnel (fig. 11). Prior to release, the release compartment operator ascertained the species and estimated the length of each fish. Upon releasing the fish, he alerted an observer stationed on a walkway above the entrance to the test channel. When the fish entered the channel, this observer followed its movements from the walkway above the channel and noted the maximum distance which the fish attained.

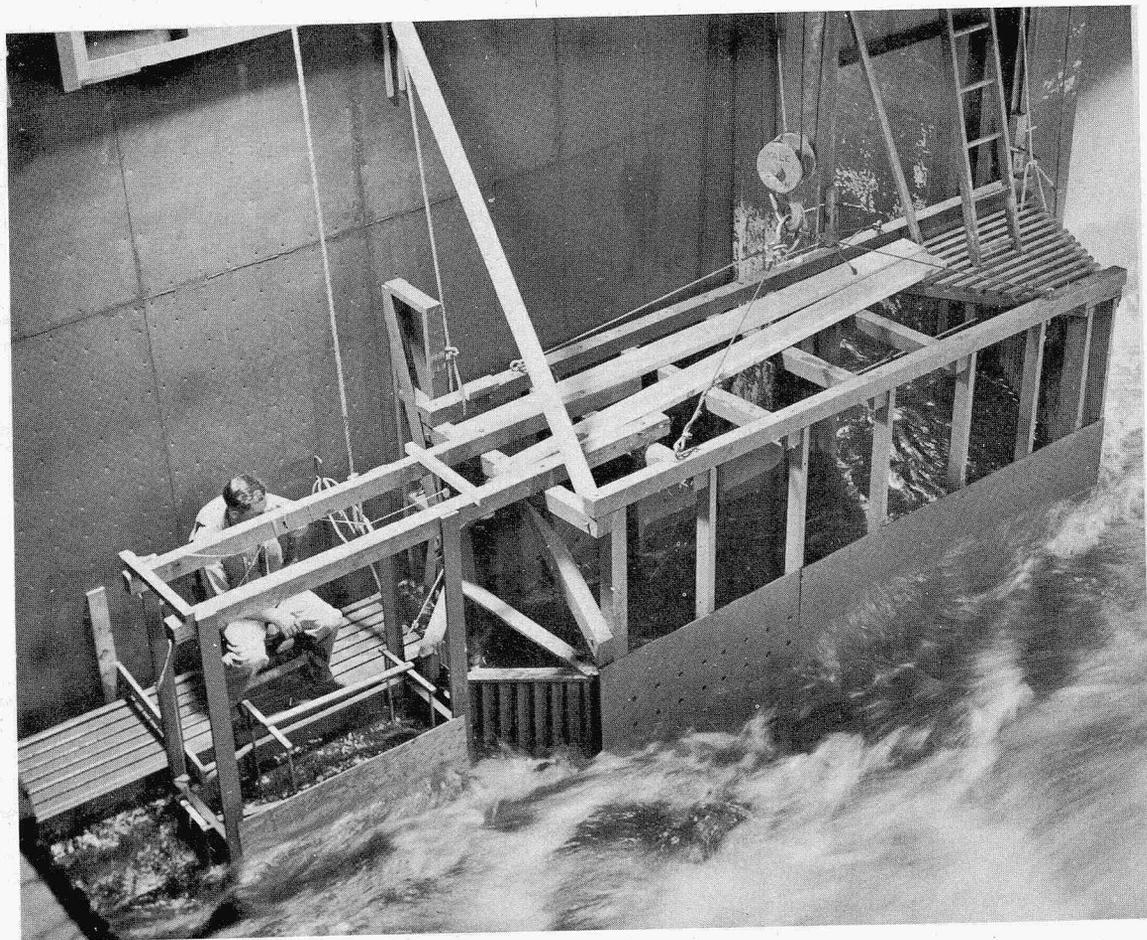


FIGURE 11.—View of entrance tunnel and release compartment utilized in the 13.4 and 15.8 f.p.s. velocity experiments.

Throughout the course of the experiments (especially in the 15.8 f.p.s. tests) fish that failed to pass through the channel and were swept back downstream often reentered and attempted to negotiate the channel again. Generally when this occurred, testing was merely delayed until the fish either passed through the channel or was again swept back downstream to the introductory area; the distance negotiated was recorded, and testing was resumed. If, however, these re-entries became so numerous as to pose difficulty is distinguishing the fresh fish being introduced from the release compartment, the test was terminated or at least delayed until the fish could be cleared from the introductory area by reducing the channel velocity.

As many fish as possible were tested each day. The number varied from 30 to 60 fish depending upon availability. At the end of each day the channel velocity was reduced so that the fish which had accumulated in the introductory area could pass through the laboratory during the night.

RESULTS

The 13.4 f.p.s. velocity tests were conducted on September 5, 6, and 7, and the 15.8 f.p.s. tests were made on September 9, 10, 14, and 15. A total of 47 steelhead trout and 91 chinook salmon were tested in the 13.4 f.p.s. velocity flow, and 67 steelhead and 130 chinook, in the 15.8 f.p.s. flow.

A cursory examination of the data revealed that there was considerable variation in the swimming abilities of the fish tested in the two velocities. The distances attained by individual steelhead trout ranged from 10 to 85 feet (total length of channel) in the 13.4 f.p.s. velocity and from 14 to 85 feet in the 15.8 f.p.s. velocity. Chinook salmon ranged from 15 to 85 feet in the 13.4 f.p.s. velocity and from 0 feet (one fish failed to reach the channel entrance) to 85 feet in the 15.8 f.p.s.

The performances of the two species tested on different days are compared in table 16. The only consistent variation in performance between days occurred with the chinook tested in the 15.8 f.p.s. velocity. In this instance there was a decline in the median distance negotiated by the four groups of fish tested during the 7-day period. Since there were only slight differences in the mean lengths of the fish in the four tests, a real

TABLE 16.—Median distances attained by chinook salmon and steelhead trout tested on different days in velocities of 13.4 and 15.8 f.p.s.

Velocity	Date	Number of fish		Mean length ¹		Median distance negotiated in 85-foot channel ²	
		Chinook salmon	Steelhead trout	Chinook salmon	Steelhead trout	Chinook salmon	Steelhead trout
13.4	Sept. 5	16	12	30.5	27.3	75	85
	Sept. 6	46	14	27.6	26.0	85	85
	Sept. 7	29	21	29.8	24.1	70	85
	Sept. 9	44	13	27.3	25.1	30	74
15.8	Sept. 10	40	25	27.4	26.1	28	85
	Sept. 14	21	9	26.0	24.0	21	79
	Sept. 15	25	20	26.6	24.9	19	78

¹ Based on estimated lengths.

² Values of 85 feet represent a minimum estimate of median as length of channel was only 85 feet.

decline in the swimming ability of the chinook salmon tested during the 7-day period is indicated.

The pooled data from the individual tests at each velocity are presented graphically to show the respective distances negotiated by the two species in the 85-foot channel (fig. 12). Each species has been divided into two general-size groups (small fish consisting of individuals estimated to be less than 25 inches in length and large fish consisting of individuals 25 inches and larger) to indicate the relationships between performance and fish size. These data clearly illustrate that

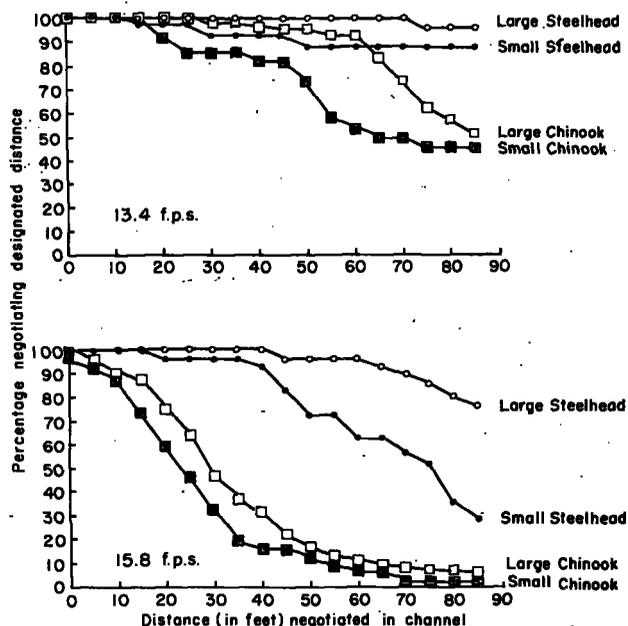


FIGURE 12.—Performances of small (estimated to be less than 25 inches in length) and large (25 inches and larger) steelhead trout and chinook salmon in velocities of 13.4 and 15.8 feet per second.

steelhead trout were more successful than chinook salmon in negotiating the two test flows and larger fish of both species were more successful than smaller fish. In the 13.4 f.p.s. tests 92 percent of the steelhead negotiated the entire 85-foot channel. In comparison, only 51 percent of the chinook salmon traveled this distance. The performances of both species declined significantly in the 15.8 f.p.s. velocity. Only 51 percent of the steelhead and 5 percent of the chinook negotiated the entire length of the channel. In comparing the performances of the two size groups it is interesting to note that the decline in the performance of steelhead between the 13.4 and 15.8 f.p.s. velocity tests was due largely to the influence of the smaller fish. The proportion of large steelhead negotiating the entire 85-foot channel was reduced by only 20 percent while that of the smaller fish was reduced by 66 percent. In comparison, the proportions of large and small chinook salmon negotiating the channel were reduced by nearly the same proportion (90 and 95 percent, respectively) between the 13.4 and 15.8 f.p.s. velocity tests.

In considering the performance curves in figure 12 we should bear in mind that: (1) the velocities of 13.4 and 15.8 f.p.s. are mean values, (2) the distances given apply only to measurements made within the confines of the channel and, (3) the performance curves are based upon the distances attained by the fish in their first attempt to negotiate the channel.

Reference to appendix (fig. 1) illustrates that fish may have encountered velocities somewhat higher or lower than 13.4 and 15.8 f.p.s. as they ascended the channel depending upon the course they followed. Observations made during the course of the experiments indicated that although some fish traversed back and forth across the channel they generally ascended the channel near the walls and were posited near the floor or at least below middepth. The performance curves in figure 12, therefore, are probably associated with velocities slightly lower than the mean values given.

On the other hand the distances given in figure 12 may be somewhat less than the actual distances which the fish negotiated in the two velocities, especially in the 15.8 f.p.s. tests. In these tests the flow was not dissipated upon entering the approach area to the extent that it was in the

13.4 f.p.s. tests, and a high-velocity jet continued through the approach area to the introduction pool (fig. 10). A number of fish followed this jet as they approached the channel and were subjected to velocities of 15.8 f.p.s. or greater for distances up to 20 feet before entering the channel. The distances given in figure 12 apply only to the distance attained after entering the channel and may lead to an underestimation of the performance of the fish in this velocity.

It has been mentioned that fish which failed to negotiate the entire channel in their first attempt and were swept back downstream to the introductory area frequently reentered and attempted to negotiate the channel again. Although the mean distance negotiated by both steelhead trout and chinook salmon reentering the channel was slightly less than the mean distance achieved by the two species in their first attempts in both velocities, there was evidence that at least some of the fish were capable of achieving greater distances in the two velocities than they demonstrated in their first attempt. The maximum distances which all (100 percent) steelhead trout and chinook salmon were capable of negotiating in the two velocities may, therefore, be somewhat greater than is indicated in figure 12.

RATE OF MOVEMENT EXPERIMENTS

METHODS AND MATERIALS

These experiments were conducted concurrently with the choice and high-velocity experiments and utilized the same fish. Rates of movement were determined by simply recording the time required for the fish to pass through a 30-foot timing zone in the lower portion of the channels. Gray lines on the floor of the channels marked the boundaries of these zones. The downstream boundary or "start" line and the upstream or "finish" line are designated as points *A* and *B*, respectively, in figures 3 and 9.

Rates of movement in water velocities of 2, 4, 6, and 8 f.p.s. were measured during the velocity-preference experiments and in velocities of 13.4 and 15.8 f.p.s. during the high-velocity experiments. In the high-velocity experiments the upper end of the channel was not obstructed with the Denil ladder or stoplogs as it was in the choice experiments. It was possible, therefore, to obtain an additional measure of the rate of movement

TABLE 17.—Distribution of times required by steelhead trout to negotiate the 30-foot timing zone in water velocities approximating 2, 4, 6, 8, 13, and 16 f.p.s.

Time interval in seconds	Water velocity											
	2 f.p.s.		4 f.p.s.		6 f.p.s.		8 f.p.s.		13.4 f.p.s.		15.8 f.p.s.	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number ¹	Percent	Number ¹	Percent
0-0.9												
1.0-1.9					2	.3	1	.2				
2.0-2.9	8	2.5	11	2.3	17	2.9	15	3.1				
3.0-3.9	37	11.4	37	7.8	61	10.5	89	15.4			1	1.6
4.0-4.9	38	11.7	63	13.3	114	19.6	140	24.2	2	4.9	5	7.8
5.0-5.9	34	10.5	66	14.0	80	13.7	108	18.6	13	31.7	15	23.4
6.0-6.9	36	11.1	63	13.3	56	9.6	93	16.1	8	19.5	22	34.4
7.0-7.9	31	9.6	49	10.4	31	5.3	58	10.0	8	19.5	10	15.6
8.0-8.9	25	7.7	51	10.8	34	5.8	29	5.0	5	12.2	7	10.9
9.0-9.9	21	6.5	28	5.9	21	3.6	11	1.9	2	4.9	1	1.6
10.0-10.9	16	4.9	23	4.9	15	2.6	10	1.7				
11.0-11.9	8	2.5	21	4.4	16	2.7	5	.8	3	7.3	1	1.6
12.0-12.9	12	3.7	17	3.6	13	2.3					2	3.1
13.0-13.9	7	2.2	6	1.3	8	1.4	1	.3				
14.0-14.9	11	3.4	6	1.3	7	1.2	2	.3				
15.0-15.9	11	3.4	5	1.1	6	1.0	1	.2				
16.0-16.9	4	1.2	5	1.1	3	.5	1	.2				
17.0-17.9	4	1.2	5	1.1	4	.7						
18.0-18.9	2	.6	3	.6	3	.5	1	.3				
19.0-19.9	4	1.2	3	.6	2	.3	1	.2				
20.0-20.9	2	.6			3	.5						
21.0-21.9	1	.3	1	.2								
22.0-22.9	1	.3	1	.2	3	.5	1	.3				
23.0-23.9	2	.6			1	.2						
24.0-24.9			1	.2	1	.2						
25.0-25.9							1	.2				
26.0-26.9			2	.4	2	.3						
27.0-27.9	3	.9										
28.0-28.9					1	.2						
29.0-29.9	1	.3	2	.4								
30.0+	5	1.5	3	.6	79	13.6	8	1.4				
Total number of fish	324		472		583		579		41		64	

¹ Represents only fish which were able to negotiate timing zone.

(from point B to the upstream end of the channel) for those fish which negotiated the entire length of the channel.

PROCEDURE

Fish were timed through the 30-foot zone with stopwatches by an observer stationed on the catwalk above the entrances of the channels. During the choice experiments a single watch was used. It was started as the fish crossed point A and stopped when the fish crossed point B.

During the high-velocity studies two watches were employed. One was used as above to record the time required to negotiate the 30-foot zone. The second watch was started as the fish crossed point B at the end of the 30-foot zone and stopped when the fish reached the upstream end of the channel. If the fish failed to negotiate the entire channel, the watch was stopped when the fish started to fall back downstream.

RESULTS

The distributions of individual times required by steelhead trout, chinook, and silver salmon to negotiate the 30-foot timing zone in the various water velocities tested are given in tables 17, 18,

and 19. Passage times listed for velocities from 2 to 8 f.p.s. were measured during the choice experiments and include all fish tested at a given velocity regardless of choice condition. Passage times listed for water velocities of 13.4 and 15.8 f.p.s. were measured during the high-velocity experiments and include only those fish which were able to negotiate the timing zone.

Relationship Between Water Velocity and Rate of Movement by Species

Since the passage times do not conform to a normal type distribution in all instances, a non-parametric method was considered appropriate in comparing passage times between species and water velocities. The median passage time with 95-percent confidence limits was selected as the test statistic. These values for each species and velocity are presented in table 20. Rates of movement in each velocity, calculated by dividing the length of the timing zone (30 feet) by the median times in table 20, are compared in figure 13. Rates of movement ranged from 3.1 to 6.9 f.p.s., varying with species and water velocity.

A comparison of median times in table 20 reveals the following with respect to differences between

TABLE 18.—Distribution of times required by chinook salmon to negotiate the 30-foot timing zone in water velocities approximating 2, 4, 6, 8, 13, and 16 f.p.s.

Time interval in seconds	Water velocity												
	2 f.p.s.		4 f.p.s.		6 f.p.s.		8 f.p.s.		13.4 f.p.s.		15.8 f.p.s.		
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number ¹	Percent	Number ¹	Percent	
0-0.9													
1.0-1.9	1	1.1											
2.0-2.9	14	15.2	20	10.9	20	9.1	7	3.5					
3.0-3.9	24	26.1	41	22.4	35	16.0	19	9.6					
4.0-4.9	18	19.5	39	21.3	44	20.1	41	20.7			1	2.6	
5.0-5.9	14	15.2	25	13.7	57	26.0	50	25.2		2	2.3	4	10.2
6.0-6.9	7	7.6	19	10.4	14	6.4	37	18.7		9	10.7	4	10.2
7.0-7.9	3	3.3	10	5.5	14	6.4	18	9.1		17	20.2	10	25.6
8.0-8.9	5	5.4	4	2.2	7	3.2	14	7.1		23	27.4	9	23.1
9.0-9.9	2	2.2	6	3.3	5	2.3	5	2.5		21	25.0	6	15.4
10.0-10.9	3	3.3	7	3.8	5	2.3	1	.5		10	11.9	4	10.2
11.0-11.9			4	2.2	2	.9	3	1.5		1	1.2	1	2.6
12.0-12.9			1	.5			1	.5					
13.0-13.9			2	1.1						1	1.2		
14.0-14.9	1	1.1			2	.9							
15.0-15.9			3	1.6			1	.5					
16.0-16.9													
17.0-17.9					2	.9							
18.0-18.9					1	.5	1	.5					
19.0-19.9					1	.5							
20.0-20.9			1	.5									
21.0-21.9													
22.0-22.9					2	.9							
23.0-23.9					1	.5							
24.0-24.9					2	.9							
25.0-25.9													
26.0-26.9			1	.5									
27.0-27.9													
28.0-28.9					1	.5							
29.0-29.9													
30.0+					4	1.8							
Total number of fish	92		183		219		198		84		39		

¹ Represents only fish which were able to negotiate timing zone.

TABLE 19.—Distribution of times required by silver salmon to negotiate the 30-foot timing zone in water velocities approximating 2, 4, 6, and 8 f.p.s.

Time interval in seconds	Water velocity							
	2 f.p.s.		4 f.p.s.		6 f.p.s.		8 f.p.s.	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
0-0.9								
1.0-1.9								
2.0-2.9					1	2.6		
3.0-3.9					2	5.3	1	3.1
4.0-4.9	1	11.1	2	12.5	3	7.9	6	18.7
5.0-5.9	1	11.1	5	31.3	4	10.5	11	34.4
6.0-6.9			1	6.2	7	18.4	5	15.6
7.0-7.9	1	11.1	2	12.5	4	10.5	7	21.9
8.0-8.9	1	11.1			6	15.8	1	3.1
9.0-9.9	1	11.1					1	3.1
10.0-10.9	1	11.1	2	12.5	1	2.6		
11.0-11.9			1	6.2	1	2.6		
12.0-12.9			1	6.2	1	2.6		
13.0-13.9	1	11.1						
14.0-14.9					1	2.6		
15.0-15.9								
16.0-16.9								
17.0-17.9								
18.0-18.9								
19.0-19.9	1	11.1						
20.0-20.9					1	2.6		
21.0-21.9					1	2.6		
22.0-22.9								
23.0-23.9								
24.0-24.9					1	2.6		
25.0-25.9								
26.0-26.9								
27.0-27.9								
28.0-28.9			1	6.2				
29.0-29.9								
30.0+	1	11.1	1	6.2	4	10.5		
Total number of fish	9		16		38		32	

species: (1) chinook salmon moved significantly faster (required less time to negotiate the 30-foot timing zone) than steelhead trout or silver salmon in velocities of 2, 4, and 6 f.p.s., (2) the rates of movement of the three species were approximately equal at 8 f.p.s., and (3) chinook salmon were

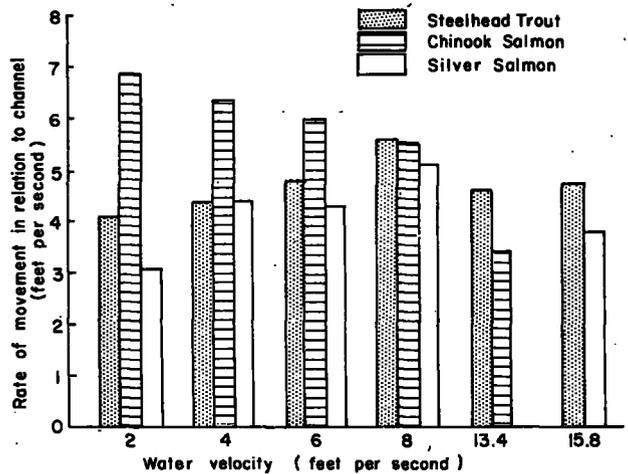


FIGURE 13.—Average rates of movement maintained through the 30-foot timing zone by steelhead trout, chinook salmon, and silver salmon in the six velocities tested. Rates are based on the median time required to negotiate the timing zone.

TABLE 20.—Median passage times of steelhead trout, chinook and silver salmon through the 30-foot timing zone in water velocities approximating 2, 4, 6, 8, 13, and 16 f.p.s.

Species	Median and ¹ 95% confidence limits	Passage time in seconds						Sample size					
		Water velocity (f.p.s.)						Water velocity (f.p.s.)					
		2	4	6	8	13.4	15.8	2	4	6	8	13.4	15.8
Steelhead trout	Lower limit	6.6	6.4	5.7	5.0	5.8	5.9	324	472	583	579	41	64
	Median	7.4	6.8	6.2	5.4	6.5	6.3						
	Upper limit	8.0	7.5	6.7	5.6	7.6	6.9						
Chinook salmon	Lower limit	3.7	4.2	4.6	5.1	8.0	7.0	92	183	219	198	84	39
	Median	4.3	4.7	5.0	5.5	8.7	8.0						
	Upper limit	5.2	5.5	5.3	6.0	9.0	8.9						
Silver salmon	Lower limit	5.8	5.4	6.4	5.4	---	---	9	16	38	32	0	0
	Median	9.7	8.8	7.0	5.8	---	---						
	Upper limit	19.2	11.0	8.3	6.9	---	---						

¹ If the median passage time listed for a given species and velocity does not lie between the lower and upper limits listed for another velocity or species, the two passage times are considered to be significantly different.

significantly slower than steelhead trout in water velocities of 13.4 and 15.8 f.p.s.

Definite trends are noted when rates of movement and water velocities are compared (fig. 13). Steelhead moved progressively faster as the water velocity increased from 2 to 8 f.p.s.; then slowed down somewhat in velocities of 13.4 and 15.8 f.p.s. The rate of movement at 8 f.p.s. was significantly faster than at any other velocity (table 20). Silver salmon, although slightly slower than steelhead, also moved faster as the water velocity increased

from 2 to 8 f.p.s. Chinook salmon differed from steelhead trout and silver salmon in that their rate of movement decreased with an increase in water velocity; the fastest rate of movement being achieved in the 2 f.p.s. velocity.

Examination of the relationship between fish size and rate of movement illustrates the differences previously noted in the rate of movement between species cannot be attributed to differences in size of the fish (fig. 14). Comparisons of the rates of movement between species by length groups agrees closely with the trends noted in figure 13. A direct relationship between size and rate of movement is also indicated. Steelhead were consistent in this respect throughout the various velocities tested. With the exception of the fish tested at 2 f.p.s., chinook demonstrated a similar consistency. Silver salmon were not as consistent. At 2 and 8 f.p.s. the larger fish move fastest, while at velocities of 4 and 6 f.p.s. the smaller fish moved fastest. It should be noted, however, that the silver salmon data represent comparatively small sample sizes and thus may not be reliable.

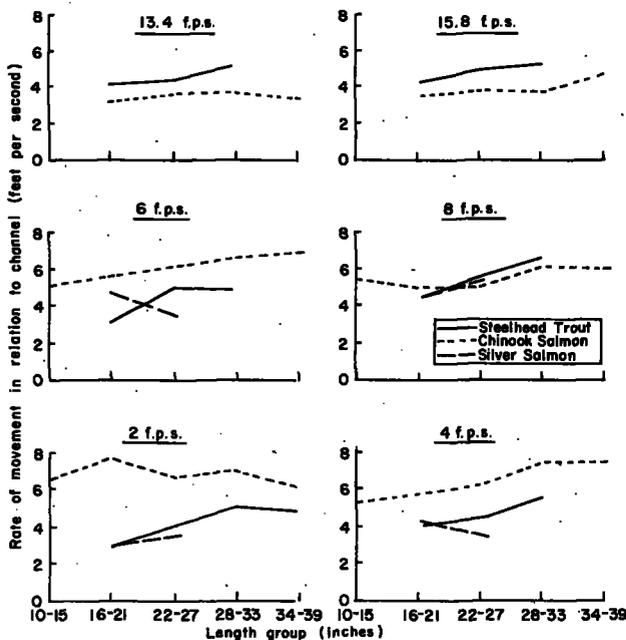


FIGURE 14.—Relationship between fish size and rate of movement. Rates are based on the median passage time of each length group. Lengths of individual fish were estimated. Underscored headings represent water velocities.

Maximum Observed Swimming Speeds

The preceding rates of movement were based upon the speed of the fish in relation to the channel and did not take into account the water velocity in which they were measured. Swimming speeds may be calculated by adding the velocity of the flow to these rates of movement.

Maximum observed swimming speeds for steelhead trout, chinook, and silver salmon at each velocity are given in table 21. The fastest fish timed was a 24-inch steelhead which maintained

an average swimming speed of 26.8 f.p.s. while passing through the 30-foot timing zone. Maximum observed swimming speeds for chinook and silver salmon were 21.9 and 17.5 f.p.s., respectively.

Here again the water velocities given are mean values and may be somewhat lower or higher than the actual velocities which the fish encountered depending upon the course they followed ascending the channel (appendix fig. 1). The maximum swimming speeds based on these values, therefore, are subject to an unknown degree of error depending upon the distribution of velocities within the channel and the course the fish followed.

TABLE 21.—Maximum observed swimming speeds of steelhead trout, chinook, and silver salmon timed through the 30-foot timing zone in water velocities ranging from 2 to 15.8 f.p.s.

Species	Water velocity	Water temperature	Estimated length	Rate of movement through timing zone		
				F.p.s.	F.p.s.	M.p.h.
Steelhead trout	2.0	66.5	24	12.0	14.0	9.5
	4.0	66.5	28	13.6	17.6	12.0
	6.0	66.5	30	15.7	24.7	16.3
	8.1	66.5	24	18.7	28.8	18.3
	13.4	67.0	32	6.5	19.9	13.6
	15.8	66.5	24	7.7	23.5	16.0
Chinook salmon	2.0	66.0	20	15.8	17.8	12.1
	3.9	66.5	28	14.3	18.2	12.4
	5.9	66.0	32	14.3	20.2	13.8
	7.9	66.0	32	13.6	21.5	14.7
	13.4	65.5	32	5.8	19.2	13.1
	15.8	67.0	38	6.1	21.0	14.9
Silver salmon	2.1	66.0	18	7.3	9.4	6.4
	3.9	66.0	14	7.0	10.9	7.4
	5.9	66.5	14	11.5	17.4	11.9
	8.4	66.5	24	9.1	17.5	11.9

¹ Swimming speed equals rate of movement maintained through 30-foot timing zone plus the velocity of flow in which the rate was measured.

Other Factors Related to Rate of Movement

Effect of nonuniform flow upon rate of movement.—At a water velocity of 6 f.p.s. a standing wave was created in the channel. Although the position of the wave varied somewhat in relation to the channel during the different test conditions, it was generally posited within the limits of the timing zone. During the course of the experiments it became apparent that this wave was affecting the rate at which fish swam through the timing zone. Some of the fish would stop when they reached the wave and remain for periods ranging from a few seconds to several minutes. This accounts for the comparatively greater percentages of steelhead, chinook, and silver salmon requiring 30 seconds or more to negotiate the timing zone in the 6 f.p.s. velocity tests. A comparison of the distributions of passage times in

tables 17, 18, and 19 indicates that the occurrence of the wave affected steelhead trout and silver salmon more than it did chinook salmon; 13.6 percent of the steelhead trout and 10.5 percent of the silver salmon required 30 seconds or longer to negotiate the timing zone in contrast to 1.8 percent of the chinook salmon.

Relationship between swimming ability and rate of movement.—Data on samples of fish tested at water velocities of 13.4 and 15.8 f.p.s. were examined to determine whether there were significant differences in time required to negotiate the timing zone between fish which were able to negotiate the entire channel and those that failed to do so. The distribution of sample sizes restricted the comparisons to chinook salmon at 13.4 f.p.s. and steelhead trout at 15.8 f.p.s. Passage times were obtained for only three steelhead trout which failed to negotiate the channel at 13.4 f.p.s. velocity and for only six chinook salmon which were able to negotiate the entire channel at 15.8 f.p.s. The limited data indicate that the ability of the fish to negotiate the channel was not reflected in the passage time through the timing zone (table 22).

The data for steelhead trout and chinook salmon which were able to negotiate the entire channel in the 13.4 and 15.8 f.p.s. tests were further examined to determine whether the rates of movement decreased as the fish ascended the channel. A comparison was made of rates of movement measured through the first 30 feet of the channel and those measured through the next 50 feet of the channel (table 23). By inspection, no decrease in the rate

TABLE 22.—Differences between mean passage times of fish which negotiated entire channel and those which failed to do so.

[Data are for chinook in 13.4 f.p.s. velocity and steelhead in 15.8 f.p.s. velocity]

Water velocity	Species	Size ¹ group	Mean time required to negotiate 30-foot timing zone		Difference (B-A)	Sample size	
			A Negotiated entire channel	B Failed to negotiate entire channel		A	B
13.4	Chinook salmon	small	9.03	9.14	+ .11 N.S.	7	12
		large	8.48	8.31	-.17 N.S.	32	33
15.8	Steelhead trout	small	7.29	6.94	-.45 N.S.	10	25
		large	5.95	7.36	+1.41 N.S.	22	7

¹ Small fish consist of individuals 24 inches and less in length, large fish consist of individuals 25 inches and greater in length.
N.S.—Not significant.

TABLE 23.—Comparison of steelhead and chinook rates of passage through the lower and upper sections of the channel in water velocities of 13.4 and 15.8 f.p.s.

Water velocity	Species	Size group	Sample size	Mean rate of movement through	
				First 30 feet	Next 50 feet
13.4	Steelhead trout	small	15	F.p.s. 4.0	F.p.s. 3.8
		large	21	4.7	4.7
	Chinook salmon	small	6	3.2	3.3
		large	31	3.5	3.6
15.8	Steelhead trout	small	7	4.4	3.3
		large	20	5.0	4.0
	Chinook salmon	small	—	—	—
		large	4	5.2	4.6

of movement is apparent among either steelhead trout or chinook salmon at 13.4 f.p.s. At 15.8 f.p.s. both steelhead and chinook showed a declining rate of movement as they ascended the channel.

DISCUSSION AND CONCLUSIONS

The results of the preceding experiments clearly demonstrate that water velocity is an important consideration in the design and operation of fishways.

The general response for the high-velocity flow in the choice experiments emphasizes the importance of maintaining adequate attraction flows at fishway entrances. The variation in the response for a given flow velocity among the different experimental conditions suggests that the relative attractiveness of a fishway entrance may vary with the magnitude of the flows adjacent to the entrance, and if these contrasting flows are strong enough, a significant proportion of the fish approaching the fishway might be diverted from the entrance. This may be especially true at low head dams on the Columbia River where entrance flows must often compete with comparatively strong spillway or turbine discharges. The results of the two exploratory tests involving a choice between velocities of 2.7 and 12.9 indicate that at least some fish might repeatedly enter and attempt to negotiate velocities beyond their swimming ability even though a low-velocity passage was near at hand.

Admittedly the responses demonstrated in the laboratory may not be directly applicable to conditions normally existing at fishway entrances. The interaction of other factors such as turbulence;

turbidity; differences in water quality, temperature, or light intensity; and possibly tendency of the fish to follow the shoreline might influence the response to flow differences in the vicinity of fishway entrances. We have no assurance, therefore, that the relative attractiveness of a fishway could be greatly improved by striving to maintain the entrance velocity at a higher level than adjacent flows from spillway or turbine discharges. Furthermore, since the high-velocity channel in these experiments always carried a proportionally greater quantity of water, we have not definitely established that the fish were responding solely to velocity differences. Additional studies should be conducted to determine the relative importance of flows in attracting adult salmonids.

The results of the high-velocity experiments demonstrate that the maximum water velocity which may be employed at the entrance or within a fishway will be governed by the species and size of fish involved and the distance which the fish are required to negotiate. When a fishway is designed to pass several species simultaneously the maximum allowable velocities should be determined by the swimming ability of the weakest species. It is evident that velocities of 13 and 16 feet per second could not be utilized in passage facilities designed for both steelhead trout and chinook salmon unless relatively short distances are involved (fig. 12). From the performances of the two species in the choice experiments we would conclude that the maximum velocity which could be employed for distances of approximately 85 feet would lie somewhere between 8 and 13 f.p.s. It is recognized that determination of a maximum velocity which may be safely utilized in passage facilities must not rely solely on the demonstrated ability of the fish to negotiate a required distance. The latent effects of the strenuous effort which may be required to negotiate the passage must also be considered. Paulik, DeLacy, and Stacy (1957) have demonstrated that salmonids may require a period of several hours to recover from exhausting swimming efforts, and Black (1958) has discussed the possible lethal effects and reduction of swimming ability brought about by sustained severe muscular exertion.

The recent findings of Paulik and DeLacy (1958) indicating that the swimming ability of adult salmonids may vary as the fish proceed up the river suggest that caution must be exercised in

applying the results of the Bonneville experiments to situations farther up the river.

The results of the rate of movement experiments demonstrate that certain water velocities may be more conducive to passing fish through channels than others. The differences in the rate of movement between species in these experiments preclude a definite decision as to which velocity would be most effective in passing these fish through channels. Chinook salmon demonstrated the fastest rate of movement in the 2 f.p.s. velocity while steelhead trout and silver salmon moved fastest in the 8 f.p.s. velocity. Perhaps the present standard (Bureau of Commercial Fisheries, 1958) of 2 f.p.s. is adequate when dealing with the species utilized in these experiments. This velocity appears strong enough to keep the fish orientated and moving through the channel at a satisfactory rate and would certainly require the least effort of the various velocities tested. It is significant to note, however, that our observations were made in a shallow, well-lighted, relatively narrow channel; somewhat different patterns of movement might be demonstrated in deeper, wider, and often darker passage channels frequently encountered at dams.

The fact that some fish were observed to hesitate in the standing wave created by the 6 f.p.s. velocity suggests a laminar-type flow might be more conducive to a uniform rate of passage through channels.

SUMMARY

The purpose of these experiments was to examine the influence of water velocity upon the orientation, performance, and rate of movement of adult migrating salmonids of the Columbia River. Experiments were conducted at the Fisheries-Engineering Research Laboratory, Bonneville Dam, during the months of August and September 1957. Steelhead trout and chinook salmon were the principal species involved in these experiments. A few silver salmon were also tested. The various experiments which were conducted and their results are outlined below.

Velocity-preference experiments

The orientative influence of water velocity was examined by offering the fish a choice of two channels carrying flows of different velocities. The following six velocity combinations were

tested: 8 vs. 2, 8 vs. 4, 8 vs. 6, 6 vs. 2, 6 vs. 4, and 4 vs. 2 feet per second. The response for the high or low velocity in each test condition was measured by the number of fish selecting each channel. The responses of 2,064 steelhead trout, 750 chinook salmon, and 108 silver salmon were observed during the period August 8-30. The following results were obtained:

1. The percentages of steelhead choosing the high-velocity channel in order of the choice conditions listed above were 79.4, 59.0, 52.2, 73.1, 63.8, and 67.2, respectively. This preference for the high velocity was statistically significant for all except the 8 vs. 6 f.p.s. choice condition.

2. The percentages of chinook choosing the high-velocity channel for the above choice conditions were 93.0, 67.5, 45.4, 87.1, 62.3, and 73.4, respectively. Again, as in the case of steelhead, the preference for the higher velocity was statistically significant for all except the 8 vs. 6 f.p.s. choice condition. Chinook demonstrated a more positive response than steelhead for the high velocity in four (8 vs. 2, 8 vs. 4, 6 vs. 2, and 4 vs. 2 f.p.s.) out of the six test conditions. The response was significantly greater at 8 vs. 2, and 6 vs. 2 f.p.s. No significant difference could be demonstrated between the response of large (25 inches and larger) and small (less than 25 inches) fish except in the 8 vs. 4 f.p.s. test condition. Here a greater proportion of large fish chose the higher velocity channel.

3. The limited number of silver salmon tested during these experiments indicated that this species generally preferred the higher velocity channel.

4. Results of an exploratory test in which 41 steelhead and 57 chinook were presented with a choice between water velocities of approximately 3 and 13 f.p.s. were similar to the preceding test in that 75.6 percent of the steelhead and 89.5 percent of the chinook chose the high-velocity channel.

High-velocity experiments

The performances of steelhead and chinook were measured in water velocities of 13.4 and 15.8 f.p.s. by determining the distance which the fish were able to negotiate through an 85-foot channel. The 13.4 f.p.s. tests were conducted from September 5-7, and the 15.8 f.p.s. tests were conducted on September 9, 10, 14, and 15. A total of 47

steelhead and 91 chinook were tested in the 13.4 f.p.s. flow and 67 steelhead and 130 chinook were tested in the 15.8 f.p.s. flow. The following results were obtained.

1. The performance of steelhead surpassed that of chinook in both 13.4 and 15.8 f.p.s. velocities. At a water velocity of 13.4 f.p.s., 92 percent of the steelhead negotiated the entire length of the channel whereas only 51 percent of the chinook achieved this distance. The performance of both steelhead and chinook declined at 15.8 f.p.s. velocity. Only 51 percent of the steelhead and 5 percent of the chinook negotiated the entire 85-foot channel. A decline in the swimming ability of chinook was noted during the experimental period.

2. Large fish of both species performed better than small fish in both 13.4 and 15.8 f.p.s. velocities.

Rate-of-Movement Experiments

The influence of water velocity upon rate of movement was measured by timing the fish through a 30-foot distance within the channels. Rates were determined at water velocities approximating 2, 4, 6, 8, 13, and 16 f.p.s. These experiments were conducted concurrently with the velocity-preference experiments and high-velocity experiments and utilized the same fish. The following results were obtained:

1. Rates of passage through the channels varied with species and water velocity. Based on median passage times required to negotiate 30 feet, both steelhead trout and silver salmon increased their rate of movement as the water velocity increased from 2 to 8 f.p.s.; steelhead from 4.1 to 5.6 f.p.s. and silver salmon from 3.1 to 5.1 f.p.s. In contrast the rate of movement of chinook salmon decreased from 6.9 f.p.s. in the 2 f.p.s. flow to 5.5 f.p.s. in the 8 f.p.s. flow.

The rates of movement of steelhead and chinook, based on median passage times of the fish which were able to negotiate the 30-foot timing zone, were 4.6 and 3.4 f.p.s., respectively, in the 13.4 f.p.s. velocity and 4.7 and 3.8 f.p.s., respectively in the 15.8 f.p.s. velocity.

3. A standing wave which occurred within the timing zone at a velocity of 6 f.p.s. tended to stop some of the fish for periods ranging from several seconds to several minutes. Steelhead were more affected by this wave than chinook.

4. Large steelhead and chinook were generally faster than small steelhead and chinook at each velocity tested.

5. Maximum observed swimming speeds (rate of movement in relation to the channel plus the water velocity in which the rate was measured) for each species were as follows: steelhead 26.8 f.p.s., chinook 21.9 f.p.s., and silver salmon 17.5 f.p.s. These rates are equivalent to 18.3, 14.9, 11.9 miles per hour, respectively.

6. There was no evidence that the distance which steelhead and chinook were able to negotiate in flows of 13.4 and 15.8 f.p.s. influenced their rates of movement at these velocities. Rates of movement of fish which were unable to negotiate the entire channel at these velocities did not differ significantly from those fish which negotiated the entire channel.

7. There was no apparent difference in the rates of movement maintained by steelhead and chinook through the first 30 feet and last 50 feet of the channel in the 13.4 f.p.s. flow. At 15.8 f.p.s. velocity the rates of movement of both steelhead and chinook decreased somewhat through the last 50 feet of the channel.

ACKNOWLEDGMENTS

The author gratefully acknowledges the assistance of the following individuals: Gerald B. Collins who was responsible for the original planning of the experiments; Carl H. Elling who supervised the experiments; Robert S. Rupp who was in charge of preliminary experiments conducted in 1956 and devised the methods of establishing many of the various flow conditions; and personnel of the Hydraulics Laboratory, U.S. Corps of Engineers, Bonneville Dam for technical assistance with the various hydraulic problems encountered during the experiments. The author is particularly indebted to Robert H. Lander, Biometrics Unit, Bureau of Commercial Fisheries Biological Laboratory, Seattle, for his assistance in designing the experiments and statistical treatment of the data.

LITERATURE CITED

- BLACK, EDGAR C.
1958. Hyperactivity as a lethal factor in fish. *Journal of the Fisheries Research Board of Canada*, vol. 15, no. 4, pp. 573-586.

BUREAU OF COMMERCIAL FISHERIES.

1958. Anadromous fish passage at dams in the Pacific Northwest. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Portland, Oreg., 10 pp., processed.

COCHRAN, WILLIAM G., and GERTRUDE M. COX.
1950. Experimental designs. John Wiley and Sons, New York, 454 pp.

COLLINS, GERALD B.
1952. Factors influencing the orientation of migrating fishes. U.S. Fish and Wildlife Service, Fishery Bulletin 73, vol. 52, pp. 375-396.

COLLINS, GERALD B., and CARL H. ELLING.
1961. Fishway research at the Fisheries-Engineering Research Laboratory. U.S. Fish and Wildlife Service, Circular 98, 17 pp.

PAULIK, GERALD J., and ALLAN C. DELACY.
1958. Changes in the swimming ability of Columbia River sockeye salmon during upstream migration. University of Washington College of Fisheries, Technical Report No. 46, 67 pp., processed.

PAULIK, GERALD J., ALLAN C. DELACY, and EDWIN F. STACY
1957. The effect of rest on the swimming performance of fatigued adult silver salmon. University of Washington School of Fisheries, Technical Report No. 31, 24 pp., processed.

SNEDECOR, GEORGE W.
1956. Statistical methods applied to experiments in agriculture and biology. 5th ed., Iowa State College Press, Ames, Iowa, 534 pp.

APPENDIX A

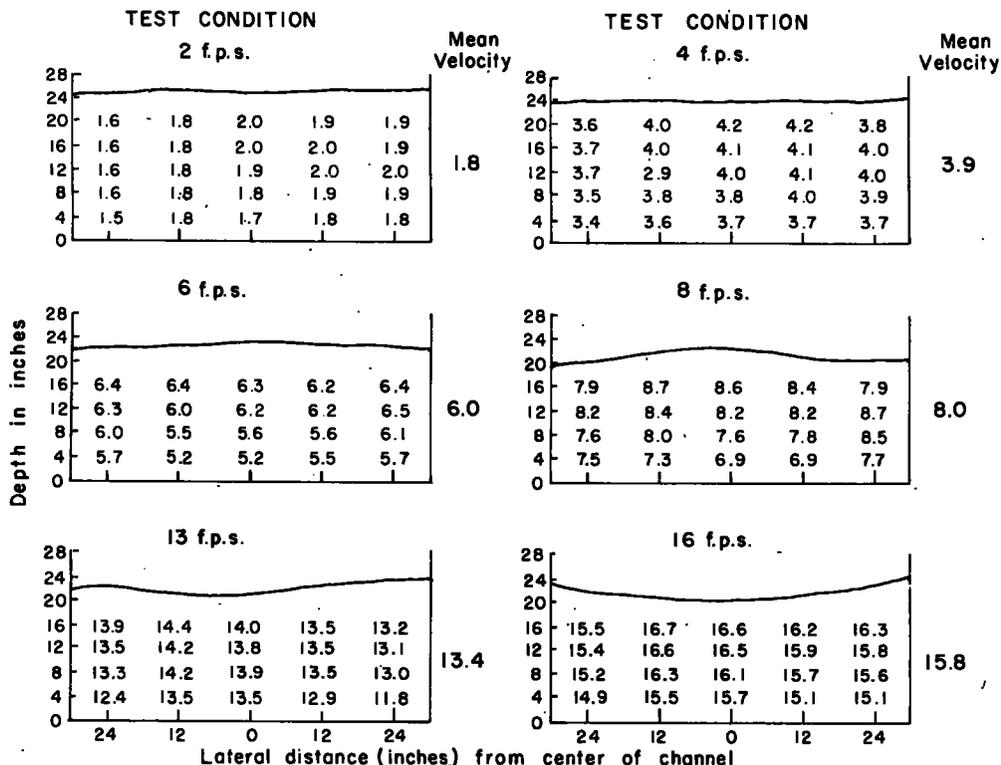


FIGURE A-1.—Examples of the distribution of water velocities in the channel for each of the six test conditions. Entries for each measuring point (depth and distance from the center of the channel) are mean values derived from measurements taken at these points at five different stations between the downstream end of the channel and the upstream limit of the timing zone (point B, figs: 3 and 9). Line at top indicates water surface.

DEVELOPMENT OF A MATHEMATICAL RELATIONSHIP BETWEEN ELECTRIC-FIELD PARAMETERS AND THE ELECTRICAL CHARACTERISTICS OF FISH

By GERALD E. MONAN, *Fishery Biologist*, and DEREK E. ENGSTROM, *Physicist*

ABSTRACT

A few of the electrical characteristics of fish were defined and studied as the criteria for producing a specific, observed reaction. Voltages and currents applied to a small test cell containing a live fish were measured. With the use of an electrical analogue of the cell contents, these data were reduced to the equivalent parameters applied to a mathematical model representing the fish. The resulting values of resistivity and power

density computed for this model were then used to describe the corresponding fish characteristics. Application of pulsed voltages to the cell demonstrated a minimum power density below which no reaction was observed. Equations were then derived to relate this value to corresponding electrical conditions that would exist at an electrical guiding installation.

The use of electric fields is presently being investigated as a possible method of diverting fish for safe passage around hydroelectric dams, thus aiding in the preservation of the salmon fisheries.¹

A major problem of this investigation is the evaluation of an electric field as a motivating stimulus. Prior to the research reported upon here, few, if any, methods have been developed to observe or determine accurately those portions of a field pattern which motivate the behavior of a fish. Therefore, the optimum electrical parameters of a particular, effective guiding installation may not apply at some other site. In other words, so little is known about how an electrical field stimulates a fish that it is difficult to design a successful electrical-guiding device. Extensive and costly experimentation has been necessary at each new installation to obtain the necessary parameters for an effective electrical-guiding device.

NOTE.—Approved for publication April 17, 1962.

¹ Mason, James E., and Rea Duncan. Manuscript in preparation. The development and appraisal of methods of diverting fingerling salmon with electricity at Lake Tapps. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

An investigation of this problem indicates that an adequate solution would include a mathematical method of relating electric-field parameters to the electrical characteristics of the fish. These characteristics control the response of the fish to electricity and thus define for the fish specific regions in an electrical field. However, because of the complexity of the biological structure involved, a precise description of these characteristics is impossible. The mathematical process therefore, must utilize an electrical analogue to facilitate such a description.

The research presented here has three objectives: (1) To develop a mathematical model to serve as the electrical analogue of a fish, (2) to find an evaluation procedure which will determine the electrical properties and processes within the model, and (3) to develop a method to relate these model characteristics to the parameters of the electric fields to be used in proposed fish-guiding devices.

MATERIALS AND METHODS

The experiments were conducted at the Bureau of Commercial Fisheries Biological Laboratory;

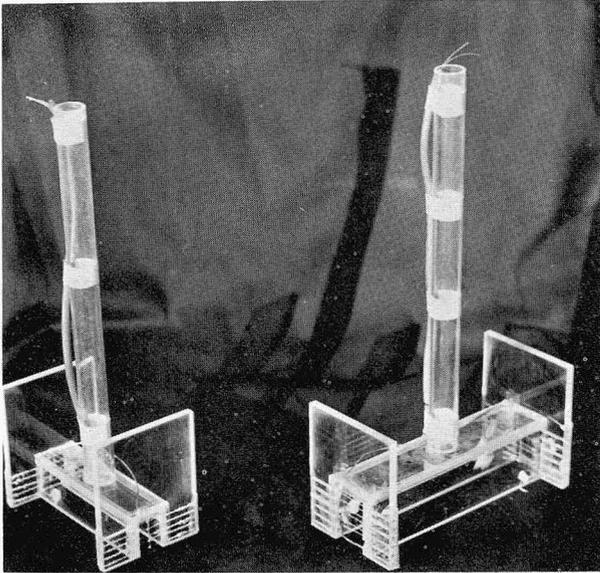


FIGURE 1.—Plastic cells used to contain fish while testing.

Seattle, Wash., from November 27, 1958, to January 9, 1959. The fish used were 0 age-group sockeye salmon (*Oncorhynchus nerka*). These fish were obtained from the Winthrop National Fish Hatchery in September, 1958, and were kept in the laboratory holding facilities until their transfer to the experimental area.

The general method of laboratory investigation involved measuring voltages and currents applied to a small, plastic test cell (fig. 1) containing a live fish. Measurements were carried out with the fish facing either the positive or the negative electrode. These parameters were measured coincident with a specific observable reaction of the fish. Measurements of applied voltage were made from electrodes positioned within, and at opposite ends of, the cell. These electrodes were designed so the electrical resistance between them would be completely controlled by the contents of the cell. It was also necessary to reduce the volume of the surrounding body of water to a minimum in order to obtain measurements which were analogous to functions of the electrical characteristics of a fish. Reactions produced in the fish were created by applying the necessary voltage across the cell.

The cell voltages used in the calculations were the lowest applied values to which the fish appeared to respond. This response was selected because it could be easily observed and because the stimulus threshold was well defined. When the applied

voltage reached the threshold value, a violent swimming motion was observed. This reaction could be considered equivalent to the muscle response caused by the rheobase potential (Mitchell, 1948), and would correspond to the threshold reaction reported in later publications (Fisher, 1950; Cattley, 1955). Since this observed threshold phenomenon is a property of the biological structure of the fish, any corresponding electric-field gradient should produce the same effect. Therefore, this response defined a characteristic of the fish that could be related to field-pattern parameters.

HOLDING FACILITIES

Holding facilities were set up adjacent to the experimental area in order to provide ease of operation and to minimize any change in water conditions between the holding troughs and the cell. Fish were held here at least 4 hours prior to testing.

Equipment for this installation included three wooden troughs, 22 cm. wide by 24 cm. deep by 196 cm. long, and a 1042-liter wooden tank. Dechlorinated city water was supplied to the tank through a float valve. From the tank, water was pumped to a head trough which in turn supplied the three holding troughs. Approximately 70 percent of the flow from the holding troughs was diverted back into the main tank, and 30 percent was drawn off as waste. A thermostatically controlled refrigeration unit kept the water temperature at approximately 50° F.

APPARATUS

The major portion of the experimental apparatus was made up of the plastic tank and test cells and the electronic measuring and testing equipment. The plexiglass tank had inside dimensions of 25 cm. by 25 cm. by 38 cm. and had one fixed partition and one adjustable partition. A test cell (fig. 2) was placed between these partitions, and the adjustable partition was positioned and clamped in such a manner as to hold the cell tightly between the two partitions. Electrodes made of duralumin were placed at both ends of the tank to permit the application of the test currents.

Two cells of different size were used in order to accommodate the range of fish sizes tested. Cell number one had inside dimensions of 2.54 cm. wide, 3.81 cm. deep, and 15.88 cm. long; whereas

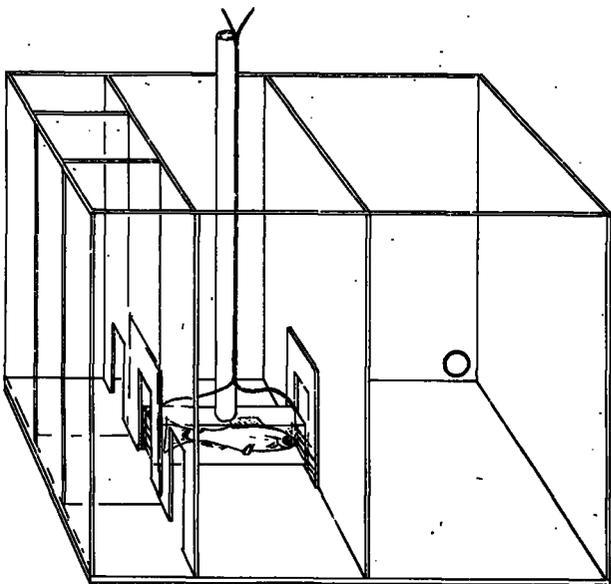


FIGURE 2.—A test cell in position within the experimental tank.

cell number two was 1.59 cm. wide, 2.54 cm. deep, and 11.43 cm. long. Each cell was equipped with nylon restraining threads stretched horizontally across both ends. The quantity of restraining material was kept at a minimum by using only six threads per end for cell number one and three threads per end for cell number two. Monitoring electrodes were placed in each cell opening to measure the voltage drop across the cell. The leads for these electrodes were routed through the cell wall and up the handle to the external circuit.

Three types of monitoring electrodes were used. The first arrangement consisted of a ¼-inch wide, stainless steel strip, cemented to the top wall, just inside each cell opening. The second type was a ¼-inch mesh screen which covered the two ends of the cell, and the third type consisted of a single wire stretched horizontally across the cell openings. Experimentation with all three types revealed that the fish were not sensitive to the proximity of a conducting plane. This information was important for consideration in the design of future cells.

Water was obtained from the holding facilities and was gravity fed to the tank from a 14-gallon reservoir. The rate of flow through the test cell was kept at approximately 2 gallons per hour. Water resistivity was controlled by the introduction of NaCl.

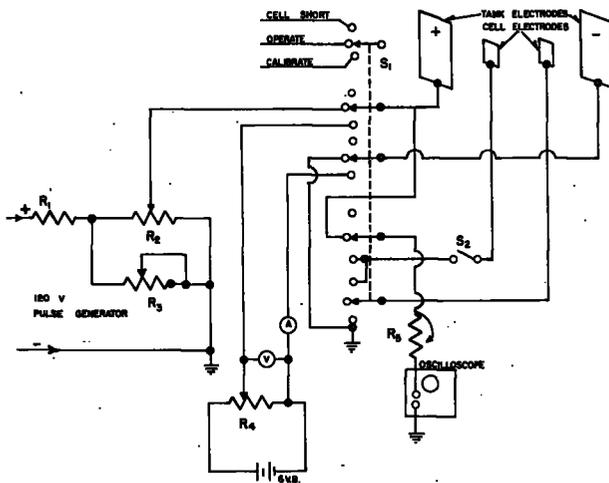


FIGURE 3.—Circuit diagram of the complete testing unit.

The electronic circuitry enabled a square wave pulse of the desired amplitude and duration to be applied to the cell (fig. 3). Electronic switching equipment, controlled by the investigator (described in detail by Volz (1962)) connected the output of a d.c. (direct current) generator to the test circuit at preset intervals and for preset durations. The voltage applied to the circuit was essentially a square wave pulse with an amplitude of 120 volts and a duration of 50 milliseconds.

The circuit functions as follows: When switch S_1 is in the operate position, the functioning circuit is the operate circuit (fig. 4a). In this case, resistors R_1 , R_2 , and R_3 combine to form an adjust-

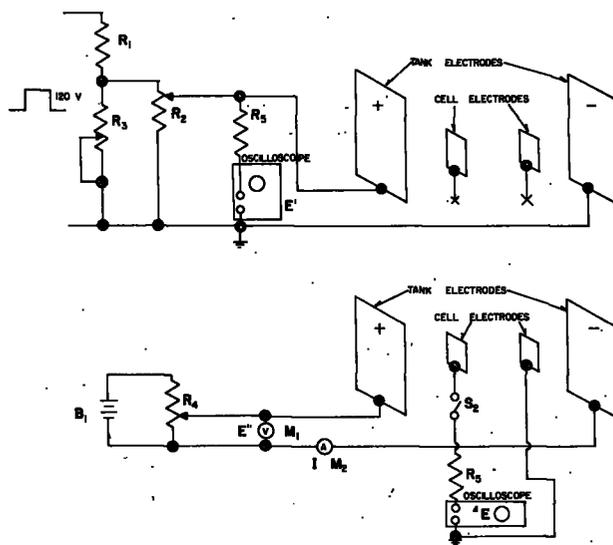


FIGURE 4.—Circuit diagram of the testing unit: (above) operate configuration; (below) calibrate configuration.

able voltage divider that reduces the 120-volt input pulse to the required voltage applied to the tank. This voltage is applied to the tank electrodes and is monitored on the oscilloscope by means of the monitoring electrodes. Resistor R_s is used to change scale readings on the oscilloscope by one-half, when necessary, in order to achieve the maximum possible accuracy.

When switch S_1 is placed in the calibrate position, the functioning circuit is the calibrate circuit (fig. 4b). In this case battery B and resistor R , supply an adjustable d.c. voltage to the tank electrodes. The voltage drop across the cell is now measured on the oscilloscope. Switch S_2 prevents current from flowing in the monitoring circuit until the operator is ready to record the reading. This operation is necessary in order to prevent the electrodes from becoming polarized and giving erroneous readings. After the readings have been taken, depolarization is accomplished by closing switch S_2 and placing switch S_1 in the "cell short" position. With the switch in this position, the cell electrodes are shorted, thus returning the circuit to equilibrium.

MEASUREMENT PROCEDURE

After preliminary experimentation, a specific measurement procedure was adopted. The fish to be tested was taken from the holding trough and was placed in the plexiglass tank. The test cell was then lowered over the fish and positioned so that the openings at the ends of the cell coincided with the openings in the partitions. The resistivity of the water entering the test cell was then measured with a standard resistivity bridge.

After the fish was allowed a two-minute rest, switch S_1 was placed in the operate position, and the electronic pulsing device was triggered. Pulses with a duration of 50 milliseconds were then automatically applied at intervals of 20 seconds. Between each pulse application, the potentiometer (R_2) was manually rotated to increase the pulse amplitude. When the reaction level was reached, the fish jumped violently, and the operator, observing this reaction, recorded the pulse voltage from the oscilloscope.

The battery voltage (B_1) was used to establish the relationship between the pulse voltage across the tank and the actual voltage across the cell. The desired level of current was set, and the voltage was recorded from the voltmeter (M_1).

With switch S_2 closed, switch S_1 was moved to the cell short position and the cell electrodes were shorted for 30 seconds. With switch S_2 open, switch S_1 was turned to the calibrate position. Switch S_2 was then closed, and the voltage was immediately recorded from the oscilloscope. Three levels of current were used for each fish tested, and measurements were repeated at least twice at each level to insure accuracy.

After being tested, each fish was lifted from the cell in a net, and after the excess water, clinging to the fish, was eliminated, the fish was placed in a graduated cylinder partially filled with water. The volume of the displaced water was then recorded as the volume of the fish.

The complete testing procedure took approximately 15 minutes per fish. After the volume measurement was completed, each fish was returned to the appropriate trough, where it was held for several days. No mortalities occurred among the fish tested.

ANALYSIS PROCEDURE

The symbols listed below are used in the discussions that follow:

- ρ_f = fish resistivity.
- ρ_w = water resistivity.
- V_f = fish volume.
- V_c = cell volume.
- L = fish length.
- D = distance between cell electrodes.
- R = resistance of the cell containing the fish.
- R_a = resistance of the cell without the fish.
- E = d.c. voltage drop across the cell.
- E' = d.c. voltage applied to the tank.
- E'' = reaction voltage applied to the tank.
- V = guiding-field gradient.
- P_f = power density in the fish.
- P_w = power density in the water.
- I = d.c. current through the cell.
- m = empirical function of ρ_w and ρ_f .

Appendix A contains a glossary which may be useful to readers who are not familiar with electrical laws and terms. The following discussion is purposely brief; however, the subject is covered in more detail in appendix B. The mathematical model of the fish was developed by constructing an electrical analogue of the contents of the test cell. The analogue was developed by dividing the cell into a number of rectangular parallelepipeds, one of which represented the fish and the remaining ones represented the water within the cell. The size of the parallelepiped representing

the fish was dependent upon the size of the fish, whereas the dimensions of the remaining parallelepipeds were functions of both cell and fish geometry.

The correct partitioning of the cell's contents into parallelepipeds was governed by the following requirements: (1) the calculated fish resistivity must remain constant as the water resistivity is varied over a specified range, (2) there must be a practical limitation on the complexity of the resulting equations, and (3) the accuracy requirements of the resulting equations must not exceed the capabilities of existing measuring techniques. These are the restrictions which were used in devising the mathematical model of the fish.

In the partitioning scheme, each parallelepiped of the cell model was treated as a resistive-circuit component. The end or cross sectional boundaries served as connecting terminals, whereas the remaining surfaces were considered nonconducting. The resistance of each of the parallelepipeds was related to the resistivity of its enclosed medium by using Ohm's Law. The result was a set of equations called component equations which related cell dimensions, fish dimensions, water resistivity, and fish resistivity to the resistance of a corresponding circuit component. Thus, an analogue circuit of the cell's contents was devised by replacing each parallelepiped of the cell model with an equivalent two-terminal resistive component. The total resistance of this analogue circuit was designated to be the cell's resistance. An equation was obtained by using the known properties of resistors to relate this resistance to the resistance of each component. This equation was called the circuit equation. By substitution of the component equations for the resistance values in the circuit equation, a relationship was obtained between the cell resistance and the resistivity of the fish model. Thus, the resulting equation provided a method of evaluating a specific property of the fish.

The transformation from the actual cell to that of the model of the cell's contents can be more clearly visualized by mentally subdividing the actual cell volume into infinitesimal volume elements. These elements would be of equal volume and can be called differential volume elements (similar to the units used in the differential theory of calculus).

The transformation consists of transferring each

element of the cell volume into a parallelepiped in the model of the cell's contents. The correct distribution of volume elements should be carried out in such a way that the total power in each parallelepiped will be equal to the power dissipated in a corresponding circuit component for all values of water resistivity. In order to complete the transformation, the lines of current flow can be rotated in each differential element without changing the power dissipated by the element. This allows these current lines to be arranged to correspond with those current lines which would be expected to exist in each parallelepiped. After considerable preliminary experimentation, two configurations were chosen which best fulfilled the previously established criteria.

The first partitioning plan divided the cell's contents into four parallelepipeds; three represented the total water in the cell. The fourth parallelepiped, which represented the fish, was designated as the fish model. The corresponding analogue circuit was composed of four resistors (R_1 , the fish; and R_2 , R_3 , and R_4 , the water) connected in a series-parallel network. This arrangement was satisfactory in all ranges of water resistivities tested except when the resistivity of the fish was greater than the resistivity of the surrounding water. It was in this region that this arrangement had a point of discontinuity.

In order that this difficulty might be avoided, the volume elements were resolved in a different manner for this area of operation. In this partitioning system, the cell's contents were divided laterally into two rectangular parallelepipeds, one representing the fish and the other representing the total water in the cell. The corresponding analogue circuit was composed of two resistors (R_1 , the fish; and R_2 , the water) connected in series.

EVALUATION PROCEDURE

The resistivity of the fish model was found by using the measured resistivity of the water in the cell and the resistance of the cell. The values of R were found from the slope of a plot of cell voltage (E) vs. cell current (I) for each fish tested. Figure 5 shows an example of one of these graphs. A similar graph (fig. 5) was made from data taken with the cell empty in order to find the value of R_a . One of these graphs was made for each series of fish tested. Because the value of R_a is directly proportional to the resistivity of the

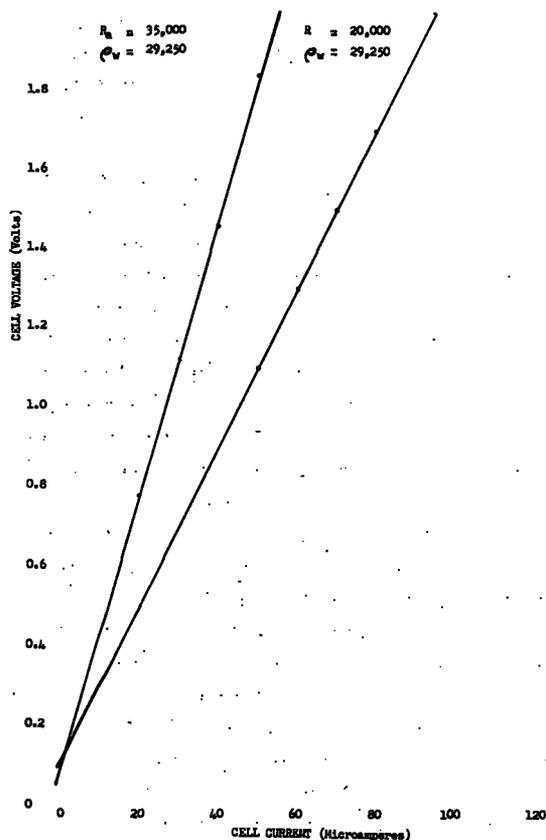


FIGURE 5.—A plot of cell voltage (E) vs. cell current (I); first for an empty cell and then for the cell with the test fish enclosed. The resistance of the empty cell (R_e) and the resistance of the cell with the fish enclosed (R) were found from the slope of their respective graphs.

water in the cell, it was easy to calculate from this single value of R_e the R_e 's for the rest of the series. With the use of these values and other measured parameters, such as fish volume, fish length, and distance between electrodes, the values of fish resistivity (ρ_f) were found. The figures for fish length were obtained from the graph illustrated in figure 6.³

The power density in the fish model was determined by applying Kirchhoff's Voltage Law to the analogue circuit of the cell's contents. With this approach, the total power in the fish model was related to a voltage applied across the cell's contents. The voltage that was applied to the cell was considered as being applied to the analogue

³ When the four-body equation was derived, it became necessary to add a previously unneeded parameter, fish length (L). The lengths and volumes of a random sample of experimental fish were measured and a plot of fish length (L) vs. fish volume (V_f) was made to obtain this measurement. From this graph, approximate values of fish length were obtained by using the recorded values of fish volume (V_f) from the previous experiments.

circuit terminals, as represented by the ends of the cell. The voltage value used in the computation was the applied cell voltage which produced the specific swimming like motion chosen as our desired reaction. By application of Kirchhoff's Voltage Law and our component equations, the actual voltage applied across the fish model was determined. The power density in the fish model was determined by using Joule's Law, the fish model's dimensions, the voltage applied to the model, and the component resistance of the model. The equation describing this relationship provided a method of evaluating the rate at which an electrical process takes place within a fish.

The range of water resistivities, over which the configurations and their corresponding equations were useful, was established by varying the water resistivity (ρ_w), calculating the resistivity of the fish (ρ_f), and observing within what range of water resistivities the resistivity of the fish remained relatively constant.

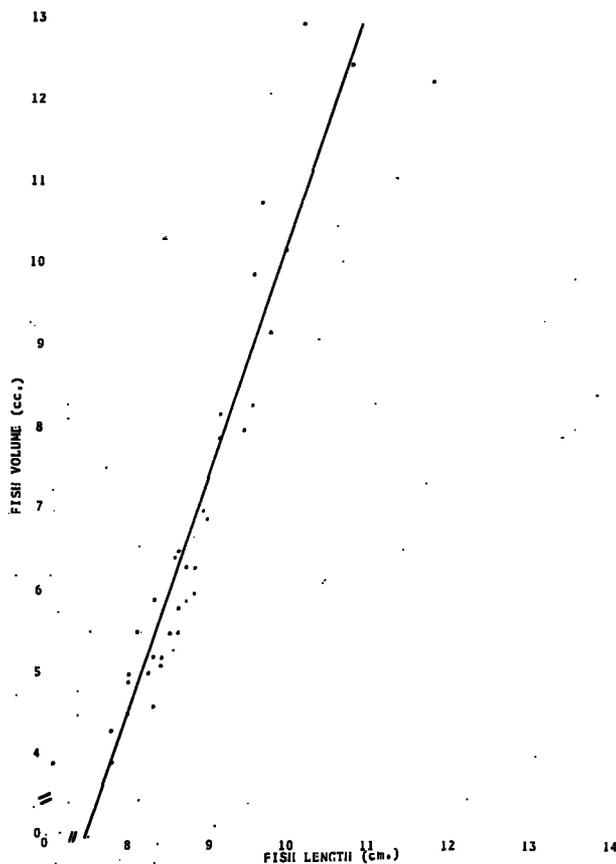


FIGURE 6.—Length-volume relationship used to provide the additional parameter fish length (L) in the four-body equation.

The theory and complete mathematical derivations of the formulas used in computing fish resistivity and power density are found in appendix B.

In order that the third objective of our research might be fulfilled, the power density in the fish (P_f) was related to the corresponding power density (P_w) and voltage gradient (V) in an open body of water. The complete derivation and explanation of the relationship between P_f and P_w can be found in appendix C.

RESULTS AND DISCUSSION

Table 1 shows the models of the test cell that were derived, the corresponding analogue circuits, the range of water resistivities for each and the equations used, to solve for ρ_f and P_f .

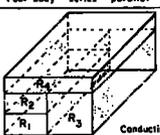
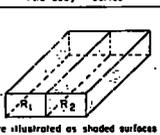
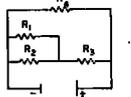
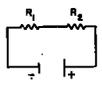
The formula derived for relating cell voltage gradients and power densities to open water gradients and power is as follows:

$$\rho_w P_w v = (m^2 \rho_f P_f) = V^2 \text{ where } m = f(\rho_w, \rho_f)$$

The complete derivation and explanation of this formula can be found in appendix C.

The symmetry of the equations and configurations is similar to those experienced with standard series and parallel electrical circuits. Basic laws of electricity can be applied to these configurations just as if they were composed of common commercial resistors. For example, in a resistance network with two resistors in parallel, if one resistance approaches zero and the other remains constant, the total resistance approaches zero.

TABLE 1.—Formulas derived for computing fish resistivity and power density; shown with the corresponding test-cell models and analogue circuits. The limits of usefulness, based on water resistivity, are also shown.

DERIVED TEST	Four body - series - parallel	Two body - series
CELL MODELS		
ANALOGUE CIRCUIT		
EQUATION FOR ρ_f	$\rho_f = \frac{P_w [R_1 R_2 \sqrt{L} - 2 \sqrt{L} R_1 (R_2 - R_1) D - L]}{R R_2 \sqrt{L} - W R_1 (R_2 - R_1) D - L} \rho_w D^2 [L R_2 - R]$	$\rho_f = P_w \frac{D^2}{R_2^2 \sqrt{L}} [R - R_2]$
EQUATION FOR P_f	$P_f = \left(\frac{E \sqrt{L}}{D} \right)^2 \left(\frac{\rho_w D}{R_2 \rho_w D^2 L + 2 R_1 \sqrt{L} D - L} \right)^2 L^2 D$	$P_f = \left(\frac{E \sqrt{L}}{D} \right)^2 \left(\frac{R_2 \sqrt{L}}{R} \right)^2 \left(\frac{D}{D^2} \right)$
LIMITS OF USEFULNESS	$1 \leq \frac{\rho_w}{\rho_f} \leq 20$	$1 \geq \frac{\rho_w}{\rho_f} \geq 0.75$

If, on the other hand, two resistors are connected in series and the value of the first resistor approaches zero and that of the second resistor remains constant, the total resistance of the circuit approaches the value of the second resistor. These same principles are applied to the resistance elements of the model of the cell's contents.

In order that the situation in which the resistivity of the water (ρ_w) is greater than the resistivity of the fish (ρ_f) might be accurately represented, the configuration and corresponding equation starting with two resistors in parallel are used. This equation reaches an extreme limit when the resistivity of the water (ρ_w) is infinite. When the resistivity of the water (ρ_w) is infinite, the resistance of the cell is equal to the resistance of the fish. By expanding this two-body, parallel configuration into a four-body, series-parallel network, this limit disappears. In the four-body, series-parallel network, when the resistivity of the water (ρ_w) is infinite, the resistance of the cell (R) is infinite; and when the resistivity of the water (ρ_w) is zero the resistance of the cell (R) also is zero.

In order that an accurate reflection of the situation in which the resistivity of the water (ρ_w) is less than the resistivity of the fish (ρ_f) may be achieved, the configuration and corresponding equation with two resistors in series are used. This equation reaches an extreme limit where the resistivity of the water (ρ_w) is zero. In this case, the resistance of the cell (R) is equal to the resistance of the fish.

The equation developed to relate power density in the cell to power density in an open body of water is not completely satisfactory. When the volume of the cell is expanded to infinity in our configuration, the boundaries no longer enclose finite regions and therefore exhibit an impossible field condition. For elimination of the effects of this property it was necessary to put an empirical function (m) of ρ_w and ρ_f into the equation. This empirical function will have to be determined by further experimentation.

Appendix D illustrates some qualitative values of fish resistivity and power density that were calculated to observe the practicability and validity of the derived analytical processes. With the use of the formulas that were derived, according to their restrictions, the average value of fish resistivity was calculated for the fish tested. When measured from end to end, with the fish

acclimated at 49° F., this resistivity was 1,380 ohm centimeters. The large deviations in the values for the fish tested are primarily due to two causes: (1) a lack of accurate data on fish length and, (2) leakage current between the cell flange and the tank partitions. If the cell was not placed exactly in the same position each time, the dimension changes of the minute spaces between the cell flange and the tank partitions caused an error between the resistance of the cell with the fish in (R) and the resistance of the cell empty (R_0). Because of these errors, further work should be done before the absolute numerical values can be considered correct.

During the experiment, several interesting phenomena were observed. One of these was the apparent dependence of the reaction threshold upon pulse-rise time. Although the available equipment prohibited the variation of pulse-rise time, the fish was observed to withstand, without irritation, a much greater level of voltage when it was applied as a continuous voltage gradient. Mitchell (1948) found this to be true also in work with individual nerves.

It was also noticed that the reaction level appears to be a function of fish size when the fish is facing the positive pole; yet, when the fish faces the negative pole, this level is constant. When the fish was facing the negative pole, the reaction level was generally lower than it was when the fish was facing the positive pole (table 2). This has also been observed by other investigators (Eggen and Sheckels, 1954; McMillan, Holmes, and Everest, 1937³).

CONCLUSIONS

1. A mathematical model can be devised to serve as the electrical analogue of a fish.

2. The techniques developed in this work can provide a means of evaluating the electrical properties and processes within the model and thus provide a practical method of evaluating some electrical characteristics of a fish.

3. Power density can be used to describe an electrical criterion required to produce a specific reaction in a fish.

³ McMillan, F. O., H. B. Holmes, and F. Alton Everest. 1937. The response of fish to impulse voltages. A report on investigations conducted at the Tablerock site near Medford, Oreg., between August 25, 1937 and September 18, 1937. 15 p. Typewritten. A copy of this report is available at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

TABLE 2.—The relationship of the average reaction power density to fish volume and polarity orientation

Pole fish is facing		Fish volume (cc.)		P_f , ¹ (microwatt per cc.)	
Positive	Negative	Range	Average	Range	Average
.....	x.....	3.9 to 9.0.....	6	0.51 to 2.51.....	0.9
.....	x.....	11.0 to 22.0.....	15	0.32 to 1.64.....	0.8
x.....	3.9 to 9.0.....	6	0.61 to 3.31.....	1.4
x.....	11.0 to 22.0.....	15	0.84 to 3.44.....	3.8

¹ P_f must be applied within 2 milliseconds, since a pulse with a rise time of not greater than 2 milliseconds was used.

4. The mathematical techniques developed here indicate that power density, as a reaction criterion, can be related to electric field parameters.

5. Additional experimentation will be required to develop the relationship between power density and the corresponding voltage gradient in an unbounded body of water.

RECOMMENDATIONS

The experimentation reported here should be furthered, and the following improvements should be employed:

(a) The test cell used in future experiments should resemble, in principle at least, the cell in figure 7. This design reduces the possibility of leakage currents, provides easier access to the cell, and enables closer observations of the fish.

(b) The electronic equipment should be well shielded and grounded.

(c) Alternating current should be used wherever possible to avoid polarization effects.

(d) The ends of the cell should be perforated conducting planes, erected perpendicular to the major cell axis.

(e) The incremental increase in pulse amplitude should be small in magnitude and constant in rate.

(f) A consistent handling procedure should be used for each fish.

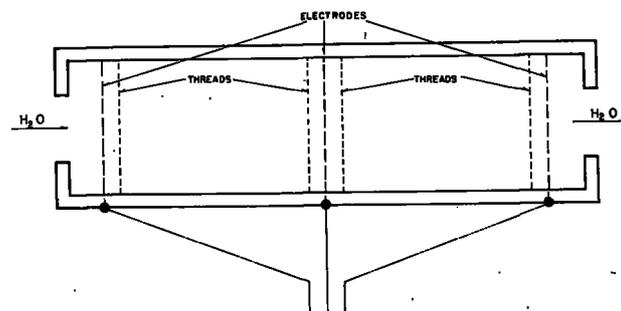


FIGURE 7.—Proposed test cell, incorporating the recommended improvements to eliminate leakage currents.

(g) The length of each fish tested should be accurately measured and recorded.

SUMMARY

Electrical fish guiding is being developed for use in protecting natural fish runs where their migration is threatened by manmade obstacles. A major problem in this development is the evaluation of an electric field as a motivating stimulus. In order that a precise method of evaluation might be established, a method of analysis was developed which employed a mathematical model of a fish.

The fish was confined in a small plastic test cell, through which water was circulated. The electrical characteristics of the cell's contents (water and fish) were determined by measuring voltages and currents applied to the cell. A mathematical model of the cell's contents was then devised by mentally dividing the test-cell volume into several parallelepipeds. One of the parallelepipeds was designated to represent the fish, whereas the others represented the water within the cell. The characteristics of this model were defined as those properties necessary to produce an electrical analogue of the cell's contents. Since the properties of the water portion of the analogue were known, the characteristics of the fish portion were determined by measuring the electrical parameters applied to the cell. The entire process utilized: (1) the voltage applied between the cell electrodes; (2) the electrical resistance of the cell, with the fish and without the fish; (3) the water resistivity; (4) the length of the fish; (5) the volume of the fish; (6) the cell length or separation of the cell electrodes; and (7) the formulas derived to relate the resistivity and power density of the model to the measured parameters.

One model characteristic, power density, was determined to be a criterion for producing an observed reaction. The applied voltages used in these power calculations were the minimum values to which the fish appeared to react. Therefore, the resulting power density value was a property controlled by the fish.

Study of the variations in the threshold of reaction revealed that the power density necessary for this reaction increased as the size of the fish increased, provided the fish was facing the positive pole. If the polarity was reversed, the threshold remained constant over the range of

fish sizes tested. The two levels of power density converged as the fish size decreased. With the fish facing the positive pole, the average value of power density ranged from 1.4 to 3.8 $\mu w/cc.$ over a corresponding fish-volume variation of 6 to 15 cc. When the fish faced the negative pole, values of 0.8 to 0.9 $\mu w/cc.$ were obtained over the same volume range.

By expanding the cell dimensions, in our calculations, we found it possible to obtain a simple relationship between power density and the equivalent voltage gradient in an unbounded body of water. This gradient is the variable that would be applied in an electrical fish-guiding field pattern. The calculated gradient would permit the identification of portions of any field pattern as being capable or incapable of producing the reaction observed in the laboratory. Because of the manner in which the test cell's contents were subdivided, the equations derived for the open-water gradient contain a proportionality function, with constants that must be evaluated empirically. Therefore, this particular phase of the work is incomplete. Examination of the results of this work, however, indicates that a mathematical model can be devised to serve as the electrical analogue of a fish, and the techniques that were developed can provide a practical method of evaluating some electrical characteristics of fish. Additional experimentations, incorporating the techniques developed herein and incorporating the recommended improvements, will certainly be of value to the electrical-guiding program.

LITERATURE CITED

- CATTLEY, J. G.
1955. Your guide to electrical fishing (1). *World Fishing*, vol. 4, No. 3, pp. 125-127.
- EGGEN, ARMON M., and G. DALE SHECKELS.
1954. Susceptibility of rainbow trout to electric shocks. *Montana State College Bulletin, Engineering Experiment Station*, No. 19, 14 pp.
- FISHER, KENNETH C.
1950. Physiological considerations involved in electrical methods of fishing. *The Canadian Fish Culturist*, No. 9, 26 pp.
- MITCHELL, PHILIP H.
1948. *General physiology*. 4th ed. McGraw-Hill Book Company, Inc., New York, 927 pp.
- VOLZ, CHARLES D.
1962. Ignition-pulsed electric fence guides migrating salmon. *Electronics*, vol. 35, No. 16, pp. 50-53.

APPENDIX A

GLOSSARY

1. Joule's Law: That portion of the power input to any device which is equal to the product of the resistance of the conductors forming the winding of the device and the square of the current through this winding is always converted into heat. That is, when a current I flows through a resistance r , heat is always "dissipated" in this resistance, and the rate of dissipation is $P_h = rI^2$ ¹

2. Kirchhoff's Network Laws: (a) The algebraic sum of the currents coming to any junction in a network of conductors is always zero. (b) The algebraic sum of the potential drops around any closed loop in a network of conductors is always zero.¹

3. Ohm's Law: If a steady difference of potential V (in volts) is impressed across a con-

ductor which (a) is held at constant temperature and in which (b) there is no internal emf, $V = rI$ where I is the steady current in amperes which will flow through the conductor and r is the factor of proportionality called the resistance of the conductor. The drop in potential V is therefore equivalent to the drop in potential rI , this latter being called the resistance drop.¹

4. Resistance: The opposition offered by a substance or body to the passage through it of an electric current.²

5. Resistivity: The proportionality factor between current density and electric intensity. A property of a medium having the same value as the resistance measured between opposite faces of a unit cube of the medium, expressed in ohm-units.³

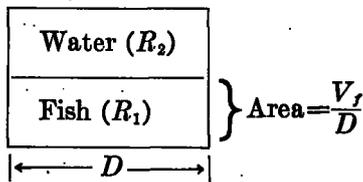
¹ This definition is taken from the following sources: Eshbach, Ovid W. 1955. Handbook of Engineering Fundamentals. 2d ed., John Wiley and Sons, Inc., New York. 1262 pp.

² This definition is taken from the following source: 1946. Webster's Collegiate Dictionary. 2d ed. G. C. Merriam Co., Springfield, Mass. 1,174 pp.
³ Author's definition.

APPENDIX B

Theory and mathematical derivation of the formulas used in computing ρ_f and P_{fv} .

The two-body equations for (ρ_f) and (P_{fv}) were developed in the following manner:



Then, for the total cell resistance R :

$$R = \frac{R_1 R_2}{R_1 + R_2} \quad (1)$$

Where:

$$R_1 = \frac{\rho_f D^2}{V_f} \quad R_2 = \frac{\rho_w D^2}{V_c - V_f}$$

$$V_c = \frac{\rho_w D^2}{R_a} \quad R_2 = \frac{\rho_w D^2 R_a}{\rho_w D^2 - R_a V_f}$$

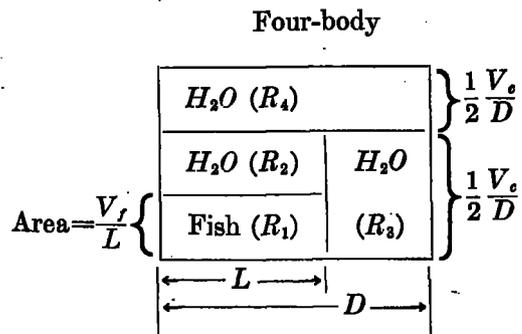
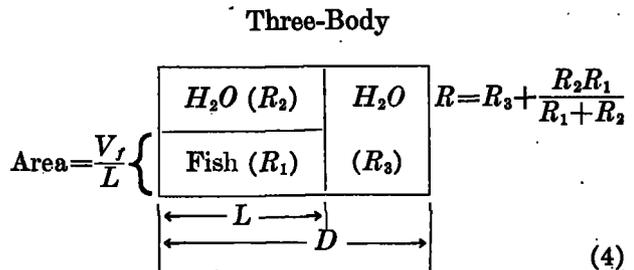
Substituting for R_1 and R_2 in (1) and solving for ρ_f we get:

$$\rho_f = \frac{\rho_w R R_a V_f}{R R_a V_f + \rho_w D^2 (R_a - R)} \quad (2)$$

and for power density:

$$P_{fv} = \left(\frac{E'E}{E'''} \right)^2 \frac{1}{R_1 V_f} = \left(\frac{E'E}{E''' } \right)^2 \frac{1}{\rho_f D^2} \quad (3)$$

The expansion to a three-body and a four-body arrangement was done in the following manner:



$$R = \frac{(R_4) \left(R_3 + \frac{R_1 R_2}{R_1 + R_2} \right)}{R + \left(R_3 + \frac{R_1 R_2}{R_1 + R_2} \right)} \quad (5)$$

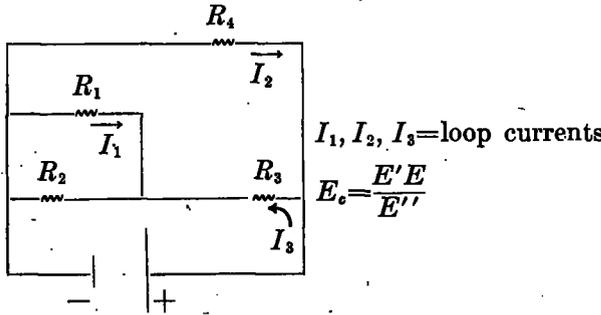
$$R_4 = \frac{\rho_f L^2}{V_f}, \quad R_2 = \frac{\rho_w L}{V_c - V_f} = \frac{2\rho_w L^2 R_a}{(\rho_w L D - 2V_f R_a)}$$

$$R_3 = \frac{\rho_w (D-L)}{V_c} = \frac{2R_a (D-L)}{D}, \quad R_4 = \frac{\rho_w D}{V_c} = 2R_a$$

Substituting into (5) and solving for ρ_f gives:

$$\rho_f = \frac{\rho_w [RR_a V_f L - 2V_f R_a (R_a - R)(D-L)]}{RR_a V_f L - 2V_f R_a (R_a - R)(D-L) + \rho_w D^2 L (R_a - R)} \quad (6)$$

Then, for power density we solve for the current in R_1 in the following network.



$$\begin{vmatrix} I_1 & I_2 & I_3 \\ (R_1 + R_2) & R_2 & R_2 \\ R_2 & (R_4 + R_3 + R_2) & (R_2 + R_3) \\ R_2 & (R_2 + R_3) & (R_2 + R_3) \end{vmatrix} = \begin{matrix} 0 \\ 0 \\ E_c \end{matrix}$$

The power density in the fish is:

$$P_{fv} = I_1^2 R_1 \frac{1}{V_f} \quad (7)$$

Solving for the current I_1 :

$$I_1 = \frac{E_c \begin{vmatrix} R_2 & R_2 \\ (R_4 + R_3 + R_2) & (R_2 + R_3) \end{vmatrix}}{\begin{vmatrix} (R_1 + R_2) & R_2 & R_2 \\ R_2 & (R_4 + R_3 + R_2) & (R_2 + R_3) \\ R_2 & (R_2 + R_3) & (R_2 + R_3) \end{vmatrix}} = E_c \frac{R_{21}}{\Delta R}$$

Then:

$$P_{fv} = E_c^2 \left(\frac{R_{21}}{\Delta R} \right)^2 \frac{R_1}{V_f} \quad (8)$$

Expanding the determinant factors and substituting for the resistance values in the resulting equation we obtain the following:

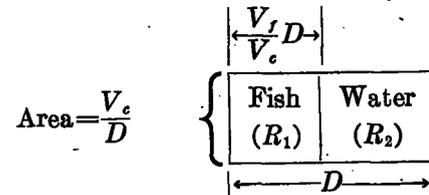
$$P_{fv} = \left(\frac{EE'}{E''} \right)^2 \left(\frac{\rho_w D}{\rho_w \rho_f D^2 L + 2R_a V_f (D-L)(\rho_w - \rho_f)} \right)^2 L^2 \rho_f \quad (9)$$

The simplicity of the resulting power density equation was achieved by the manner in which the dimensions of the individual volume elements were chosen. The geometric similarity between these elements reduced the complexity, indicated by the expansion of (8), to the simplicity of equation (9). Such a simplification is desirable for the practicability of processing data. However, it can be expected to limit the range of usefulness of the equation.

In the course of our studies, there was reason to reduce the water resistivity to a value below that obtained for the fish. We did this to check the results of previous measurements. When we attempted to evaluate our data, we found that the measured parameters forced us to work in and near a region of discontinuity that was a characteristic of our equation for (ρ_f) . This condition occurred when, for (6):

$$RR_a V_f L - 2V_f R_a (R_a - R)(D-L) + \rho_w D^2 L (R_a - R) = 0$$

To avoid this difficulty, we resolved our volume elements in a different manner for this region of operation. Hence, for the two-body case:



$$R = R_1 + R_2$$

$$R_1 = \frac{\rho_f \frac{V_f}{V_c} D}{\frac{V_c}{D}} = \frac{\rho_f V_f R_a^2}{\rho_w^2 D^2}$$

$$R_2 = \frac{\rho_w \left(D - \frac{V_f}{V_c} D \right)}{\frac{V_c}{D}} = R \left(1 - \frac{V_f R_a}{\rho_w D^2} \right)$$

Substituting and solving for ρ_f we get:

$$\rho_f = (\rho_w^2) \left(\frac{D^2}{R_a^2 V_f} \right) (R - R_a) + \rho_w \quad (10)$$

And:

$$P_{fv} - \left(\frac{E'E''}{E'''} \right)^2 \left(\frac{R_a}{R} \right)^2 \frac{\rho_f}{\rho_w^2 D^2} \quad (11)$$

Notice that for equation (10), there exists no point of discontinuity, as was present in equation (6).

Having derived these equations, we determined that they satisfied our requirements by using the following methods:

1. If the fish model is electrically homogeneous and has a characteristic resistivity ρ_f , then when $\rho_w = \rho_f$, $R_a = R$. Observing equations (2), (6), and (10), we see that in each case, where $R_a = R$, this condition is satisfied.

2. If the resistance R were measured continuously as ρ_w was varied from $\rho_w = 0$ to $\rho_w = \infty$, we would expect the functions R and $\frac{\delta R}{\delta \rho_w}$ to be continuous over the range of variation. This is because we consider our cell to contain linear, bilateral resistive elements. To check the fulfillment of this condition, we examined the ratio $\frac{1}{R} \frac{\delta R}{\delta \rho_w}$ at the point where $\rho_w = \rho_f$. If the condition is satisfied, then:

$$\left[\frac{1}{R_{2s}} \frac{\delta R_{2s}}{\delta \rho_w} = \frac{1}{R_{4P}} \frac{\delta R_{4P}}{\delta \rho_w} \right] @ \rho_w = \rho_f$$

Where:

R_{2s} = the two-body series function

R_{4P} = the four-body parallel function

Using equation (6) and solving for R as a function of ρ_w , we get:

$$R = \frac{A \rho_w B \rho_f + C(\rho_w - \rho_f)}{B \rho_f + (C + F)(\rho_w - \rho_f)} \quad (12)$$

Where:

$$A = \frac{D^2}{V_c}, B = V_c D^2 L, C = 2V_f D^2 (D - L), F = V_f L D^2$$

And:

$$\frac{\delta R}{\delta \rho_w} \frac{A(C \rho_w + B \rho_f) + AC(\rho_w - \rho_f)}{B \rho_f + (F + C)(\rho_w - \rho_f)} - \frac{[AB \rho_f \rho_w + AC(\rho_w^2 - \rho_f \rho_w)](F + C)}{[B \rho_f + (F + C)(\rho_w - \rho_f)]^2} \quad (13)$$

When: $\rho_w = \rho_f$ equations (12) and (13) reduce to:

$$R = \rho_f A = \rho_f \frac{D^2}{V_c}$$

And:

$$\frac{\delta R}{\delta \rho_w} = A \left(1 - \frac{F}{B} \right) = \frac{D^2}{V_c} \left(1 - \frac{V_f}{V_c} \right)$$

Therefore:

$$\left(\frac{1}{R_{4P}} \frac{\delta R_{4P}}{\delta \rho_w} \right) = \frac{1}{\rho_f} \left(1 - \frac{V_f}{V_c} \right) \quad (14)$$

Next, we solve equation (10) for R as a function of ρ_w and obtain the following:

$$R = \frac{D^2 V_f}{V_c^2} \left[\rho_w \frac{V_c}{V_f} - (\rho_w - \rho_f) \right] \quad (15)$$

And:

$$\frac{\delta R}{\delta \rho_w} = \frac{D^2}{V_c} \left(1 - \frac{V_f}{V_c} \right)$$

When:

$\rho_w = \rho_f$ equation (15) reduces to:

$$R = \frac{\rho_f D^2}{V_c}$$

Then:

$$\left(\frac{1}{R_{2s}} \frac{\delta R_{2s}}{\delta \rho_w} \right) = \frac{1}{\rho_f} \left(1 - \frac{V_f}{V_c} \right) \quad (16)$$

Comparing (16) with (14) we see that our requirement is satisfied.

It should be noted that in equations (2) through (11) the parameter V_c has been eliminated. This was done because the cell boundaries at the ends of the cells were not clearly defined owing to the different grid structures used. It was hoped that, by allowing this degree of freedom, the errors caused by this effect would be minimized.

APPENDIX C

Derivation and explanation of the relationship between P_{fs} and P_{ws} :

To relate our results to the electrical conditions present when the fish is not confined in a cell, we used the following procedure:

In the four-body configuration, the power density in the water of R_4 is:

$$P_{ws} = \left(\frac{EE'}{E''} \right)^2 \frac{1}{\rho_w D^2} \quad (1)$$

From this:

$$\left(\frac{EE'}{E''} \right)^2 = P_{ws} \rho_w D^2 \quad (2)$$

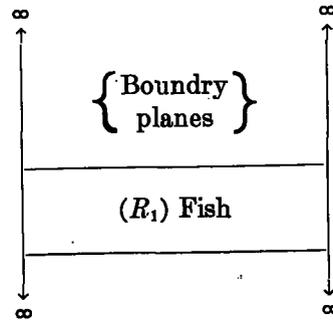
Substituting this value into equation (9) of Appendix B and expanding V_c to infinity (the expansion was carried out holding $\frac{D^2}{V_c}$ constant), we obtain the following result:

$$P_{ws} = P_{fs} \frac{\rho_f}{\rho_w} \frac{V^2}{\rho_w} = \lim_{V_c \rightarrow \infty} P_{ws}$$

Or:

$$P_{ws} = \rho_f P_{fs} = V^2 \quad (3)$$

By expanding V_c to infinity our volume configuration is as pictured below:



This illustration demonstrates the greatest weakness in our resolution model. That is, when we expand our configuration, our boundaries no longer enclose finite regions and therefore exhibit an impossible field condition. For correction of equation (3) and elimination of the effects of this property, it appears that it will be necessary to multiply (3) by some empirical function (f) of ρ_w and ρ_f .

Thus:

$$\rho_w P_{ws} = m^2 \rho_f P_{fs} = V^2$$

Where:

$$m = f(\rho_w \rho_f)$$

This empirical function will have to be determined by further experimentation.

APPENDIX D

Tables A-1: How derived formulas were applied, and A-2: A sample of some of the numerical values of ρ_f and P_{fs} that were obtained.

TABLE 1.—Original measurement data

Fish number	Polarity orientation	E' (volts)	E'' (volts)	E (volts)	I (μ amps)	P_w (ohm cm.)	Water temp. ($^{\circ}$ F.)	V_f (cc.)	D (cm.)	Date
6a	Negative	2.3	3.18 2.77 2.37	1.70 1.48 1.30	80 70 60	29,250	47.0	15.3	15.8	1/5/59

TABLE 2.—Calculation sample (ρ_f)

Fish number	R_s (ohms) ¹	R (ohms) ¹	$R_s - R$ (ohms)	L (cm.) ²	$D - L$ (cm.)	A ($\times 10^{11}$) ³	B ($\times 10^{11}$) ⁴	$A - B$ ($\times 10^{11}$)	C ($\times 10^{11}$) ⁵	ρ_f (ohm cm.) ⁶
6a	35000	20000	15000	11.6	4.20	1.24	0.675	0.565	12.72	1,244

¹ R_s and R (from graph)

² $L = 1/3 V_f + 6.5$ (from graph)

³ $A = R R_s V_f L$

⁴ $B = 2 V_f R_s (R_s - R) (D - L)$

⁵ $C = \rho_w L D^2 (R_s - R)$

⁶ $\rho_f = \frac{\rho_w (A - B)}{A - B + C} = \frac{(29,250)(.565)}{.565 + 12.72} = 1,244$ ohm cm.

TABLE 3.—Calculation sample (P_{1v})

Fish number	E^2 (volts) ¹	D ($\times 10^3$)	G ($\times 10^{10}$) ²	H ($\times 10^3$) ³	$D-L$ (cm.)	$\rho_w - \rho_f$ (ohm cm.)	F ($\times 10^{-6}$) ⁴	F^2 ($\times 10^{-12}$)	$L^2 \rho_f$ ($\times 10^8$)	P_{1v} (μw) ⁵
6a.....	1.54	4.62	10.55	10.71	4.20	28006	2.00	4.00	1.67	1.03

¹ $E_c^2 = \left(\frac{EE'}{E''}\right)^2$

² $G = \rho_f \rho_w D^3 L$

³ $H = 2R_s V_f$

⁴ $F = \frac{\rho_w D}{G + H(D - L)(\rho_w - \rho_f)}$

⁵ $P_{1v} = (E_c^2)(F^2)(L^2 \rho_f) = (1.54)(4.00)(1.67) = 1.03$

TABLE 4.—A sample of the numerical values obtained for fish resistivity (ρ_f) and reaction power density (P_{1v}) using our derived equations

Fish number	Polarity orientation (fish facing)	Water temp. ($^{\circ}$ F.)	Fish volume (cc.)	ρ_f (ohm cms.)	P_{1v} ($\mu w/cc.$)
1.....	—	49.0	5.9	1979	1.26
2.....	—	49.0	6.0	1446	1.19
3.....	+	49.0	5.3	1677	1.20
4.....	+	49.0	8.0	1092	0.94
5.....	+	49.5	6.1	1832	0.88
6.....	+	49.5	7.1	1119	1.00
7.....	—	49.0	9.0	1030	0.83
8.....	—	49.0	8.0	1000	0.50
9.....	—	49.0	6.5	1800	0.74
10.....	+	49.5	6.0	1470	0.96
11.....	+	49.5	6.2	790	1.39
12.....	—	49.5	5.4	1330	0.52

USE OF PLANT HEMAGGLUTININS IN SEROLOGICAL STUDIES OF CLUPEOID FISHES

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ABSTRACT

As part of a general immunogenetic study of marine animals, the use of hemagglutinins in seed extracts has been investigated. Individual variations were found in reactions of alewife, blueback herring, and Atlantic herring erythrocytes with certain extracts, particularly those of lima beans. Reactions of Atlantic

herring cells with one lima bean extract paralleled those found with certain rabbit antisera. Evidence was obtained for heterogeneity among four spawning populations of alewives with quantitative tests of erythrocyte antigens using an extract of one variety of lima bean.

Plant extracts, particularly those of legume seeds, have been useful in differentiating human erythrocyte antigens (Boyd and Reguera, 1949; Makela, 1957; Boyd, Everhart, and McMaster, 1958; Bird, 1959). This work has engendered interest in possible use of such extracts for blood-grouping studies of other animal species (Bird, 1953). The definitive separations of antigens possible with plant extracts suggest that plant hemagglutinins or lectins may prove useful in systematic and racial studies of fish, as an adjunct to current immunogenetic studies using sera and antisera of animal origin. Several laboratories are presently investigating the use of plant agglutinins in studies of teleosts, and Sprague (1961) has reported their use in studies of oceanic skipjack.

This paper describes the use of selected plant hemagglutinins to distinguish individual differences within species of clupeoid fishes and to characterize spawning populations of alewives.

METHODS

Blood samples were obtained from five species of clupeoid fishes (alewife, *Alosa pseudoharengus*;

blueback herring, *Alosa aestivalis*; American shad, *Alosa sapidissima*; Atlantic herring, *Clupea harengus*; and Atlantic menhaden, *Brevoortia tyrannus*) taken in commercial trap nets at Belford, N.J., in April of 1960 and 1961. All fish were adults, although all species were not in the same condition of maturity in April. Blood samples from prespawning populations of alewives were obtained at Narragansett, R.I., in May, 1961; Bourne, Mass., in May, 1961; Damariscotta Mills, Maine, in May, 1961; and Tusket, Nova Scotia, in June, 1961. All samples were from upstream migrants, taken shortly after they had left the sea. Fish were bled by heart puncture with Pasteur pipettes. Whole-blood samples were refrigerated overnight, and serum decanted for other studies. Erythrocytes were washed from clots as needed, washed twice in 1.4 percent saline solution, and used in approximately 5 percent suspensions for testing.

Seeds from several species of Leguminosae were used: lima bean (*Phaseolus limensis*), lentil (*Lens culinaris*), and garbanzo bean (*Cicer arietinum*). Extracts were prepared by addition of 10 ml. of 1.4 percent saline to each gram of powdered seeds. After extraction for 3 hours at 37° C. and over-

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night at 4° C. the mixture was filtered and centrifuged. The supernatant fluid (the extract) was frozen in 3 ml. aliquots until use.

Tube agglutination tests used 0.2 ml. extract dilution and 0.05 ml. cell suspension. Presence and degree of reaction were observed macroscopically after 1 hour incubation at room temperature and 30 seconds centrifugation. Results were recorded conventionally as (++++) complete agglutination, (+++) strong agglutination with a few large clumps, (++) moderate agglutination with numerous smaller clumps, (+) weak agglutination with many very small clumps, and (-) no agglutination. Cells were tested within 72 hours from the time the sample was taken.

Absorptions of extracts in an attempt to obtain specific reagents were carried out with washed cells. One part extract was added to one part packed cells. The mixture was shaken briefly to suspend the cells and incubated at room temperature for varying periods up to 2 hours. Absorbing cells were then settled by centrifugation, and the supernatant absorbed extract tested with a previously removed aliquot of the cells used for absorbing.

RESULTS

Individual Variations in Erythrocyte Antigens

A battery of extracts, including several varieties of lima beans, was used to determine whether individual differences could be detected among fish of each of the species studied. Tests with cells of 10 individuals from each of the five clupeoid species produced results shown in table 1.

Most of the extracts agglutinated herring cells, some extracts agglutinated alewife and blueback cells, only large lentil extract agglutinated men-

haden cells, and none of the extracts agglutinated shad cells.

Several extracts gave sufficient distinction among individuals to suggest further study. Individual differences were detected in alewives, blueback herring, and Atlantic herring with hemagglutinins from lima bean varieties 5, 21, 92, 106, and 121, as well as large lentils. Lima bean variety 21, provided in quantity by J. A. Harding, University of California, was selected to determine the extent of individual differences in the three species. Twenty-five individual blood samples from each species were tested, and examples of results obtained are presented in table 2.

Using three doubling dilutions of lima bean variety 21 extract, some individuals were positive at all dilutions, while others were negative at the same dilutions. Most definitive separation of individuals occurred in Atlantic herring. Possible subtypes or dosage effects may be indicated by differences in reactivity of individual fish.

Reactions of Atlantic herring cells with extract 21 were similar to those with certain dilutions of a rabbit antiherring serum (GBH5R), as illustrated in table 3. Since rabbit antisera such as GBH5R have been sources of reagents for detection of erythrocyte antigens of herring, particularly the C antigen (Sindermann and Mairs, 1959; Sindermann, 1961), the similarity of reactions suggested that certain extracts might be useful as substitutes for antisera. A comparison of 70 individual herring blood samples whose C antigens had been previously determined disclosed that C-negative fish were negative at all dilutions of extract 21 and that C-positive fish were all positive with extract 21.

TABLE 1.—Reactions of erythrocytes from individual fish of five clupeoid species with seed extracts

Seed extract	Cells																														
	Alewife										Blueback herring										American shad										
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	
Lima 121.....	+	+	++	+	+	+	++	+	++	-	-	-	-	++	-	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-
106.....	-	-	+	-	-	-	++	+	++	-	-	-	-	++	-	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-
123.....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75.....	+++	-	++	++	-	+	++	+	++	-	-	-	-	++	-	-	++	-	++	++	-	-	-	-	-	-	-	-	-	-	-
5.....	+	-	++	++	-	+	++	+	++	-	-	-	-	++	-	-	++	-	++	++	-	-	-	-	-	-	-	-	-	-	-
21.....	+	-	+	+	+	+	++	+	++	-	-	-	-	++	-	-	++	-	++	++	-	-	-	-	-	-	-	-	-	-	-
92.....	+	-	+	+	+	+	++	+	++	-	-	-	-	++	-	-	++	-	++	++	-	-	-	-	-	-	-	-	-	-	-
Garbanzo bean.....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Large lentil.....	++	-	-	+	+	++	+	+	-	-	+	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Small lentil.....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 1.—Reactions of erythrocytes from individual fish of five clupeoid species with seed extracts—Continued

Seed extract	Cells																			
	Atlantic menhaden										Atlantic herring									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Lima 121	-	-	-	-	-	-	-	-	-	-	+++	++++	++++	++++	+++	+++	+++	+++	+++	+++
106	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
128	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
75	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
5	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
21	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
92	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Garbanzo bean	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Large lentil	+	++	+	+++	+	+	++	+++	+	+	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Small lentil	-	-	-	-	-	-	-	-	-	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++

TABLE 2.—Examples of reactions of alewife, blueback herring, and Atlantic herring erythrocytes with three dilutions of lima bean variety 21

Lima bean extract	Alewife cells									
	11	12	13	14	15	16	17	18	19	20
21-undiluted	++	++	+	-	+++	++	-	++	++	-
1:1	+	+	-	-	++	+	-	++	+	-
1:2	+	-	-	-	+	-	-	+	-	-
Lima bean extract	Blueback herring cells									
	11	12	13	14	15	16	17	18	19	20
21-undiluted	+	+	-	-	+++	+++	+	-	+	-
1:1	-	+	-	-	++	++	-	-	-	-
1:2	-	-	-	-	+	+	-	-	-	-
Lima bean extract	Atlantic herring cells									
	11	12	13	14	15	16	17	18	19	20
21-undiluted	++++	++++	+++	++++	-	++++	+++	++	++++	++++
1:1	+++	+++	++	+++	-	+++	++	+	+++	+++
1:2	++	++	+	++	-	++	+	-	++	++

TABLE 3.—Examples of reactions of Atlantic herring erythrocytes with plant hemagglutinins (extract 21) and rabbit antisera (GBH5R)

Reagent	Atlantic herring cells									
	11	12	13	14	15	16	17	18	19	20
Extract 21:										
1:1	+++	++++	+++	+++	-	++++	+++	+	++++	++++
1:2	++	+++	++	++	-	+++	++	-	+++	+++
1:4	+	+	-	-	-	+	-	-	+	+
Rabbit antiherring serum (GBH5R):										
1:128	++++	++++	+++	++++	-	+++	+++	++	++++	+++
1:256	+++	+++	++	+++	-	++	++	+	+++	++
1:512	++	++	+	++	-	+	+	-	++	+

Quantitative Studies of Agglutination Reactions in Alewife Spawning Populations

In view of the marked individual differences in reactions of alewife erythrocytes with seed extracts, particularly with lima bean variety 21, widely separated spawning populations were tested for reactions with three dilutions of this extract (1:1, 1:2, 1:4). Numbers of fish negative at all dilu-

tions and positive at all dilutions are presented in table 4. A scoring system comparable to that used by Race, Sanger, and Lehane (1953) and Ridgway, Cushing, and Durall (1958), involving addition of reaction scores of individual fish, was also used. Average scores for each spawning population are presented in figure 1. A test for independence of scores (Snedecor, 1956), pooling

TABLE 4.—Individual reactions of alewives from four spawning populations with lima bean variety 21 extract

Location	Number sampled	Number positive at all dilutions	Number negative at all dilutions
Narragansett, R.I.-----	200	64 (32%)	66 (33%)
Bourne, Mass.-----	200	112 (56%)	28 (14%)
Damariscotta Mills, Maine-----	190	7 (4%)	112 (59%)
Tusket, Nova Scotia-----	73	12 (16%)	33 (45%)

frequencies of test scores of six and more (table 5) indicated that the distribution of scores was dependent on the population studied (chi square = 180.2, d.f. = 18, $p < .001$). Only four out of many possible spawning populations were sampled, and a more definitive picture of the discreteness of spawning groups may emerge as more populations are studied.

TABLE 5.—Frequencies of agglutination scores in four alewife spawning populations

Scores	Numbers of fish				Total
	Tusket, Nova Scotia	Damariscotta Mills, Maine	Bourne, Mass.	Narragansett, R.I.	
0-----	33	112	28	66	239
1-----	15	41	17	27	100
2-----	11	22	31	30	94
3-----	3	6	15	22	46
4-----	1	7	20	14	42
5-----	6	1	44	15	66
6 or more-----	4	1	45	26	76
Total-----	73	190	200	200	663

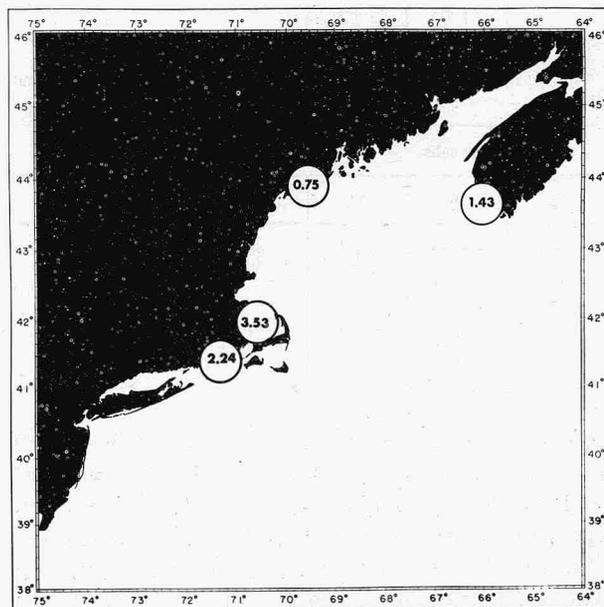


FIGURE 1.—Average reaction scores of four alewife spawning populations with lima bean variety 21 extract.

DISCUSSION

Immunogenetic studies of fishes have advanced rapidly during the past decade, so that quantitative information has already accumulated for subpopulations of several species (Ridgway, Cushing, and Durall, 1958; Sindermann and Mairs, 1959; Suzuki, Morio, and Mimoto, 1959). There must be, however, continuous exploration of new techniques, even as quantitative studies proceed, since adequate serological characterization of subpopulations depends on description and use of several different factors or blood-group antigens. An examination of the possible utility of plant hemagglutinins in serological research constitutes a phase of such exploratory work.

It is premature to attempt genetic explanations for the results of the present work, but the fact that reactions of clupeoid erythrocytes with certain extracts paralleled those obtained with specific rabbit antisera suggests that discrete antigenic factors are involved in the agglutinations. Also, the distributions of reaction scores for several alewife spawning populations lacked the continuous gradation characteristic of polygenic inheritance, but resembled distributions obtained with a series of alleles at a single locus. Individual differences in clupeoid species have been recognized, and this is significant, but information from fractionation of extracts, or from study of known crosses, should precede proposals of genetic systems that may control such differences.

There are advantages and difficulties in the use of plant extracts. Many varieties of many species of plants may be tested, relatively easily and inexpensively. Once a satisfactory variety has been found, any desired amount of extract may be prepared, whereas the amounts of specific antisera are dependent on the blood volume of the experimental animal used. Specific reagents for detection of individual antigenic variation are usually derived from absorptions of sera or antisera. Plant extracts have thus far proved resistant to normal methods of absorption with clupeoid fish cells. Use of unabsorbed extracts may provide valuable information, but further attempts to refine the extracts as reagents should be carried out. Also, the nature of the reaction between animal erythrocyte and extract that produces often highly specific agglutination is poorly

understood, and requires further study. Despite such limitations, plant hemagglutinins offer a promising approach to recognition and characterization of subpopulations of fishes. Plant extracts can form part of a wide spectrum of serological tools available to fishery research.

SUMMARY

Erythrocytes of the five dominant clupeoid species of the western North Atlantic: alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), American shad (*Alosa sapidissima*), Atlantic menhaden (*Brevoortia tyrannus*), and Atlantic herring (*Clupea harengus*) were studied for reactivity with plant extracts. Individual variations were found in reactions of alewife, blueback herring, and Atlantic herring erythrocytes with hemagglutinins present in seed extracts. Several varieties of lima beans provided clear differentiation of individuals. Evidence for population heterogeneity was obtained when blood samples from four spawning populations of alewives were tested against an extract of one variety of lima bean.

ACKNOWLEDGMENTS

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LITERATURE CITED

- BIRD, G. W. G.
1953. Some interrelationships of the erythrocytes of various species with plant agglutinins. *Nature*, vol. 172, no. 4374, pp. 401-402.
- BIRD, G. W. G.
1959. Haemagglutinins in seeds. *British Medical Bulletin*, vol. 15, no. 2, pp. 165-168.
- BOYD, WILLIAM C., and ROSE M. REGUERA.
1949. Hemagglutinating substances for human cells in various plants. *Journal of Immunology*, vol. 62, no. 3, pp. 333-339.
- BOYD, WILLIAM C., DONALD L. EVERHART, and MARJORIE N. McMASTER.
1958. The anti-N lectin of *Bauhinia purpurea*. *Journal of Immunology*, vol. 81, no. 5, pp. 414-418.
- MAKELA, OLAVI.
1957. Studies on hemagglutinins of leguminosae seeds. *Annales Medicine Experimentalis et Biologiae Fenniae (Helsinki)* vol. 35, suppl. II, 133 pp.
- RACE, R. R., R. SANGER, and D. LEHANE.
1953. Quantitative aspects of the blood-group antigen Fy^a. *Annals of Eugenics*, vol. 17, pp. 255-266.
- RIDGWAY, G. J., J. E. CUSHING, and G. L. DURALL.
1958. Serological differentiation of populations of sockeye salmon, *Oncorhynchus nerka*. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 257, 9 pp.
- SINDERMANN, CARL J.
1961. Serological techniques in fishery research. *Transactions Twenty-sixth North American Wildlife and Natural Resources Conference*, 1961, pp. 298-309.
- SINDERMANN, CARL J., and DONALD F. MAIRS.
1959. A major blood group system in Atlantic sea herring. *Copeia*, 1959, no. 3, pp. 228-232.
- SNEDECOR, GEORGE W.
1956. *Statistical methods*. 5th edition. 534 pp. Iowa State College Press, Ames, Iowa.
- SPRAGUE, LUCIAN M.
1961. Erythrocytes of the oceanic skipjack (*Katsuwonus pelamis*) recognized by phytoagglutinins. *Genetics*, vol. 46, no. 8, p. 901.
- SUZUKI, AKIMI, TADAO MORIO, and KOICHI MIMOTO.
1959. Serological studies of the races of tuna. II. Blood group frequencies of the albacore in Tg system. Nankai Regional Fisheries Research Laboratory, Report No. 11, pp. 17-23.

SOME ASPECTS OF THE OCEANOGRAPHY OF LITTLE PORT WALTER ESTUARY, BARANOF ISLAND, ALASKA

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ABSTRACT

In connection with studies on the survival of the pink salmon, *Oncorhynchus gorbuscha*, certain aspects of the oceanography of Little Port Walter estuary were investigated. Efforts were directed principally toward studies of the patterns and mechanisms of circulation; water exchange; flushing; and temporal and spatial distribution of salinity, temperature, transparency, and dissolved oxygen.

A shallow sill separates the estuary into two basins, the innermost possessing the structural and three-layered circulatory characteristics of a fiord. A net upbay movement of intermediate and deep water responded to a salt pump activated by the inflow from the estuary's single tributary stream, Sashin Creek. The

During the spring and summer of 1959, studies were made of certain aspects of the oceanography of the estuary of Little Port Walter, Alaska. These studies were supported by the Bureau of Commercial Fisheries and were based at the Biological Field Station at Little Port Walter. They constituted part of a series of investigations on the biology of pink salmon, *Oncorhynchus gorbuscha*. Little Port Walter estuary is the site of an annual spawning run of this commercially important species, and knowledge of environmental conditions within the estuary is pertinent to investigations of their biology.

The oceanographic studies were designed to obtain information on the following: spatial distribution of temperature and salinity, at high

rate of pumping increased materially during periods of heavy precipitation. The pattern of circulation in a shallow top layer containing the fresh water was strongly affected by the discharge from Sashin Creek but was not greatly affected by winds, since the estuary is well sheltered.

The average flushing time for the fresh water of the inner basin, computed by the method of Ketchum, Redfield, and Ayers (1951), showed a correlation with the rate of stream discharge: flushing time decreased as stream discharge increased. The total water exchange between the inner and outer basins varied in magnitude with the monthly tide range and fresh water runoff and showed some response to wind.

and low tides, under various conditions of fresh-water runoff; temporal distribution of temperature, salinity, dissolved oxygen, and transparency at selected reference stations; circulation and flushing of the estuary and the relation of these factors to the discharge of Sashin Creek; and total water transport into and out of the estuary. The methods of studying these various features and parameters are presented in the discussion of methods of investigation and observation.

We were not equipped to operate in adjacent large open waters, although observations there would have been desirable and helpful. Work was therefore limited to the estuary.

The estuary is located near the tip of Baranof Island in southeastern Alaska, about 40 airline miles from Sitka. A stream, Sashin Creek, enters the inner end over a small waterfall which

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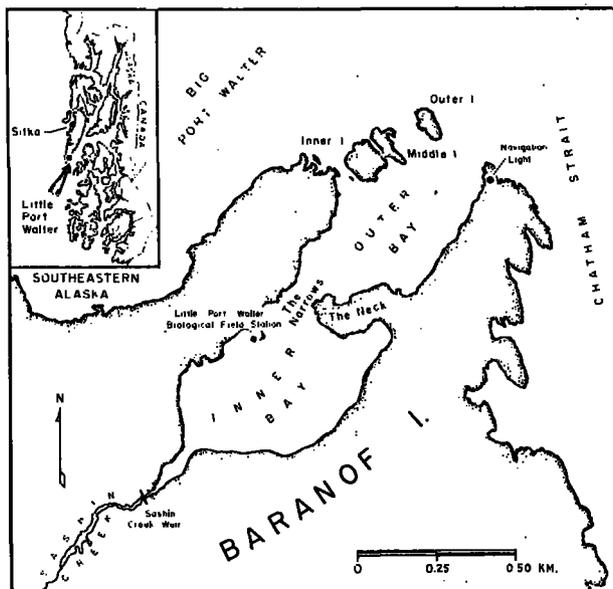


FIGURE 1.—Little Port Walter estuary, Baranof Island, southeastern Alaska.

marks the limit of salt-water intrusion. At its seaward end the estuary connects with Chatham Strait and Port Walter Bay (fig. 1).

The distance from the waterfall to Chatham Strait is 1.5 kilometers (km.); the distance across the widest part of the estuary is about 0.4 kilometer (km.). A peninsula, The Neck, extends from the south shore and divides the estuary into two bays of approximately equal area, Inner Bay and Outer Bay. These are connected by a short channel, the Narrows, between The Neck and the north shore.

The maximum observed depth of Inner Bay was 21 meters (m.) and of Outer Bay, 44 m. (referred to mean lower low water).¹ The depth at The Narrows, where a shallow sill is present, was almost 5 m. Because of this sill, Inner Bay has the structural characteristics of a fiord; Outer Bay does not, since it connects directly with Chatham Strait through a channel approximately 36 m. deep.

Three small rocky islands partially separate Outer Bay from Port Walter Bay to the north. Proceeding in a seaward direction, they are Inner, Middle, and Outer Islands. Three shallow channels connect with Port Walter Bay, but the channel between Inner and Middle Islands floods

¹ In this discussion, all depths to bottom are referred to the datum of the U.S. Coast and Geodetic Survey: mean lower low water (U.S. Coast and Geodetic Survey, 1959).

only during spring tides and has no functional significance.

The basins of both Inner and Outer Bays are steep sided, with practically no shelf formation except for a small shoal area at the head of Inner Bay. The surface area of the estuary consequently undergoes little change between low and high waters. Basins of this type are characteristic of Baranof Island as well as much of the rest of southeastern Alaska. The coastline is frequently indented by long narrow, deep embayments from which mountains rise sharply to heights of several thousand feet.

Tides in the estuary exhibit the exaggerated diurnal inequality typical of the west coast of North America. The range of spring tides at Little Port Walter was as much as 4.6 m., the range of neap tides less than half of this. Within the estuary the tide has the characteristics of a standing wave, with high and low slack waters occurring at about the same time over the entire basin.

The coastal region of southeastern Alaska is a zone of heavy precipitation. Little Port Walter receives an average of 221 inches per year.

John C. Ayers gave much valuable advice during the writing of this paper.

METHODS OF INVESTIGATION AND OBSERVATION

CRUISES

Five cruises were conducted to obtain basic oceanographic data over the entire estuary during different conditions of fresh-water runoff. Cruises were made at slack before ebb plus or minus one-half hour and at slack before flood plus or minus one-half hour. Eighty-nine stations were occupied during three cruises at slack before ebb, and 62 during two cruises at slack before flood. Station positions (fig. 2) were the same for all five cruises except where indicated. To show the stage of tide on which a particular cruise was conducted, cruise numbers bear the prefix "H" for slack before ebb and "L" for slack before flood. During each daily cruise period, as many stations as possible were visited at both slacks so that "H" and "L" cruises bearing the same number were conducted during the same time interval. Cruises H-1 and L-1 were made between June 25 and July 2, cruise H-2 between July 7 and 29,

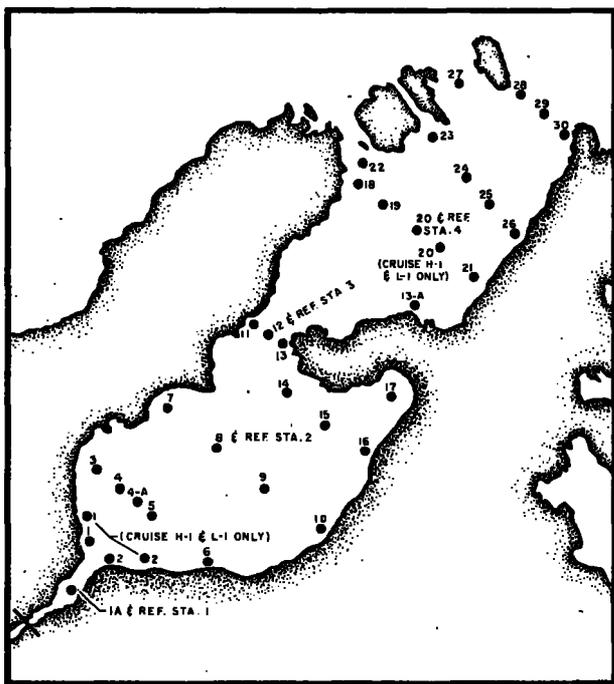


FIGURE 2.—Numbered stations for study of Little Port Walter estuary. Except where indicated, numbers refer to stations of cruises H-1, L-1, H-2, H-3, and L-3.

and cruises H-3 and L-3 between July 29 and August 4. Cruise L-2 was missed because of a series of boat engine failures. Cruise H-2 ended when about two-thirds completed because of rapidly changing conditions in the estuary, brought on by heavy rains.

At each of the 151 stations water samples for salinity determinations were obtained by Kemmerer bottle at selected depths, temperature was determined by bathythermograph, transparency was measured by white Secchi disk, and wind speed and direction and weather conditions were recorded. Wind speed was estimated, according to the Beaufort scale, from the condition of the water surface; whereas direction was estimated by reference to the geographical orientation of the axis of the estuary. Salinity was determined in the laboratory at the field station by hydrometry, and the results expressed in grams per kilogram (parts per thousand: ‰). Data from the cruise stations are on file at the laboratory at the Little Port Walter Field Station.

ANCHOR STATIONS

In addition to the stations included in the five cruises, anchor stations were occupied in The

Narrows, in the two functional channels between Outer Bay and Port Walter Bay, and in the entrance to Chatham Strait. These stations furnished data on current profiles and water transport. At anchor stations hourly determinations of the current profile from surface to bottom were obtained throughout the complete tidal cycle with a von Arx current meter (von Arx, 1950). With each lowering of the meter, water samples, temperature determinations, and wind and weather observations were obtained in the same manner as described for cruise stations.

Data from all anchor stations are on file at the station laboratory.

REFERENCE STATIONS

To obtain knowledge of temporal changes in the parameters studied, four reference stations (fig. 2) were occupied each week. Stations 1 and 2 were located in Inner Bay—station 1 just below the mouth of Sashin Creek and station 2 in the deep part of Inner Bay. Station 3 was over the sill in The Narrows. The three stations were occupied on April 3 and thereafter at intervals of approximately 1 week until August 21. Salinity, temperature (by resistance thermometer), and transparency were determined, and wind and weather were noted. Dissolved oxygen was measured on June 6, and weekly from July 11 to August 21 at stations 2 and 3 only. On July 11 reference station 4 was added. Located in the center of Outer Bay at the deepest part, it was occupied weekly until August 21. The observations were the same as those made at stations 2 and 3, except that transparency was not measured, and temperature was measured by a bathythermograph which was calibrated against the resistance thermometer. Reference stations were always visited at slack before ebb, plus or minus one-half hour. The remaining data are on file at the station laboratory.

MEASURING RUNOFF

Except during periods of intense precipitation, the entire fresh-water runoff into the bay was from Sashin Creek. This stream was not gaged, but it was possible to estimate its volume of flow. From early spring until July 20, the stream was dammed near its mouth by a fish weir with two rectangular spillways. A recording gage continuously monitored the level of the water impounded by the weir. The gage record gave the head of water



FIGURE 3.—Bathymetry in feet of Little Port Walter estuary, based on sonic soundings corrected to datum.

over the spillways, and from this the velocity of effluent through the spillways was computed by:

$$v = \sqrt{2gh}$$

where g was the acceleration due to gravity and h the head of water. Multiplying the velocity of

effluent by the cross-sectional area of the spillways gave the volume of flow.

After the dam was removed on July 20, volume of flow was calculated by the method of Robins and Crawford (1954), utilizing cross-sectional area and timed observations of floats where the stream flowed through the open weir.

BATHYMETRY

Since navigation charts give only a sketchy bathymetry of the estuary a bathymetric chart was constructed (fig. 3). Sounding transects were made with a battery-powered portable recording echo sounder by running the boat at constant speed from one side of the estuary to the other between objects on shore whose positions were charted. Depths were corrected to datum before contouring, using predicted water levels for the days when the sounding operations were made (U.S. Coast and Geodetic Survey, 1959). These corrections are only approximate, their accuracy being limited by differences that may have existed between predicted and actual water levels.

METEOROLOGY

Meteorological data collected daily at Little Port Walter were maximum and minimum air temperatures and precipitation. These data, along with daily observed maximum and minimum temperatures of Sashin Creek, are presented graphically in figure 4.

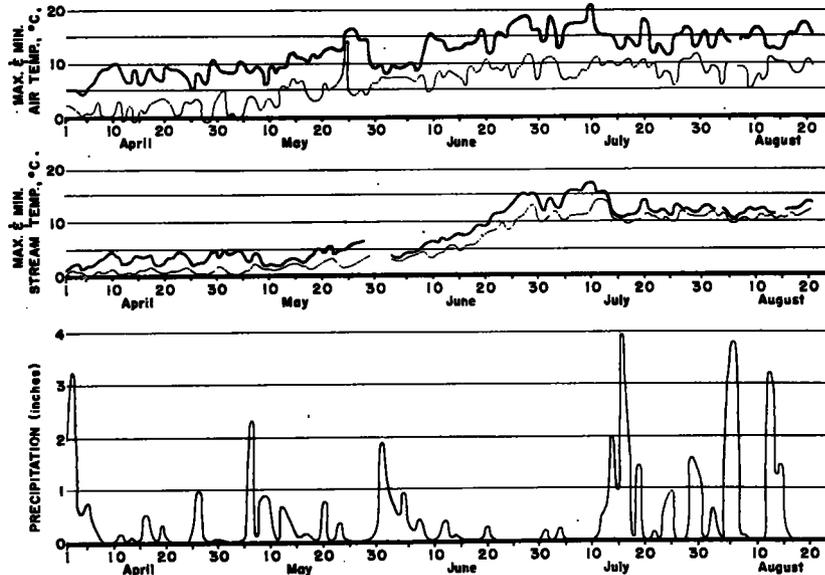


FIGURE 4.—Regimes of air temperature, stream temperature, and precipitation at Little Port Walter, April 1 to August 21, 1959.

Air temperature was measured with a sheltered glass-mercury maximum-minimum thermometer located near the station laboratory on Inner Bay. Temperature of the creek was taken daily just above the weir with a stem thermometer at approximately 0800 and 1800 hours. Rainfall was measured with a standard U.S. Weather Bureau rain gage located near the laboratory.

Routine meteorological observations at the laboratory did not include wind conditions, but they were recorded at all stations and are on file at the station laboratory. Wind conditions for the five cruises and the concurrent precipitation regimes are shown in table 1. Veloc-

TABLE 1.—Meteorological observations on five cruises in Little Port Walter estuary

Cruise number and date	Station	Average wind direction and force	Precipitation (inches)
<i>1959</i>			
H-1:			
June 25	1A-7	Calm to SW.-1	0
June 26	16	Calm	0
June 27	11-15, 17	Calm	0
June 30	19-21	NE.-1	0
July 1	18, 22-24, 26	NE.-1	0.20
July 2	25, 27-30	Calm to SW.-1	0
H-2:			
July 27	1A-7	Calm	0.01
July 28	8-18, 21, 22	SE.-1 to SW.-1, 2	0.05
July 29	19, 20	Calm	1.57
H-3:			
July 30	1A-6	Calm	1.43
July 31	7-10, 15	E. to SE.-1	0.03
July 31	16, 17	NW.-1	
Aug. 1	11-14	Calm to SSW.-2	0.04
Aug. 1	18, 21, 22	Calm to W.-1	
Aug. 2	19, 20, 23, 26	Calm	0.60
Aug. 3	24	E.-2	0.27
Aug. 4	25, 27-30	W.-1, 2	0.01
L-1:			
June 25	1A-10	SE.-1, 2	0
June 26	11, 12	NNE.-1, 2	0
June 26	13-17	Calm to SE.-1	
June 30	18-21	NE.-1, 2	0
July 1	26-30	SW.-1, 2	0
L-3:			
July 29	1A-7	Calm	1.57
July 30	8-10, 15, 16	SE.-1, 2	1.43
July 30	17	NW.-2	
July 31	11-13	SW.-1	0.03
July 31	14, 18, 21, 22	Calm	
Aug. 1	13A, 19, 20	Calm to W.-1	0.04
Aug. 2	23-26	E.-1	0.60
Aug. 3	27-30	W.-2	0.27

ities during the five cruises never exceeded Beaufort force 2, and, except for cruise L-1, at least the inner half of Inner Bay was always visited during periods of calm. No pronounced differences in distributions of temperature or salinity as a result of variations in wind direction were observed.

DROGUES AND DRIFT BOTTLES

Direct observations of surface current directions were made in Inner Bay with "drift bottles" and 2-foot-square (0.6 m.²) sheet metal current

drogues suspended from gallon glass jugs. The drift bottles were actually 1-pint motor oil cans ballasted with sand so that they floated nearly submerged.

OBSERVATIONS

SALINITY

Surface Salinity at Slack before Ebb

The lowest salinity in Inner Bay was generally found at the mouth of Sashin Creek, although during cruise H-2 it was found at station 17 in the small cove at The Neck. In cruises H-1 and H-3 (figs. 5 and 6) this freshened water showed a definite tendency to hold toward the north shore. This tendency was not as noticeable during cruise H-2 (fig. 7), probably as a result of reduced outflow of the stream at that time. Wind was not a causative factor in this distribution, since in all three "H" cruises the upper part of Inner Bay was visited during periods of calm.

The most prominent feature of the surface salinity in Inner Bay during cruises H-1 and H-3 was a large eddylike configuration of isohalines in the southeast quadrant (figs. 5 and 6). Salinity values on the side of the eddy toward the middle of the bay were continuous with those observed in The

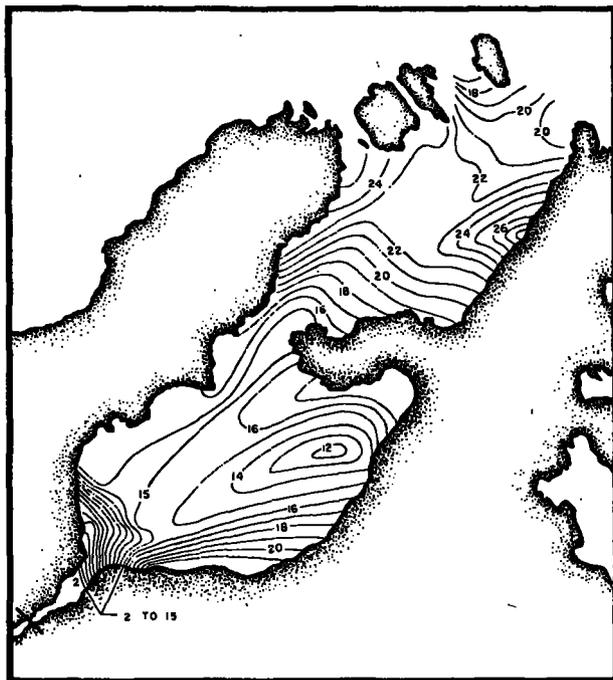


FIGURE 5.—Surface salinity; ‰, slack before ebb. Cruise H-1, June 25 to July 2.

Narrows. During cruise H-2 the eddylike structure was not present, but a series of recurved iso-

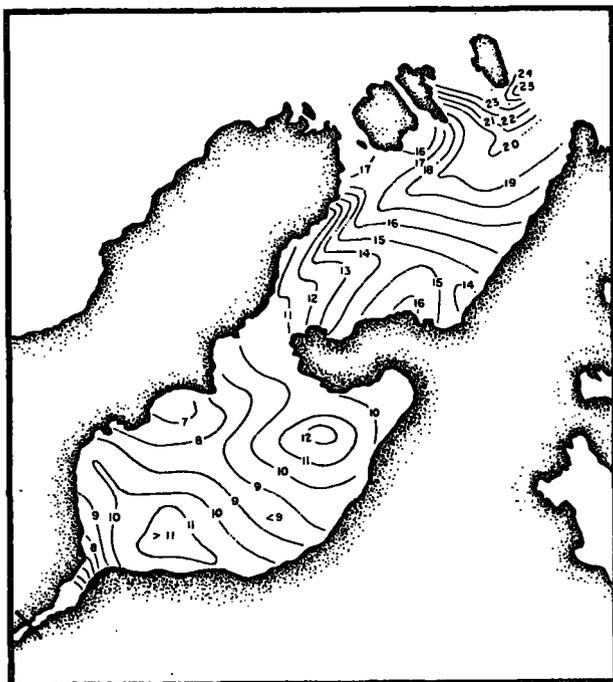


FIGURE 6.—Surface salinity; ‰, slack before ebb. Cruise H-3, July 30 to August 4.

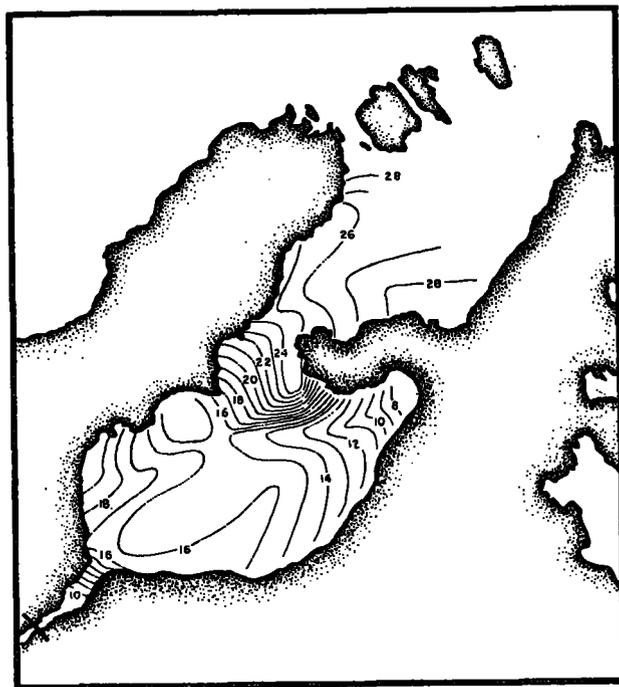


FIGURE 7.—Surface salinity; ‰, slack before ebb. Cruise H-2, July 27-29.

halines bent around The Neck from The Narrows into Inner Bay (fig. 7).

Although salinity was low at the head of Inner Bay along the north shore, it was relatively high in a comparable position on the south shore and did not appear to be appreciably affected by the direct outflow of the stream (figs. 5, 6, and 7).

During all three cruises isohalines in Outer Bay tended to parallel the north shore between the mainland-Inner Island channel and The Narrows (figs. 5, 6, and 7). Over the rest of Outer Bay, salinity tended to increase in the direction of Chatham Strait, with generally higher values in the southern portion.

Surface salinity in Outer Bay was generally higher than in Inner Bay. Average surface values for the three cruises at slack before ebb were as follows:

	Inner Bay	Outer Bay
Cruise H-1.....	14.2	22.0
Cruise H-2.....	15.0	27.4
Cruise H-3.....	10.1	18.3

The notably lower average values of surface salinity observed during cruise H-3, as compared with the previous cruises, appeared to reflect prevailing precipitation regimes. Cruise H-1 was begun June 25 and ended July 2. Precipitation was extremely low during that period, with the only measurable amount (0.20 inch) recorded July 1.

Cruise H-2 was carried out on July 27 and 28 and the morning of the 29th. Precipitation was negligible, although 1.57 inches of rain fell on the 29th after the cruise was terminated.

Cruise H-3 was begun July 30 and completed August 4. Precipitation was only slightly less on July 30 (1.43 inches) than on the 29th. During the remainder of the cruise it varied between 0.03 inch on July 31 and 0.60 inch on August 2. The heavy rains of July 29 and 30, however, appeared to be sufficient to greatly reduce surface salinity throughout the cruise.

Surface Salinity at Slack before Flood

Stations at slack before flood were occupied during cruises L-1 and L-3.

The lowest salinity of Inner Bay was found during cruises L-1 and L-3 at the head of the estuary where the fresh water from Sashin Creek entered. It remained low along the north shore for about two-thirds of the distance to The Narrows (figs. 8 and 9). From that point, it increased both

across and down the bay. In cruise L-3 (fig. 9), isohalines within this ascendant exhibited definite

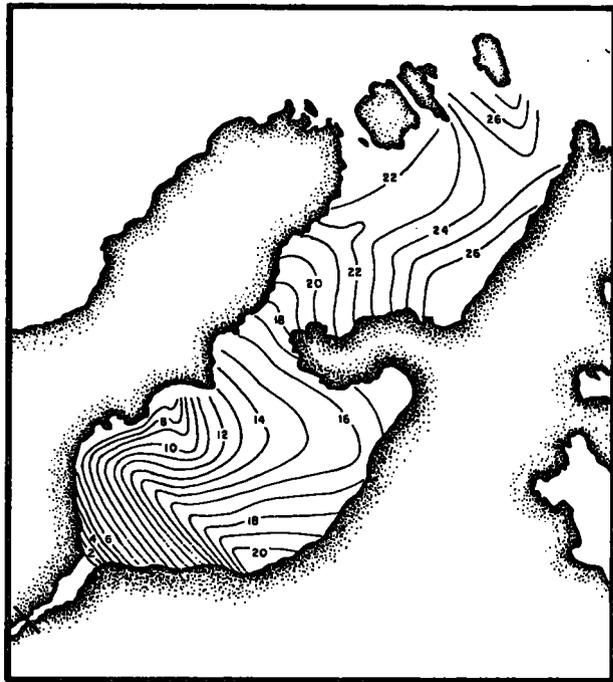


FIGURE 8.—Surface salinity; ‰, slack before flood. Cruise L-1, June 25 to July 2.

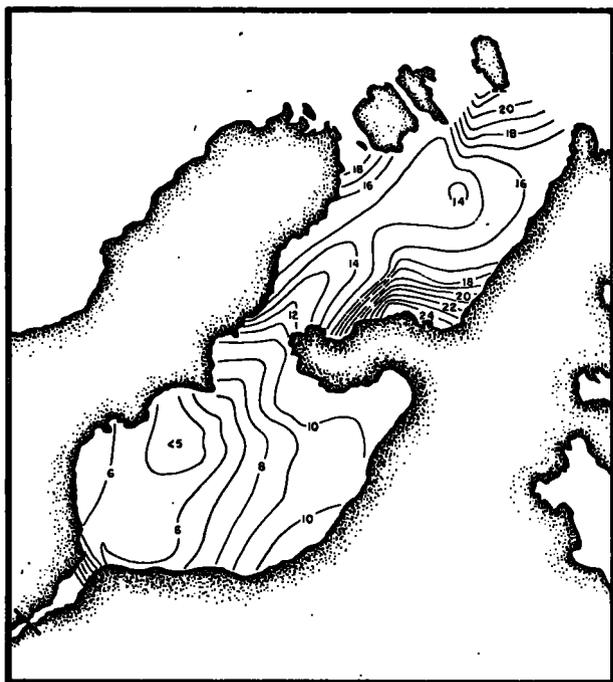


FIGURE 9.—Surface salinity; ‰, slack before flood. Cruise L-3, July 30 to August 4.

protrusions toward the cove at The Neck and toward The Narrows. Such protrusions were present, but less pronounced, in cruise L-1 (fig. 8). Near the south shore, just downbay from the shoal at the head of the bay, isohalines bent sharply and extended past the middle of the bay in the direction of the opposite shore (figs. 8 and 9).

On both cruises, the downbay increase in salinity observed in Inner Bay continued through The Narrows and into Outer Bay as a seaward-protruding tongue of isohalines. In Outer Bay this tongue occupied the north half of the bay as far as Inner Island. The south side of the tongue was continuous with a crossbay ascendant which attained maximum values in the embayment on the seaward side of The Neck.

Seaward of Middle Island, salinity increased rapidly to the end of the bay.

Average surface salinity at slack before flood was consistently greater in Outer Bay.

Values for cruises L-1 and L-3 were as follows:

	Inner Bay	Outer Bay
Cruise L-1.....	13.8	24.3
Cruise L-3.....	6.8	17.9

The greatly lowered average surface salinity of cruise L-3 was similar to the lowering observed during cruise H-3 and again appeared to reflect the effects of the heavy rains of July 29 and 30.

Vertical Salinity Distribution during Cruises at Slack before Ebb

Salinity along the axis of the estuary, as observed at slack before ebb during cruises H-1, H-2, and H-3 (figs. 10, 11, and 12), was strongly stratified. In Inner Bay, water of less than 30‰ was usually found in the upper 2 m. and never below a depth of 5 m. At greater depths the salinity was nearly constant, varying only between 30 and 32‰.

In Outer Bay stratification was generally less intense than in Inner Bay. The 30 and 31‰ isohalines rose from depths of about 20 and 30 m. in Outer Bay to about 5 m. in Inner Bay on cruise H-1. During cruise H-3, the 30‰ isohaline was near the surface over the entire estuary, but the 31‰ isohaline rose from about 35 m. in Outer Bay to less than 5 m. at the head of Inner Bay.

At depths below the superficial top layer, vertical salinity distribution at slack before flood differed little from that at slack before ebb and is not discussed here.

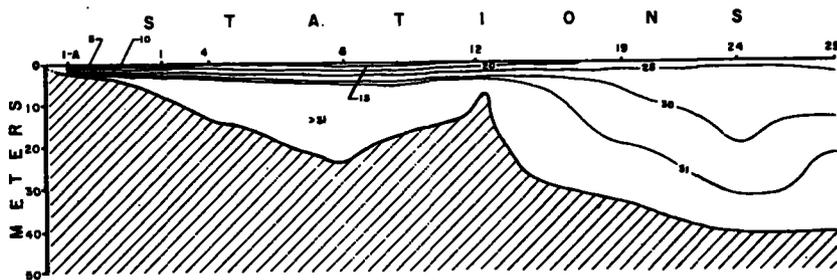


FIGURE 10.—Vertical distribution of salinity; ‰, along longitudinal axis of estuary at slack before ebb. Cruise H-1, June 25 to July 2. (Data of station 8 missing.)

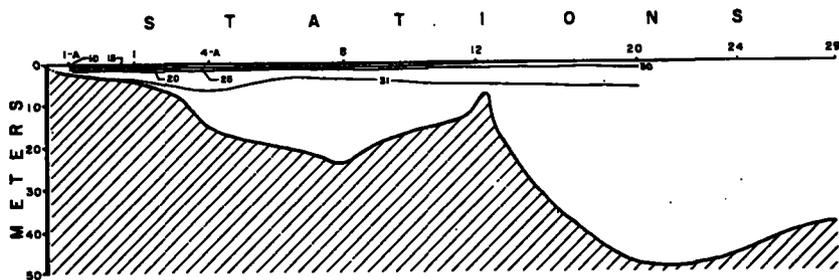


FIGURE 11.—Vertical distribution of salinity; ‰, along longitudinal axis of estuary at slack before ebb. Cruise H-2, July 27-29.

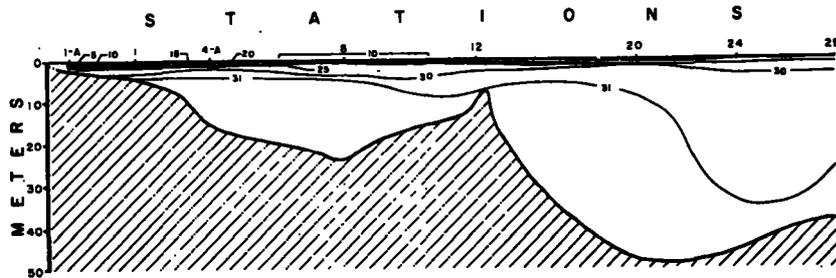


FIGURE 12.—Vertical distribution of salinity; ‰, along longitudinal axis of estuary at slack before ebb. Cruise H-3, July 30 to August 4.

Temporal Salinity Distribution

The temporal variation of salinity for Inner Bay, as observed at reference station 2 between April 3 and August 21, and daily precipitation for the period are shown in figure 13.

A strong halocline lay between the surface and 1 m. throughout most of the observation period. It was notably weakened between April 24 and May 22, probably by the mixing effects of a northeastern storm which began on April 28 and continued into the first week of May. Winds during this period attained velocities estimated at Beaufort force 6 to 7. Although heavy rains began on May 6 and continued intermittently until May 24, they or the associated heavy runoff from Sashin Creek were probably not the cause of the partial breakdown of the halo-

cline, which remained strongly intact during prolonged periods of much heavier precipitation during July and August. A comparison of precipitation and surface salinity (fig. 13) shows that surface salinity lowered appreciably with heavy rainfall. The effect of the increased fresh-water input always appeared to be restricted to a superficial surface layer. Most of the column was consistently of salinity of 30‰ or more.

TEMPERATURE

Surface Temperature at Slack before Ebb

During cruise H-1 (fig. 14), water of $> 12.5^{\circ}\text{C}$. protruded sharply into the southeastern quarter of Outer Bay from Chatham Strait. This extension reached to station 25, where temperatures decreased slightly to a low of $< 11^{\circ}\text{C}$. at The

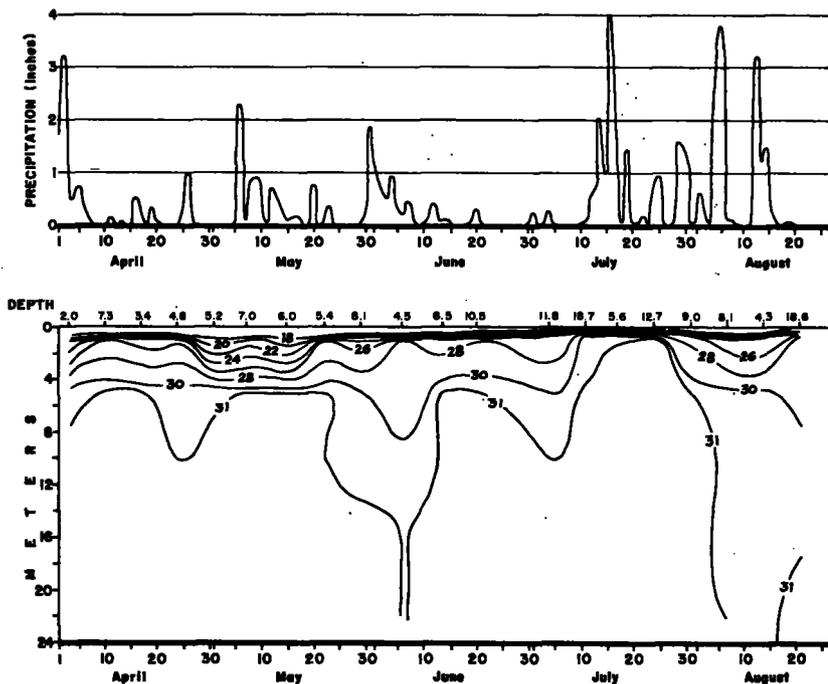


FIGURE 13.—Upper: Daily precipitation (inches of rainfall) at Little Port Walter, April 1 to August 21, 1959. Lower: Temporal sequence of salinity, ‰, at reference station 2, April 3 to August 21, 1959. Contours representing values less than 18 ‰ are omitted. Numbers at top are observed surface salinities.

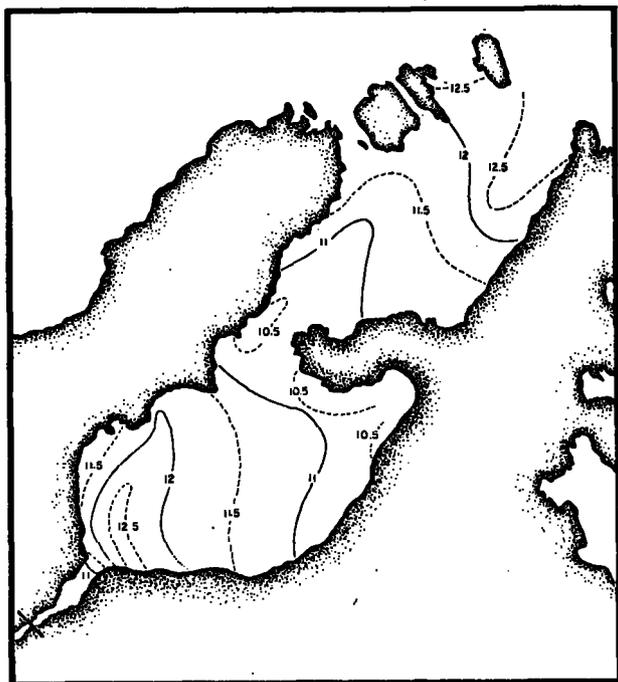


FIGURE 14.—Surface temperature, degrees C., slack before ebb, cruise H-1, June 25 to July 2.

Neck. Water of $< 11^{\circ}$ C. extended through The Narrows into the outer end of Inner Bay, then gradually warmed toward the head of the bay. Maximum temperatures in Inner Bay ($> 12.5^{\circ}$ C.) occurred as a narrow tongue extending from station 2 to station 4. Temperatures fell to $< 11^{\circ}$ C. at the mouth of Sashin Creek.

In cruise H-2 (fig. 15) a tongue of $< 11^{\circ}$ C. water extended into The Narrows from Outer Bay. This tongue was separated from the north shore by $> 11^{\circ}$ C. water that extended from the mainland-Inner Island channel into The Narrows. Slightly cooler surface waters characterized most of Inner Bay, with lows of $< 10^{\circ}$ C. in the cove at The Neck and in a narrow band in the northwest quadrant.

The nearest approach to homogeneity of surface temperatures was observed on cruise H-3 (fig. 16). The greater part of Outer Bay was occupied by water of $> 10.5^{\circ}$ C. Along the north shore a narrow band of $< 10.5^{\circ}$ C. water extended from the mainland-Inner Island channel through The Narrows, and a wider band of like temperature extended along The Neck and through The

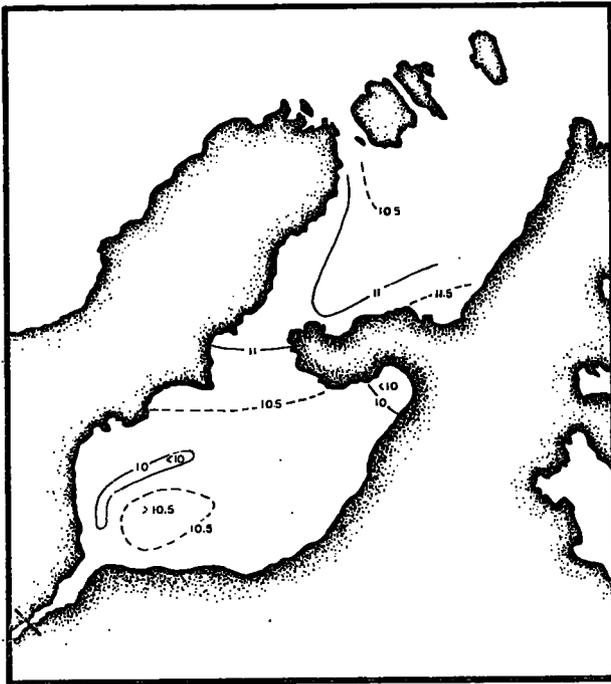


FIGURE 15.—Surface temperature, degrees C., slack before ebb, cruise H-2, July 27-29.

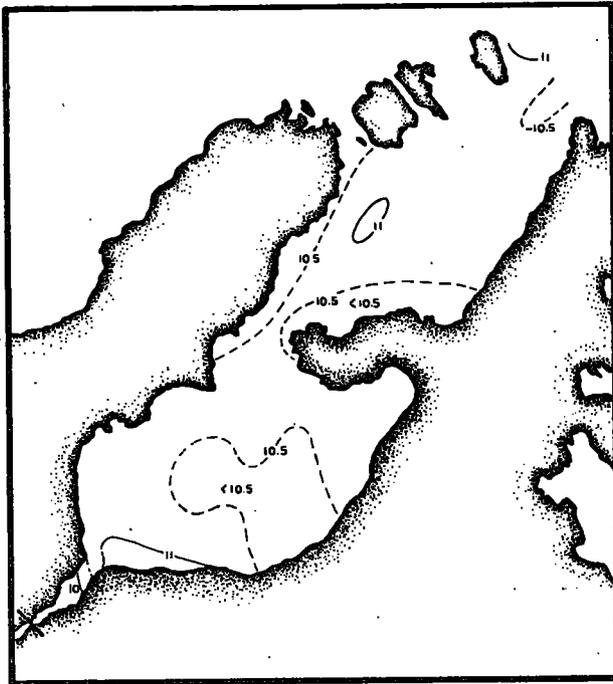


FIGURE 16.—Surface temperature, degrees C., slack before ebb, cruise H-3, July 30 to August 4.

Narrows. The $< 10.5^{\circ}$ C. water continued through The Narrows from Outer Bay and occupied a large part of Inner Bay. A large

bilobed area of $< 10.5^{\circ}$ C. water protruded from the south shore. Temperatures of $> 11^{\circ}$ C. lay over the shoal at the head of the bay; at the mouth of the stream they decreased to $< 10^{\circ}$ C.

Surface Temperature at Slack before Flood

During cruise L-1 (fig. 17) a fairly large mass of $< 11.5^{\circ}$ C. water extended from the mouth of Sashin Creek to the northwest quarter of Inner Bay. The southern half of Inner Bay was occupied by a small body of $> 12^{\circ}$ C. water that surrounded station 6 and an adjacent area of $< 11.5^{\circ}$ to $< 10.5^{\circ}$ C. water that reached to the cove at The Neck, where it warmed to $> 12.5^{\circ}$ C. A band of $> 12^{\circ}$ C. water extended from the vicinity of station 7 near the north shore, through the south side of The Narrows, and into Outer Bay where it turned back toward the north shore. It then protruded in a downbay tongue to station 24 where it recurved to the south to terminate at the south shore near station 22. The tonguelike formation was continued to the center of the Outer Island-Light Point passage by the 12.5° and 13° C. isotherms. Warmer water lay on either side of this tongue; temperature was $> 13.5^{\circ}$ C. along the south shore, and increased to 15° C. in the Middle Island-Outer Island channel.

Surface temperature structure during cruise L-3 (fig. 18) was much less complex than during cruise L-1. A large eddylike structure of $> 11^{\circ}$ C. water lay in the southern half of Inner Bay, and $> 11^{\circ}$ C. water was also found along the north shore. Water of $< 11^{\circ}$ C. ran in a wide band from the head of the bay to and through The Narrows and also extended along shore through the southern half of Inner Bay to completely surround the eddy of $> 11^{\circ}$ C. water.

From The Narrows the band of $< 11^{\circ}$ C. water reached to Chatham Strait. It was partially separated from the north shore by a narrow band of $< 10.5^{\circ}$ C. water that lay between The Narrows and the Mainland-Inner Island channel. In the southern half of the bay the extent of the $< 11^{\circ}$ C. water was interrupted by a tongue of $> 11^{\circ}$ C. water that ran from The Neck to the center of the bay, and by a cooler area of $< 10.5^{\circ}$ C. water between Light Point and Inner Island.

Vertical Temperature Distribution during Cruises at Slack before Ebb

Vertical distribution of temperature along the central axis of the estuary at slack before ebb

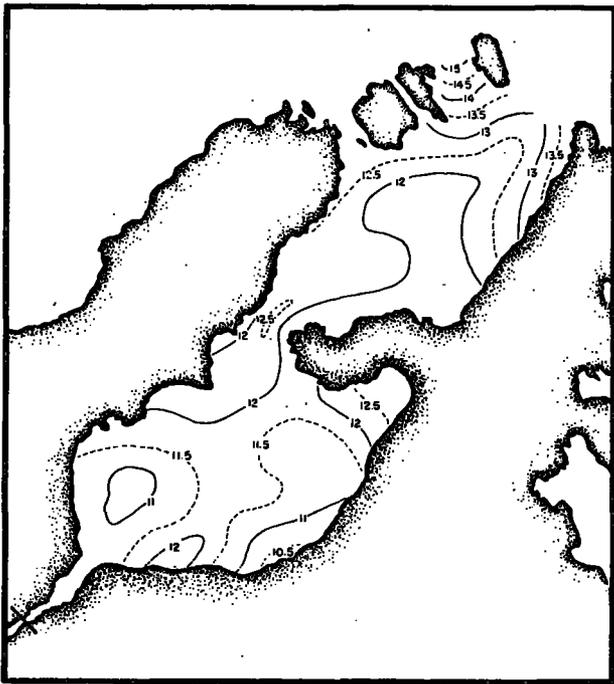


FIGURE 17.—Surface temperature, degrees C., slack before flood, cruise L-1, June 25 to July 2.

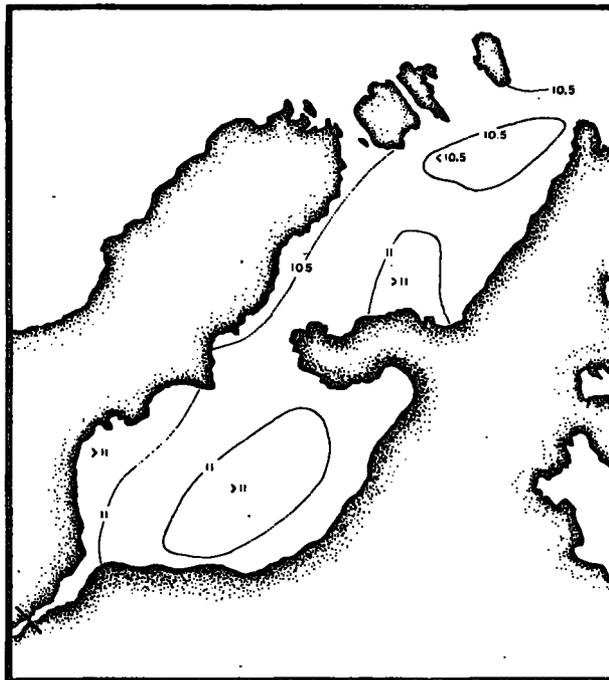


FIGURE 18.—Surface temperature, degrees C., slack before flood, cruise L-3, July 30 to August 4.

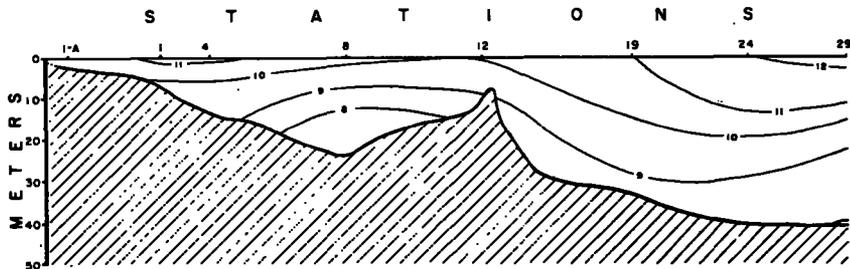


FIGURE 19.—Temperature, degrees C., along longitudinal axis of estuary at slack before ebb, cruise H-1, June 25 to July 2. (Data of station 8 missing.)

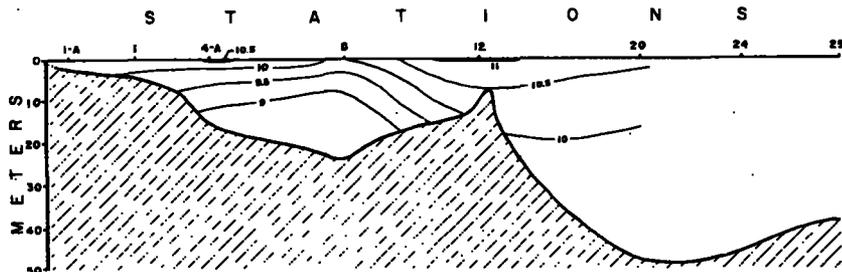


FIGURE 20.—Temperature, degrees C., along longitudinal axis of estuary at slack before ebb, cruise H-2, July 27-29.

during cruises H-1, H-2, and H-3, (figs. 19, 20, and 21) exhibited only slight gradients. Although much greater depths existed in Outer Bay, bottom temperatures remained within 1° C. of those in Inner Bay.

On cruises H-1 and H-3, all subsurface isotherms in Outer Bay sloped upward toward the sill at The Narrows. Since cruise H-2 was not completed, slopes of isotherms in Outer Bay for that cruise could not be determined.

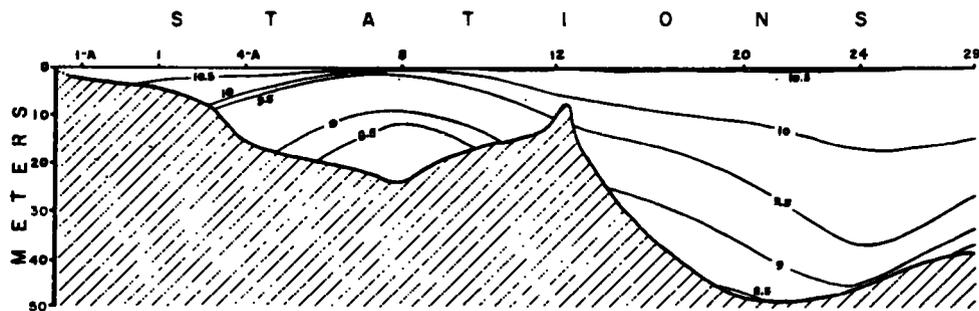


FIGURE 21.—Temperature, degrees C., along longitudinal axis of estuary at slack before ebb, cruise H-3, July 30 to August 4.

Vertical temperature distribution at slack before flood differed little from that at slack before ebb and is not discussed here.

Temporal Temperature Distribution

Figure 22 depicts the temporal variation of temperature for Inner Bay at reference station 2 between April 3 and August 21. It also includes daily maximum air temperature and daily observed maximum temperature of Sashin Creek. Conditions at reference station 2 during the first

half of April were nearly isothermal, with some slight stratification appearing during the latter part of the month and persisting into June.

Until early June, surface waters were colder than those immediately below the surface. Highest temperatures (6° to 7° C.) began at a depth of about 2 meters. Comparatively rapid warming occurred in June and July. The highest temperature of the entire period of observation (12.2° C. at the surface) was recorded on July 11. This

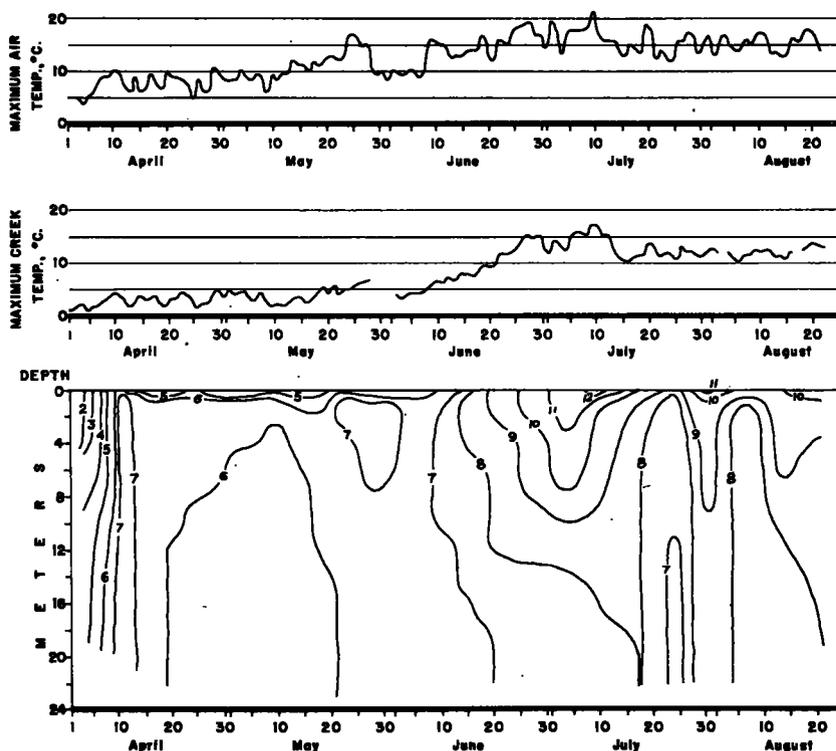


FIGURE 22.—Upper: Maximum daily air temperature, degrees C., Little Port Walter, April 1 to August 21, 1959. Center: Maximum observed daily temperature of Sashin Creek, degrees C., April 1 to August 21, 1959. Lower: Temporal sequence of water temperature, degrees centigrade, at reference station 2, April 3 to August 21, 1959.

warming trend coincided with a similar increase in air temperature which culminated in a high of 21.1° C. on July 10. Fluctuating air temperatures during the rest of the observation period were reflected in alternate warming and cooling of the water, particularly evidenced by changes in position of the 8° and 9° C. isotherms.

TRANSPARENCY AND OXYGEN IN INNER BAY

Transparency was measured weekly at reference stations 1, 2, and 3, and at all cruise and anchor stations between April 3 and August 31. Observations of this parameter at reference station 2 are presented temporally in figure 23.

Vertical distribution of oxygen was observed at reference stations 2 and 3 on June 6, and weekly at reference stations 2, 3, and 4 from July 11 to August 21. Temporal distribution at station 2 is presented in figures 23 and 24. Oxygen concentration was greater than 6 p.p.m. at all depths in all three stations except station 2 (located at the deepest part of Inner Bay). There, oxygen at depths of 20 m. and greater (22 to 24.5 m., depending on height of tide and exact point of sampling) was usually less than 6 p.p.m. The week-to-week variations in oxygen at 20 m. at station 2 are shown in table 2 (oxygen at 15 m. is included for comparison).

At 15 m. oxygen showed no tendency to become depleted, fluctuating between 6.58 and 9.00 p.p.m. At 20 m., however, changes of considerable

TABLE 2.—Comparison of week-to-week variation in oxygen at 15 and 20 m., reference station 2

Date	P.p.m. at 20 m.	P.p.m. at 15 m.
June 6.....	9.50	9.00
June 13, 20, July 4.....	(¹) 2.75	(¹) 7.68
July 11.....	7.34	6.81
July 17.....	7.66	7.87
July 24.....	5.28	7.18
July 31.....	5.45	6.78
August 7.....	5.58	7.22
August 14.....	4.15	6.58
August 21.....		

¹ No observations.

magnitude occurred. Highest observed oxygen content at that depth was 9.50 p.p.m. on June 6. It decreased by 6.75 to a low of 2.75 p.p.m. on July 11, then increased sharply to 7.34 p.p.m. on July 17. A further slight increase of 0.32 p.p.m. during the following week resulted in a secondary high of 7.66 p.p.m. on July 24. Between July 24 and 31 it decreased by 2.38 p.p.m. to a value of 5.28, then rose gradually to 5.58 on August 14. A week later it again appeared to be decreasing rather rapidly, having fallen to 4.15 p.p.m. on August 21.

Both transparency and 20-m. oxygen, as observed at reference station 2, exhibited temporal variations which correlated with the corresponding precipitation regime. In figure 23, the trend of the transparency curve correlates directly with the precipitation trends. Periods of increased precipitation corresponded with increased transparency, and periods of decreased precipitation

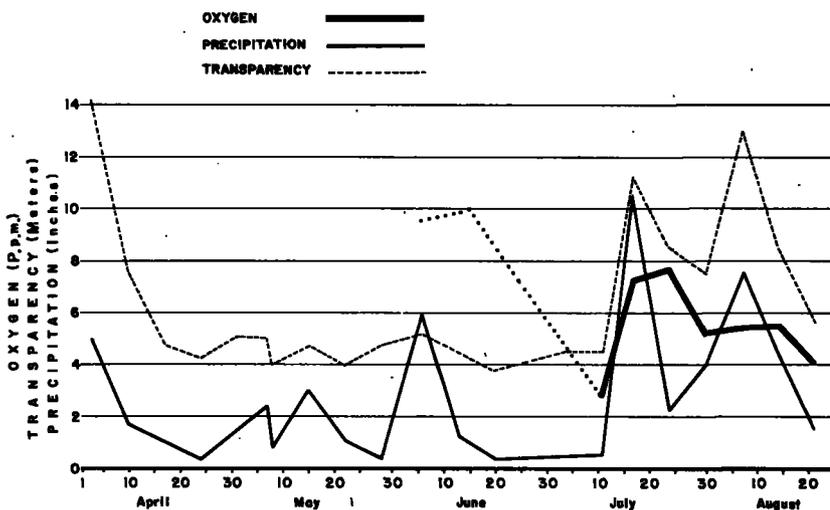


FIGURE 23.—Regimes of transparency and 20 m. oxygen at reference station 2, and precipitation as observed at Little Port Walter, April 3 to August 21, 1959. Each point on the precipitation curve represents the total for that day plus the 6 preceding days.

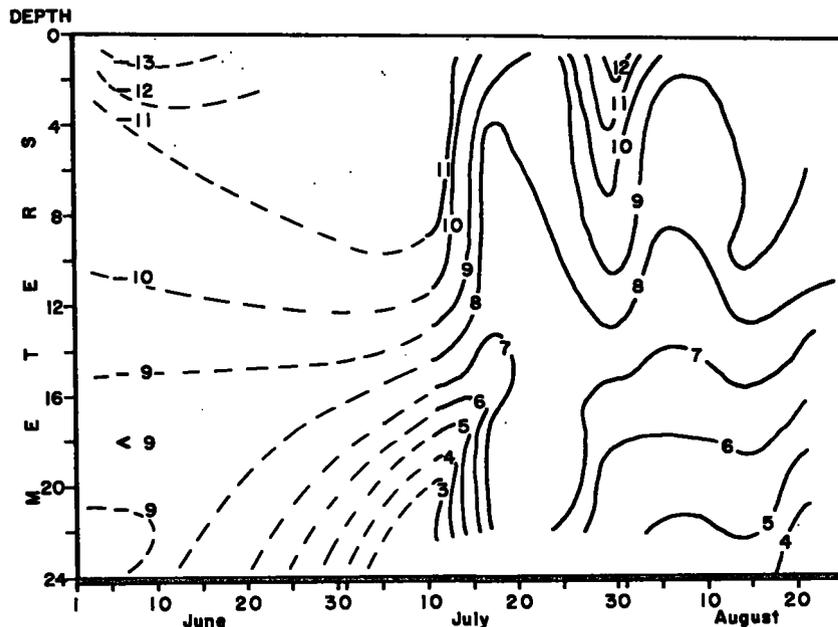


FIGURE 24.—Temporal sequence of dissolved oxygen, p.p.m., at reference station 2, June 6 and July 11 to August 21, 1959. Uppermost samples taken at depth of 1 meter.

with decreased transparency. Oxygen at 20 m. increased during two 1-week periods of heavy precipitation, continued to increase slowly during ensuing 1-week intervals of greatly reduced precipitation, and then decreased as precipitation remained low.

Between July 11 and 17, extremely heavy rainfall, 10.5 inches, coincided with large increases in transparency and 20-m. oxygen. From July 18 to 24, a period of very light precipitation, 2.4 inches, transparency decreased, while oxygen continued to increase slightly. During the week of July 25 to 31, precipitation measured a comparatively light 4.02 inches, and both transparency and oxygen decreased.

Relatively heavy precipitation (7.6 inches) between August 1 and 7 coincided with a large increase in transparency and a small increase in oxygen. Precipitation and transparency declined during the succeeding week (until August 14), while oxygen increased slightly. Precipitation was light during the last week in which observations were made, August 15–21, and both transparency and oxygen declined.

Two 3-week cycles were thus described: one between July 11 and 31, the other from August 1 to 21. Each was characterized by: (1) a week of heavy rainfall followed by 2 weeks of relatively

light precipitation, (2) changes in transparency correlating directly with intensity of precipitation, and (3) 2 weeks of increasing oxygen values at 20 m. followed by a week of decrease. In each case, the increase in oxygen corresponded with the week of heavy precipitation.

On the basis of these two cycles, the probable trend of the oxygen curve between June 6 and July 4 is shown as a dotted line on figure 23.

DROGUES AND DRIFT BOTTLES

During the summer, drogues and drift bottles were released in Inner Bay at both high and low flows of Sashin Creek.

On August 5 the rate of flow of Sashin Creek rose sharply because of heavy rains. Estimated flows on the 4th, 5th, 6th and 7th were 0.096, 0.688, 0.728, and 0.329 million cubic meters per day respectively. The direction of flow in approximately the upper meter was observed on August 7, utilizing drift bottles and drogues. The drift bottles measured the movement of the top 0.25 m. of the water column; the drogues measured the 0.60-m. layer immediately below the 0.25-m. layer. Eight bottles and one drogue (A) were released at cruise station 4, seven bottles at station 4-A, and eight bottles at station 5. All releases were made about 1½ hours after the beginning of floodtide.

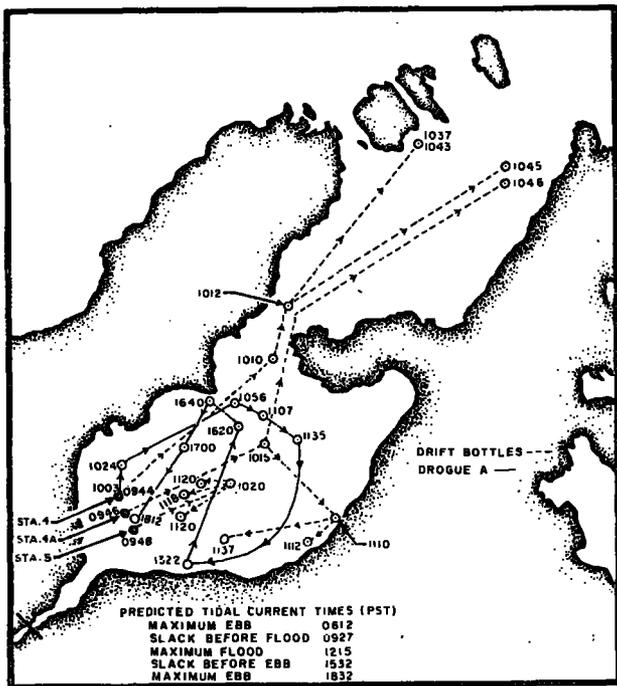


FIGURE 25.—Paths of travel of drift bottles and drogue A, August 7, 1959. Times of position fixes are indicated. Zero winds during entire period.

Wind was calm during the entire period of observation. Paths of travel of the bottles and of drogue A are presented in figure 25.

All bottles released at station 4, in the north side of the bay, moved nearly straight downbay toward the tip of The Neck, curved into The Narrows, and passed through Outer Bay to Chatham Strait in about an hour. Drogue A, released simultaneously with these bottles, did not enter The Narrows. Upon approaching the tip of The Neck it swung to the right, followed a curved path toward station 16 on the south shore, and continued upbay to the vicinity of station 10. It then moved away from shore toward The Narrows, and by the end of flood was about 150 m. southwest of the tip of The Neck. During the first 3 hours of ebb it moved toward the head of the estuary through the northern part of Inner Bay to a position near cruise station 4.

All drift bottle observations were made during floodtide (fig. 25).

The seven bottles released at station 4-A moved along the axis of the bay to between 90 and 140 m. of The Neck. Here two of them turned to the left and passed out through The Narrows, while

the remaining five turned right and moved to station 16 near the south shore. From there they drifted slowly along shore in an upbay direction. These five bottles, from their initial point of release, followed a path similar to that of the drogue, rather than that of the bottles released at station 4.

All bottles from station 5 moved downbay, paralleling the paths of those from 4-A. After drifting about 230 m., they reversed direction and fanned out, moving very slowly back toward the head of the bay.

During periods of reduced fresh-water runoff the surface layer did not run out of the estuary on floodtides. Drogues were released in Inner Bay under conditions of low streamflow to ascertain whether the basic circulation pattern was otherwise similar to that observed during high streamflow.

On August 11, when the stream was discharging about 0.07 million cubic meters per day, single drogues were released during early flood at stations 8 (drogue B) and 9 (drogue C) and recovered several hours later before the end of flood (fig. 26). Drogue B pursued a circular, clockwise course, while drogue C moved diagonally upbay and acrossbay toward the north shore.

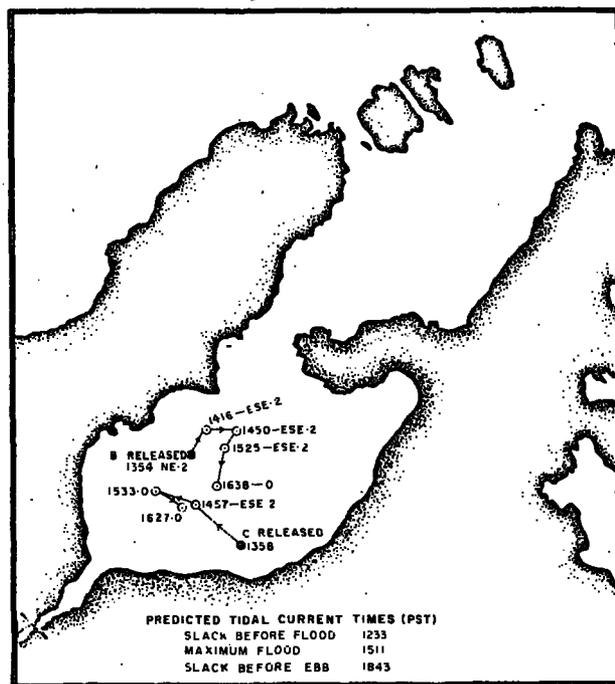


FIGURE 26.—Paths of travel of drogues B and C, August 11, 1959. Time and wind indicated at each position fix.

On August 19, when stream discharge was 0.10 million cubic meter per day, single drogues were again released at stations 8 (drogue D) and 9 (drogue E). Set adrift during early flood, they were observed until late ebb (fig. 27). Drogue

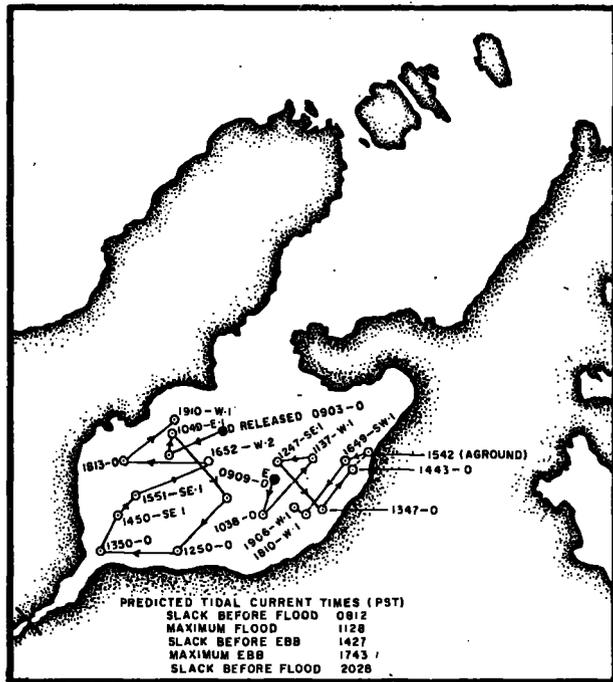


FIGURE 27.—Paths of travel of drogues *D* and *E*, August 19, 1959. Time and wind indicated at each position fix.

D followed a net clockwise path. During flood it moved toward the south shore, thence to the head of the bay near the mouth of the stream, from where it started downbay shortly before the beginning of ebb. During ebb it continued to move down through the northern part of the bay toward The Narrows. Drogue *E* followed a rather aimless spiral drift during its first several hours of travel, eventually moving very close to the south shore, along which it passed in a northeasterly direction to eventually ground shortly after the beginning of ebb. After being re-released near shore, it moved upbay along shore during the remainder of its drift. Drogues *D* and *E* were both recovered at the fifth hour of ebb.

Medusae were in the estuary throughout the summer, usually in large numbers. They were never found in the upper freshened layer, appearing to come no closer to the surface than the top of the intermediate layer. Repeated visual

observation indicated that these planktonic animals were effective neutrally buoyant drogues, and observations of their drift were helpful in discerning water movements. During times of greatly increased stream discharge, they were found in abnormally large concentrations at the extreme head of Inner Bay. Under such conditions the bottom in that region was covered with dead medusae. Their death was apparently caused by rupturing resulting from osmotic imbalance. A recent paper (Marshall and Hicks, 1962) substantiates my opinion that the medusae did not control their horizontal movements, but moved as freely floating bodies directed by the current.

DISCUSSION

CIRCULATION IN THE ESTUARY

Little Port Walter estuary exhibited normal oscillating tidal movements, which took the form of a standing wave. Slack waters coincided with high and low water, with maximum flows occurring approximately halfway between slacks. With the exception of the top 0.3 to 0.6 m. of water, which frequently ran out of Inner Bay throughout the tidal cycle, bidirectional currents were unusual, and movement of the entire water column through The Narrows was into Inner Bay during flood and out during ebb. Similar movements appeared to be the normal regime in the passages connecting Outer Bay with Port Walter Bay and Chatham Strait. For the most part, an equilibrium was apparently maintained by an excess of ebb transport over flood transport which was sufficient to carry off the fresh-water drainage. The discussion of basic circulation features which follows therefore refers to a net circulation achieved as a net product of the oscillating tidal movements.

Basic Features of Circulation

Inner Bay has the basin characteristics of a fiord. It is separated from Outer Bay by a sill at 5 m. and has a maximum depth of 21 m. The average depth is about 12 m., or approximately 2½ times the sill depth. (All depths are referred to datum.)

The fundamental net circulation of Inner Bay in the summer of 1959, as inferred from distribution of parameters and corroborated by direct observation, corresponded to that described for

fjords by Pritchard (1955) and Tully (1949). The fresh-water runoff was contained in a shallow top layer (figs. 10, 11, 12, and 13). This layer was a region of mixing between the fresh water and the underlying sea water. Salinity increased rapidly with depth in the upper few meters. The 30 ‰ isohaline was rarely found deeper than 5 m. At greater depths the water was of nearly constant salinity, varying only between 30 and 32 ‰. This water possessed the salinity and temperature characteristics of the deep water of Outer Bay (figs. 10, 11, 12, 19, 20, and 21). In figures 10 and 12, the 30 and 31 ‰ isohalines, which rose from deep positions in Outer Bay to approximately the 5-m. depth in Inner Bay, probably marked the lower limit of the intermediate layer (Pritchard, 1955) in which the net flow is directed up the estuary. The upper portion of this layer was probably delimited by the 25 ‰ isohaline, which was never observed to come to the surface in Inner Bay. Sea water entrained in the intermediate layer extended to the waterfall at the head of the estuary, where bottom salinities greater than 30 ‰ were routinely observed in 2 m. of water. Progressive seaward surfacing of isohalines less than 25 ‰ probably indicated that they were contained in the upper layer in which net flow is seaward. According to Pritchard (1955), in this layer "the salt content increases in the seaward direction as a result of advection and mixing of saltier water from below."

Deep-Water Movement in Inner Bay

The deep water below the intermediate layer exhibited an irregular upbay movement. The precipitation-transparency-oxygen cycles of July 11-31 and August 1-21 suggested a sequence of periods of alternating increase and decrease in rate of movement of this deep water. Although the increases in transparency and in oxygen at 20 meters coincided with heavy precipitation, the only appreciable lowering of salinity was confined to a very shallow surface layer (fig. 13). It was therefore evident that the increased oxygen content of the deep water was not a result of downward mixing of the additional fresh water. The increased transparency likewise could not be ascribed directly to the presence of the runoff water, the turbidity of which was greater than that of the runoff during the immediately previous conditions of low flow.

The replenishment of oxygen and increase in transparency must therefore be attributed to a movement across the sill of deep water from Outer Bay. On July 17 oxygen content near the bottom of reference station 4 in Outer Bay was higher (9.88 p.p.m.) than at any other depth sampled in that station on that day. Since this observation coincided with the increase of oxygen at 20 m. in reference station 2, it further suggested an upbay movement of deep water which could have ridden over the sill and into Inner Bay.

The relationships between precipitation, transparency, and oxygen suggested that the movement of subsurface water across the sill from Outer Bay was in response to the mechanism of a salt pump. Hachey (1934) and others described such a mechanism in which the addition of fresh water resulted in a mixed layer of lowered salinity moving seaward (away from the mixing area) and a compensating current at a deeper level moving landward (toward the mixing area). Such differential movements are usually the net result of flows occurring over a complete tidal cycle. The rate of such a pumping is directly dependent upon the rate of fresh-water discharge into the estuary. In each of the observed precipitation-transparency-oxygen cycles, a regime of decreasing oxygen values at 20 m. was transformed to one of increasing values coincident with a change from light to heavy precipitation. After rainfall and runoff had decreased, oxygen continued to increase for another week before it declined. The intermediate layer and the deep water responded differentially to the pumping mechanism. Significantly increased rates of deep circulation were probably related to an effective frictional coupling of the deep layer to the intermediate during periods of high runoff resulting from periods of very heavy precipitation. Coupling of the two layers was likely insignificant when precipitation was light and runoff small. The movement of deep water at such times was sluggish or negligible, as shown by the observed tendency toward oxygen depletion. The lag period shown by oxygen may be due to replenishment during the momentum die-out of the deep layer.

Further evidence of increased subsurface flow toward the head of the bay during periods of heavy runoff was furnished by the abnormally large concentrations and deaths of medusae at the extreme head of the bay during times of greatly increased

stream discharge. The medusae were apparently transported to the head of the bay within a counterflow that had increased its upbay rate of movement in response to the increased fresh-water discharge. Upwelling due to turbulent vertical mixing would tend to carry them into the freshened layers to which they were osmotically incompatible.

The action of a salt pump in Inner Bay was also indicated by the upbay ebbtide movements of drogoue A on August 7 (fig. 25). The drogoue was observed at a time when stream discharge had been quite heavy for several days. On the day the drogoue was set, stream discharge was 0.33 million cubic meters per day, and the day before it was 0.73 million cubic meters per day, the greatest rate measured during the entire summer. It is difficult to explain the movement of the drogoue, which was counter to the direction of the tide, on any basis other than that it was contained within a counterflow maintained by the salt pump. Water in the upper 0.3 m. was moving rapidly out of the bay at the time, and there was a complete absence of wind. Although the concept of the salt pump is generally based on net movement of water over a complete tidal cycle, it does not seem unlikely that, in a severely stratified situation such as occurred in Inner Bay, the rapid outward movement of the top layer of freshened water could have initiated and maintained an upbay movement of the more saline intermediate layer even during ebb. A somewhat analogous situation was found in Lake Ontario by Anderson and Rodgers (1959), where the flow of the warm water of the Niagara River into the lake induced a counterflow of colder bottom water from the lake toward shore.

Relation of Surface Circulation to Stream Discharge

It is evident from the foregoing discussion that the discharge rate of Sashin Creek markedly influenced the circulation of the estuary, particularly in Inner Bay. This was true not only with the vertically oriented water movements associated with the salt pump, but also with the horizontal pattern of surface circulation.

Floodtide, high stream discharge.—The paths of travel of the drift bottles and drogoue A on August 7 (fig. 25) indicated vertical differences in circulation within the northern part of Inner Bay and horizontal differences between the northern and southern parts of the bay. From the northern third of Inner Bay, that part of the water column

contained within the top 0.25 m. passed out through The Narrows, through Outer Bay, and into Chatham Strait, even though the tide was flooding. Water in the 0.6 m. layer directly below did not escape but passed into the southern part of Inner Bay. Surface water from the southern two-thirds of Inner Bay did not pass into The Narrows during flood tide, but appeared to enter an eddy.

The most striking aspect of this circulation was that it indicated at least part of the surface layer escaped throughout the tidal cycle. This continuous outflow appeared to result from the hydraulic pressure caused by increased stream discharge. Under all conditions of runoff the effluent of the stream tended to be diverted to the north side of Inner Bay by the shoal on the south side of the stream mouth. There was always an intense vertical salinity stratification, with most of the fresh water contained in a shallow surface layer. On August 7 this superficial freshened layer was subjected to sufficient head from the stream discharge to force its passage out of the northern portion of Inner Bay during both ebbtide and floodtide. That portion of the downbay surface flow which impinged upon The Neck was deflected into a clockwise eddy which occupied the southeastern quarter of the bay. Hence, only that surface water moving through approximately the northern one-third of the bay was able to escape through The Narrows. The motion of drogoue A on August 7 indicated that during floodtide on that day, no water below a depth of 0.3 m. escaped from any part of Inner Bay, but that the deeper layers responded to the normal floodtide forces rather than to the force exerted by the fresh-water discharge.

The distribution of surface salinity during cruises H-1 and H-3 (when stream discharge was high and hence similar to conditions of August 7) confirmed the positioning of the fresh-water effluent in the north side of Inner Bay and the presence of the eddy in the southern portion.

A similar condition of continuous outflow of the surface layer throughout the tidal cycle was found during a current meter anchor station in The Narrows on June 22 when melt water influx had raised the volume of flow of Sashin Creek to about 0.34 million cubic meter per day. Observations of the vertical current profile showed that the flow in the upper 0.3 to 0.6 m. was out of Inner Bay during floodtide. Below this depth

movement of water was into the bay during flood. The wind was light and variable.

Floodtide, low stream discharge.—Drogues *B*, *C*, *D*, and *E* (figs. 26 and 27), when released under conditions of reduced stream discharge drifted in the same clockwise eddy movement as they did during conditions of high stream discharge. This eddy seemed to be a dominant feature of Inner Bay under all conditions of runoff. On the day that drogue *E* was released the clockwise eddy had apparently shifted, possibly moving to a more centrally located upbay position and initiating by coupling action a counterclockwise eddy in the southeastern portion of the bay. The surface salinity of cruise H-2 (when stream flow was only 0.08 million cubic meter per day and hence comparable to that of August 11 and 19 when drogues *B*, *C*, *D*, and *E* were observed) tentatively confirmed such a shift of the clockwise eddy. The long, recurving tongue formed by the 16 ‰ isohaline in the inner central part of the bay was suggestive of eddy motion. Such an eddy might account for the relatively high salinity found near the north shore (<19 ‰ at station 3), since its motion could transport to that position the water of high salinity observed protruding in through The Narrows during the same cruise. A counterclockwise eddy geared to the clockwise motion could in turn account for the low salinity which lay in the southeast part of the bay. As the fresh water left the stream it could readily pass along the north side of the clockwise eddy and subsequently be carried south and thence downbay toward The Neck by the contiguous counterclockwise motion.

Ebbtide.—During ebbtide there was no evidence of a reversal of currents leading to counterclockwise circulation under any conditions of freshwater runoff. Drogue *E* moved upbay along the south shore as though contained in the southern edge of the clockwise eddy. Drogue *D* moved down through the northern part of the bay toward The Narrows in a clockwise pattern. The drift of drogue *A*, which appeared to be counter to the direction of ebb, has been discussed.

The distribution of surface salinity at slack before flood (cruises L-1 and L-3) tended to confirm the ebbtide circulation pattern inferred from movements of the drogues. During both cruises, salinity tended to be lower in the northern part of Inner Bay, with isohalines of greater values oc-

cupying the south shore between The Neck and the shoal at the head of the bay. Such a distribution suggested that an admixed stream effluent moved through the northern portion of the bay toward The Narrows, and a counterflow that contained lesser amounts of fresh water moved to the southern portion. The result was a clockwise motion.

Abnormal Circulation in Outer Bay

Anchor stations confirmed that the normal ebbtide pattern in Outer Bay was outflow through the three functional channels into Port Walter Bay and Chatham Strait. Occasionally, however, a reversal of flow through the Outer Island-Light Point channel took place during the first several hours of ebb. This reversal was, at least in part, caused by strong southerly currents in Chatham Strait and was not observed to occur with any degree of regularity.

The ebb current in Chatham Strait runs south. The mouth of the estuary faces partially into this current, making it possible for Chatham Strait water to flow into Outer Bay through the channel between Outer Island and Light Point. Such inflows were occasionally observed shortly after the beginning of ebb. On some ebbtides no unusual currents were observed near the mouth of the bay; on others, strong currents passed close to the mouth of the bay without actually entering; and on some the current penetrated well into the bay. This intruding current had the appearance of a typical rip current, with attendant surface ripples and swirls.

When the inflow from the strait did take place, it had the effect of damming that portion of the outflow from the estuary which normally ran between Outer Island and Light Point. Strong currents then flowed from Outer Bay into Port Walter Bay through the mainland-Inner Island and Middle Island-Outer Island channels. The escapement through these two channels was entrained in the ebbing current in Port Walter Bay and carried to the strait.

The phenomenon described was particularly evident on August 17. A line of floating kelp and other flotsam marked the advancing front of water from the strait, which penetrated through the Outer Island-Light Point channel into Outer Bay as far as a line between Middle Island and the southeast shore halfway between stations 21 and 26. This intruding water escaped into Port Walter

Bay through the Middle Island-Outer Island channel at velocities up to 80 cm./sec. (1.6 knots). The ebbing Outer Bay current passed into Port Walter Bay through the mainland-Inner Island channel at velocities of 50 to 60 cm./sec. (slightly over 1 knot). Only a weak ebb current was present at The Narrows at this time, indicating that the strong flow through the mainland-Inner Island channel was composed principally of water from Outer Bay.

The inflow from the strait began at the beginning of ebb. At the end of 1 hour, the kelp line that marked the intrusion had passed back out to the entrance of the bay, although strong currents were still running between the mainland and Inner Island and between Middle and Outer Islands. In 2 more hours the system had dissipated, and normal outflow from the estuary had become established.

On another occasion (July 8) a strong current from Chatham Strait, with surface velocities up to 50 cm./sec., was observed to approach the mouth of Outer Bay, but, although it passed just to seaward of Outer Island, it did not enter the bay and did not appear to obstruct normal outflow. This occurred during a period of spring tides, as did the events previously described when the large intrusion of water from the strait took place.

On June 22, also during spring tides, observations at anchor stations at the three channels in Outer Bay failed to reveal any operation of this system of currents.

FRESH-WATER FLUSHING OF INNER BAY

Although the feasibility of computing flushing rates for such incompletely mixed estuaries as Inner Bay has been questioned, such an operation seems logical if one carefully defines what is implied by the term "flushing." As computed here, the flushing of Inner Bay refers strictly to the flushing out of the contained fresh water, and the flushing time is the length of time required to rid the bay of an amount of fresh water equal to that of the accumulated fresh water contained within it on any given high tide (i.e., at slack before ebb). Even in this restricted sense, the flushing of an estuary has definite biological implications in that it has a direct effect upon any suspended materials or planktonic organisms which enter the bay via a stream.

The flushing time of Inner Bay was computed for each of the three cruises at slack before ebb (cruises H-1, H-2, and H-3) after the method of Ketchum, Redfield, and Ayers (1951). From contoured cross sections of salinity distribution, the cross-sectional areas of water of various salinities were determined by planimetry. The fraction of fresh water in each of these areas was calculated from the salinity, using as a reference the highest salinity observed in the entire estuary during the cruise. From the fresh-water fraction, the area of fresh water contained in the cross section was determined, and, using the known distance between sections, the volume of fresh water contained within the bay was calculated. This volume of accumulated fresh water, when divided by the average daily volume of flow of Sashin Creek during the cruise period, gave the flushing time in days. The results are:

Cruise	Fresh-water accumulation (cubic meters)	Streamflow (cubic meters/day)	Flushing time (days)
H-1-----	0.35×10 ⁶	0.33×10 ⁶	1.1
H-2-----	0.20×10 ⁶	0.08×10 ⁶	2.5
H-3-----	0.32×10 ⁶	0.24×10 ⁶	1.3

The computed flushing times correspond rather closely, varying only between 1.1 and 2.5 days. The correlation between magnitude of streamflow and flushing time, with flushing time decreasing as streamflow increases, is obvious. When flushing time is plotted against streamflow for the three cruises, the points fall nearly on a straight line. While more observations are desirable, the results are highly suggestive of a direct dependence of flushing time of Inner Bay upon volume of flow of Sashin Creek. The probability of such a relationship is enhanced by the observations and conclusions regarding surface circulation of Inner Bay, where it appeared that the pressure exerted by the flow of the stream was one of the chief determinants of the pattern of circulation of the upper layers.

WATER TRANSPORT THROUGH THE NARROWS

On August 12 and again on August 19, an anchor station was occupied in The Narrows to obtain data on water exchange between Inner and Outer Bays. The station, located in midchannel, appeared to sample adequately currents passing through The Narrows. The bottom in that

constricted passage shoaled rather rapidly toward both shores, and dense kelp beds, particularly on the south side, restricted water movements occurring outside the midchannel region.

According to Sverdrup, Johnson, and Fleming (1946, p. 568), the velocity of midchannel current in a cross section is about one-third higher than the average velocity for the entire cross section. Current velocities observed at the anchor station have accordingly been lowered by one-third to make them more nearly representative of the probable average velocity through the section. Independent estimates of total water transport through the section, using tide range and surface area of Inner Bay in the relationship

$$V = A \times 2_{70}$$

(Sverdrup et al., 1946, p. 568), indicated that this adjustment was realistic. In the above equation, V is the volume of the tidal prism (hence the volume of water that must move through The Narrows through one-half tidal cycle), A the surface area of Inner Bay, and 2_{70} the average tide range.

On August 12 the predicted mean tide range for Port Walter was 2.1 m. The current in the upper one-half meter ran out during the entire cycle of flood and ebb. The outflow during flood appeared to be caused by south to southwest winds of force 1-2, rather than by the pressure of stream discharge which measured only 0.07×10^6 cubic meters per day. The greatest observed velocity was 15 cm./sec. Below a depth of one-half meter currents were too weak to operate the current meter, which required a minimum current velocity of 7.5 cm./sec. for activation. Directional orientation of the meter, which was usually visible to the bottom, indicated that the water below one-half meter did move out of the bay during the ebb and in on the flood.

Since movement of inflowing water was not measurable, inflow was calculated from

$$S_o V_o = S_i V_i$$

where S is the weighted average salinity over one phase of tide (ebb or flood), V is volume of water, and the subscripts "o" and "i" are out and in, respectively.

Under steady state conditions, a salt balance is maintained, that is, the estuary becomes neither fresher nor saltier. Assuming such conditions, the calculated inflow represents the volume of incoming water needed to replace the measured outflow in the upper one-half meter to the extent that net salt transport through the section is zero. Any outflow which may have taken place below one-half meter could not be taken into account in this computation, since it was not known. This necessary omission had the effect of systematically lowering the estimates of total transport throughout the complete tidal cycle.

TABLE 3.—Observations at anchor stations in The Narrows, August 12 and 19

Item	August 12	August 19
Total transport out through The Narrows, m ³ /tide	0.32 × 10 ⁶	0.915 × 10 ⁶
Total transport in through The Narrows, m ³ /tide	*0.26 × 10 ⁶	0.89 × 10 ⁶
Excess, out less in (net transport), m ³ /tide	0.06 × 10 ⁶	0.025 × 10 ⁶
Volume of flow, Sashin Creek, m ³ /tide	0.035 × 10 ⁶	0.07 × 10 ⁶
Difference, net transport minus streamflow, m ³ /tide	0.02 × 10 ⁶	(-)0.04 × 10 ⁶
Weighted average salinity, incoming water, ‰	29.4	27.9
Weighted average salinity, outgoing water, ‰	23.9	25.6
Salt transport, in through The Narrows, kg./tide	7.9 × 10 ⁶	25.3 × 10 ⁶
Salt transport, out through The Narrows, Kg./tide	7.9 × 10 ⁶	23.9 × 10 ⁶

*Calculated.

On August 19 greater total transports through The Narrows were observed than on August 12. Tide ranges on August 19 were also greater; the average range during the observed cycle was 3.6 m. During the first 3 hours of flood the entire water column moved into Inner Bay, despite the fact that observed streamflow was nearly twice that observed for August 12 (0.07×10^6 m³/tide vs. 0.035×10^6 on August 12). On the 19th, however, wind was absent during most of flood, with only occasional slight gusts from the north-east. By the fourth hour of flood the upper one-half meter was running out and continued to do so until the end of ebb. The remainder of the column flowed in until slack before ebb. Current velocities were appreciably greater than those observed on August 12, with peaks of 23.5 cm./sec. and 24.0 cm./sec. at maximum flood and maximum ebb, respectively. Current velocities were consistently of sufficient magnitude for direct observation by current meter.

The results of August 12 and 19 are shown in table 3.

As a check on the results for August 12, transport was estimated from $V=A \times 2_{70}$. The average given by this method was 0.49×10^6 m.³/tide, and is appreciably greater than, but of the same order of magnitude as, the measured-calculated average of 0.295×10^6 . This difference probably resulted from the inability to measure that outflow which took place below a depth of one-half meter and not from the lowering of observed current velocities by one-third. This conclusion is substantiated by the excellent agreement between the two methods obtained on August 19, when current velocities were sufficiently strong for direct measurement at all depths.

The results for August 19 were checked in the same manner. Calculated average transport was 0.93×10^6 m.³/tide, in excellent agreement with the measured average of 0.90×10^6 .

Under steady state conditions, the excess of outflow over inflow should equal the fresh-water contribution to Inner Bay. Such an ideal balance was not obtained from the observations of either August 12 or 19. However, on both dates the estimated volume of flow of Sashin Creek must, realistically, be accepted as an approximation only. In addition, total transport in through The Narrows on August 12 could not be measured directly, and it is believed that the total transport out was only partially measured. In consideration of these factors, as well as the realization that water transport measurements of this type give, at best, approximate figures, the discrepancies between estimated streamflow and the net transport out of Inner Bay are not disturbing. The degree of agreement that was obtained is probably about all that should be expected.

LITERATURE CITED

- ANDERSON, D. V., and G. K. RODGERS.
1959. The delta of the Niagara River. Department of Research, Ontario Department of Lands and Forests, Physics Research Note No. 5, 4 pp, 7 figs.
- HACHEY, H. B.
1934. Movements resulting from mixing of stratified waters. Journal of the Biological Board of Canada, vol. 1, no. 2, pp. 133-143.
- KETCHUM, BOSTWICK H., ALFRED C. REDFIELD, and JOHN C. AYERS.
1951. The oceanography of the New York Bight. Papers in Physical Oceanography and Meteorology, vol. 12, no. 1, 46 pp.
- MARSHALL, NELSON, and STEACY D. HICKS.
1962. Drift of medusae and their distribution in relation to the hydrography of the Niantic River, Conn. Limnology and Oceanography, vol. 7, no. 2, pp. 268-269.
- PRITCHARD, D. W.
1955. Estuarine circulation patterns. Proceedings of the American Society of Civil Engineers, vol. 81, separate 717, 11 pp.
- ROBINS, C. RICHARD, and RONALD W. CRAWFORD.
1954. A short accurate method for estimating the volume of stream flow. Journal of Wildlife Management, vol. 18, no. 3, pp. 366-369.
- SVERDRUP, H. U., MARTIN W. JOHNSON, and RICHARD H. FLEMING.
1946. The oceans. Their physics, chemistry, and general biology. Prentice-Hall, Inc., N. Y., 1060 pp.
- TULLY, JOHN P.
1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. Fisheries Research Board of Canada, Bulletin No. 83, 169 pp. [University of Washington, Publications in Oceanography, Contribution No. 144.]
- U.S. COAST AND GEODETIC SURVEY.
1959. Tide tables, West Coast North and South America including the Hawaiian Islands. U.S. Government Printing Office, Washington, D.C., 224 pp.
- VON ARX, WILLIAM S.
1950. Some current meters designed for suspension from an anchored ship. Journal of Marine Research, vol. 9, no. 2, pp. 93-99.

EARLY LARVAL STAGES OF THE SEABOB, *XIPHOPENEUS KRØYERI* (HELLER)

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ABSTRACT

Five naupliar stages and the first protozoal stage of the seabob (*Xiphopeneus kroyeri*) have been described from larvae reared in the laboratory. With each molt the larva increases in length and becomes more ad-

vanced in its morphology. Differences in body structures among specimens in the same instar were noted and discussed.

The ultimate goal of shrimp research is to understand the factors affecting population numbers. This includes the dynamics of the young through the juvenile stages. To this end, studies of the abundance, distribution, and biology of larval penaeids are being pursued by the Bureau's Biological Laboratory at Galveston. In the Gulf of Mexico adjacent to this laboratory at least 13 penaeid species occur. Thus, any measurement of the seasonal and areal abundance of the young of the commercially important shrimps requires the differentiation of the various species at all developmental stages. This report gives the early stages of one of these penaeid species. Dobkin (1961) has adequately summarized the existing literature on penaeid larvae.

Xiphopeneus krøyeri is found from South Carolina to the middle Atlantic coast of Brazil. As it is also known from Puerto Rico, it probably occurs along the coasts of other Caribbean islands. Within this range the species varies greatly in abundance, having commercial importance only in the mid-Gulf States and along the northeastern coast of South America. Although its life history has not been extensively studied, the seabob is a littoral species found most often at depths less than 6 or 7 fathoms and rarely in protected bays inside the barrier islands.

METHODS AND MATERIALS

All descriptions and figures are from specimens reared in the laboratory. Gravid females were caught at sea and returned to laboratory aquaria. After spawning, eggs were pipetted from the bottoms of the aquaria into beakers of sea water and the resulting larvae observed continuously. As development proceeded, specimens of each larval stage were measured, photographed, and preserved in buffered 5 percent formalin. Details of rearing trials are included in the appendix.

Microscope magnifications ranged from 10 \times to 200 \times . Measurements to the nearest 0.01 mm. were made with an ocular grid calibrated against a stage micrometer. We observed, as did Hudinaga (1942), some growth and development of body features occurring between molts. For this reason specimens in the same instar may exhibit differences in the size and shape of body structures. Figures were drawn with the aid of a camera-lucida and represent a conscious effort to illustrate the "typical" or most prevalent form of each stage.

In the ventral aspect many details of the naupliar appendages are obscured. In order to illustrate as clearly as possible all morphological features, dextral appendages have been drawn as though they had been rotated on their axes.

NOTE.—Approved for publication July 9, 1962.

DESCRIPTION OF THE EGG AND NOTES ON HATCHING

Twenty-six viable eggs had a mean diameter of 0.16 mm. with extremes from 0.15 to 0.17 mm. Although the egg is demersal, sinking readily in still sea water, it is easily buoyed up by slight agitation of the water. The nauplius, surrounded by the embryonic membrane, fills the egg. In later stages its appendages and a well-defined ocellus (naupliar eye) can be clearly seen through the thin, transparent shell (fig. 1). Prior to hatching, rapid, vibrating movements of the nauplius occur at more or less regular intervals.

The emerging nauplius first forces one appendage through the egg shell, then moves this appendage violently to enlarge the opening through which it finally escapes. Immediately after hatching, the nauplius is curled with its appendages drawn in posteriorly along the sides of the body. It soon assumes the normal shape as shown in figure 2.

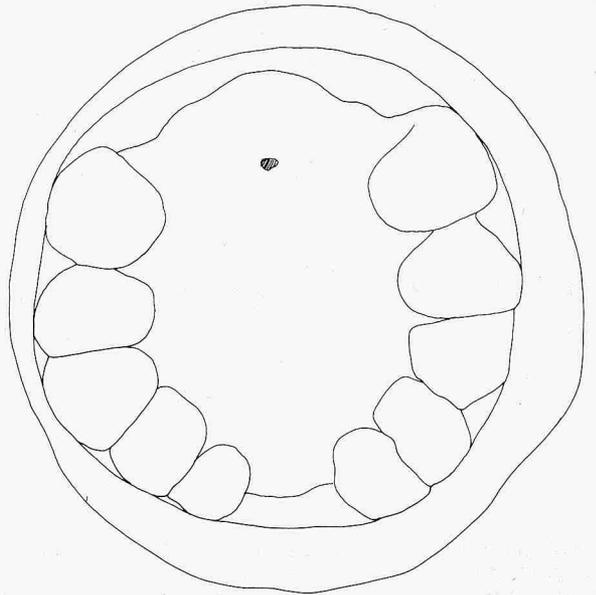


FIGURE 1.—Egg containing developing nauplius.
Photomicrograph of ventral view.

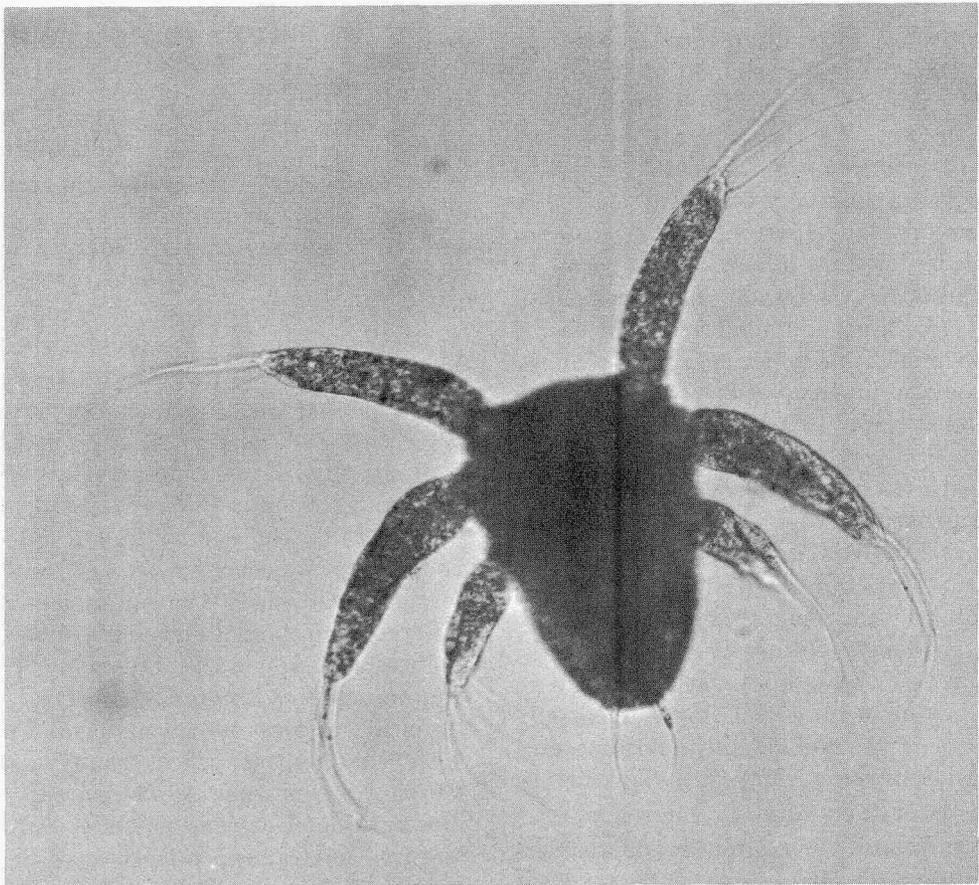


FIGURE 2.—Photomicrograph of Nauplius I, ventral view.

At rest, the nauplius lies dorsal surface down. As its appendages beat in unison, it rises a short distance then sinks when movement ceases. Active swimming lasts approximately 2 seconds with a rest period of about 8 seconds. Older nauplii swim longer and rest less.

The yolk granules filling the body give it a grainy appearance. After preservation for several weeks in 5 percent formalin, all color is lost, and the yolk granules become opaque, giving the preserved nauplius a silver, grainy appearance in strong light.

DESCRIPTIONS OF STAGES

NAUPLIUS I

The Nauplius I of *X. krøyeri* has a short, pyriform body (figs. 3 and 4). Body length of 25 specimens measured from the apical to caudal ends but excluding furcal spines averaged 0.26 mm. Measurements across the dorsal surface at the point of greatest width averaged 0.15 mm.

A small but distinct protuberance on the dorsal surface gives all naupliial stages a humpbacked appearance. The medial point of the hump falls

between the origins of the second and third appendages. A slight depression is sometimes found posterior to the hump.

The ocellus lies in the longitudinal axis of the body near the anterior end and retains its position and color in all later naupliial stages. In living specimens it is reddish or rust colored but turns black in formalin.

The labrum or upper lip appears as a protrusion of the ventral surface. It is thickest at its posterior end and extends posteriorly to or just beyond the origins of the third appendages.

Two furcal spines arising at the posteroventral end of the body generally project directly backward but curve upward in some specimens. Viewed ventrally they are seen to curve inward.

Three pairs of appendages are inserted ventrally on the anterior half of the body. The anterior pair, or first antennae, are unbranched. The middle appendages, or second antennae, are branched into ventral endopods and dorsal exopods. The posterior appendages, or mandibles, are also branched into ventral endopods and dorsal exopods. All appendages bear setae which have been assigned arbitrary numbers to facilitate their description in the text. Starting with the anterior, proximal seta on each dextral appendage, the setae are numbered counterclockwise in the figure. It must be emphasized that setae are numbered on appendages which are represented as having been rotated around their axes. A given seta does not always retain the same number in subsequent figures. That is, with addition or loss of setae on an appendage, the setae are renumbered.

Each first antenna originates at the anteroventral edge of the body and curves outward. It possesses six setae. Setae 1, 2, and 3 are inserted on the anteroventral edge of the appendage. Seta 1 may not always be distinct; its position may merely be indicated by a slight protuberance. Setae 4 and 5 are terminal, and seta 6 arises from the posterodorsal surface near the end. On most specimens a short, spikelike spine, which may be the bud of another seta, projects from the ventral surface near the end of the first antenna.

The second antennae arise immediately posterior to the origins of the first antennae and are directed obliquely backward. The endopod of each second antenna appears as an extension

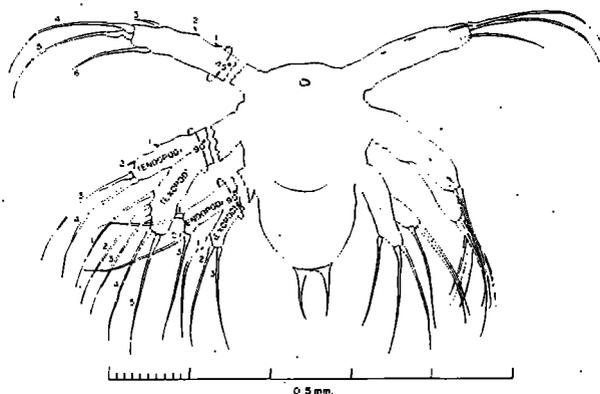


FIGURE 3.—Nauplius I, ventral view.

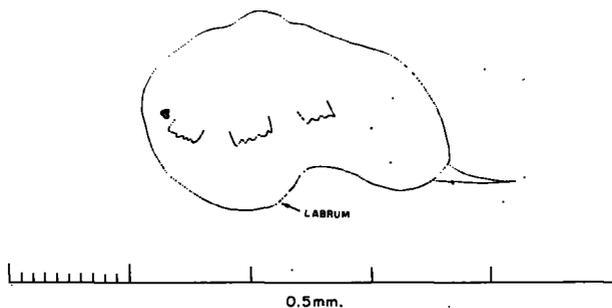


FIGURE 4.—Nauplius I, lateral view.

of the basal portion and bears four setae. Setae 1 and 2 arise along the ventral midline, while setae 3 and 4 are terminal. A small, spikelike spine projects from the ventral surface at the distal end. The exopod of each second antenna is inserted on the dorsal surface. It is slightly longer than the endopod and bears five setae. Setae 1, 2, and 3 originate along the midline on the ventral surface, and setae 4 and 5 are terminal.

The posterior appendages, or mandibles, have their origins on the ventrolateral edges of the body about halfway between the anterior and posterior ends. Each endopod is directed posteriorly and bears three setae. Seta 1 is inserted on the posteroventral surface near the distal end, and setae 2 and 3 are terminal. The exopod branches from the dorsal surface of each mandible and bears three setae of nearly equal length. Setae 2 and 3 are terminal, and seta 1 is subterminal. Setaion of the endopods and exopods of the mandibles remains constant in all subsequent naupliar stages.

NAUPLIUS II

Twenty-five Nauplius II specimens averaged 0.27 mm. in length and 0.15 mm. in greatest width (figs. 5 and 6). The labrum has a pronounced fold posteriorly, and a second fold, the labium or lower lip, can be seen behind the labrum in the lateral view. The two furcal spines are longer,

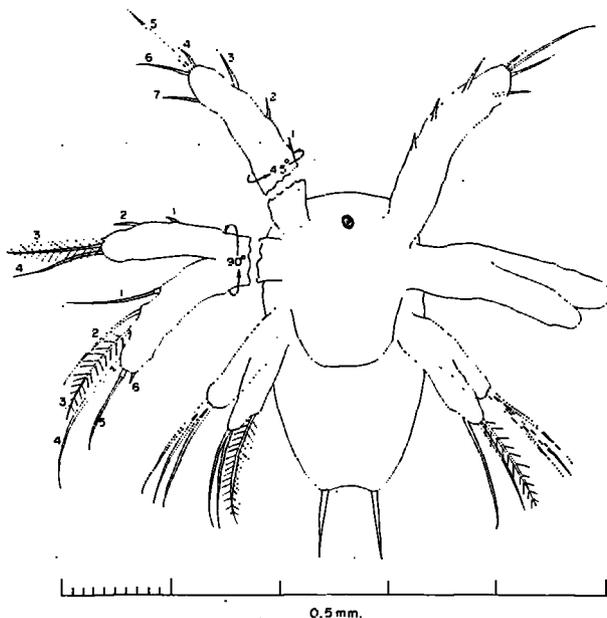


FIGURE 5.—Nauplius II, ventral view.

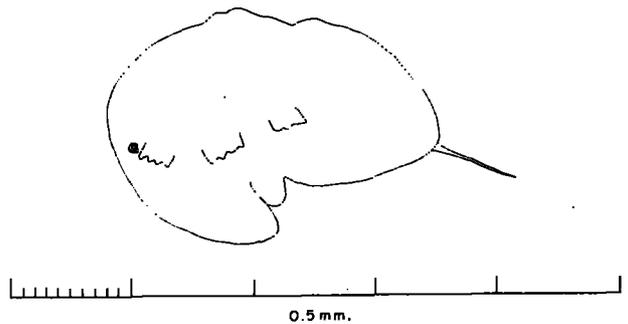


FIGURE 6.—Nauplius II, lateral view.

straighter, and inserted farther apart than those of Nauplius I.

Shapes of the appendages are not changed, but all are slightly longer. Some setae, generally the longer ones, become plumose with the addition of setules along their lengths; however, this condition varies among specimens in this stage.

The spikelike spine on each first antenna of Nauplius I has lengthened to become seta 4, while the terminal and dorsolateral setae are shorter.

The endopod of each second antenna retains the setation of Nauplius I except that the two terminal setae are shorter. Each exopod of the second antennae gains a short sixth seta terminally. Setae 4 and 5 have short, cylindrical shanks at their bases. These basal shanks are also found occasionally on other long setae of second nauplii. Setae 1, 2, 3, 4, and 5 are generally plumose.

As previously stated, setation of the mandibles remains constant in all naupliar stages.

NAUPLIUS III

Nine Nauplius III specimens averaged 0.29 mm. in length and 0.15 mm. in width (figs. 7 and 8). Both the labrum and labium are larger. Four pairs of ventral appendages, which will appear externally in the next stage, can be seen beneath the cuticle in lateral view.

Three pairs of small furcal spines have been added, two pairs laterally (spines 1 and 2) and one pair medially (spine 4). The furcal spine count thus becomes 4+4. The posterior half of the body appears slightly more slender, and the caudal end shows definite bifurcation.

All longer setae are plumose in this stage, and the basal shanks, which first appeared in the preceding stage, are longer and occur more frequently.

Setation of the first antennae is unchanged.

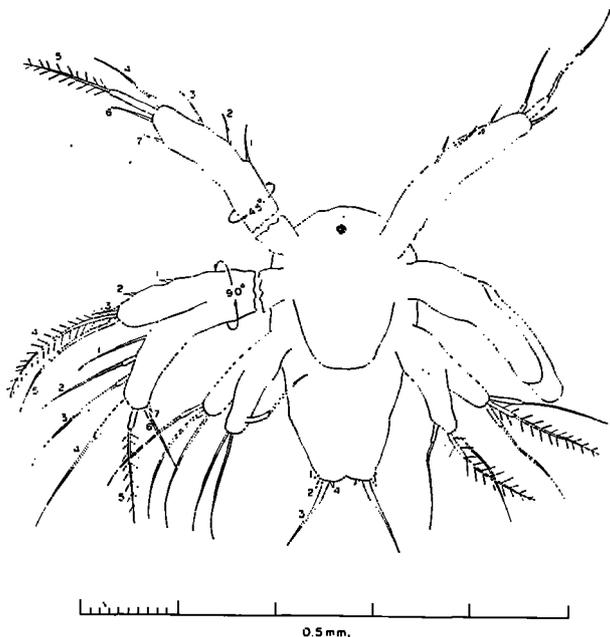


FIGURE 7.—Nauplius III, ventral view.

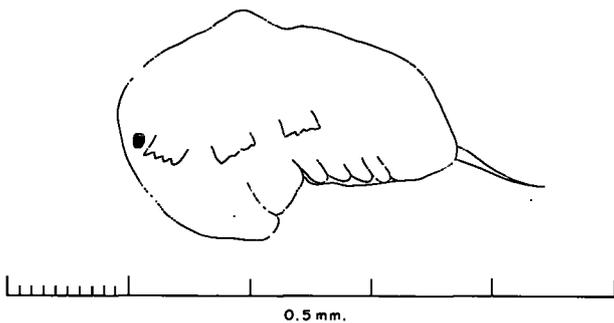


FIGURE 8.—Nauplius III, lateral view.

Setae 1, 2, 3, and 4 are longer, and seta 7 is shorter than in the last stage.

On the endopod of each second antenna the spikelike spine, which was present in the preceding two stages, has lengthened to become seta 3. The exopod of each second antenna gains a small seta (seta 7) terminally, and seta 6 has become longer.

The bases of the mandibles in some specimens appear to be swollen.

NAUPLIUS IV

Measurements of 13 Nauplius IV specimens showed their average length to be 0.34 mm. and average width 0.16 mm. The body is more elongate and slender posteriorly (figs. 9 and 10). Faint outlines of a carapace have appeared on the

dorsal surface. A pair of "frontal organs" appear as slight protuberances at the anterior margin of the body. The labrum narrows posteriorly, and the labium can now be seen in the ventral view.

Four pairs of biramous appendages (the first and second maxillae and the first and second maxillipeds) are now prominent on the ventral surface of the posterior half of the body.

Definite, lobelike furcal processes are now apparent, and with the addition of one pair of lateral spines and another pair medially, the furcal spine count is 6+6.

Setation of the first antennae does not change. On the endopods of the second antennae, setation is unchanged except for the addition of a terminal spikelike spine inserted ventrally. The exopod of each second antenna acquires an additional seta, making its total setae count eight.

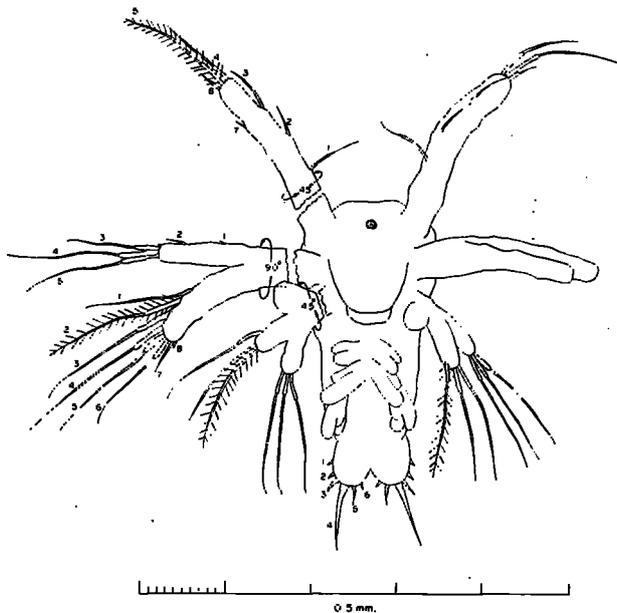


FIGURE 9.—Nauplius IV, ventral view.

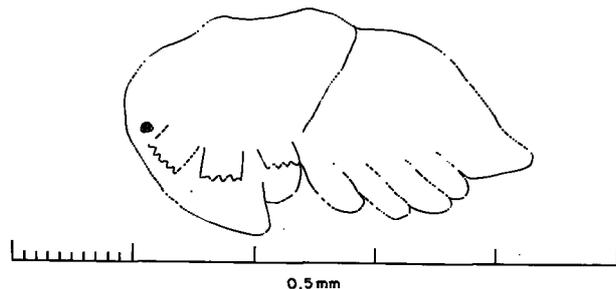


FIGURE 10.—Nauplius IV, lateral view.

Setation of the mandibles remains unchanged, but a prominent rounded lobe appears at the base of each. This is the rudiment of a masticatory organ, and combined with the appearance of the maxillae and maxillipeds, is the most characteristic feature of Nauplius IV.

NAUPLIUS V

Seven specimens of Nauplius V averaged 0.39 mm. in length and 0.16 mm. in greatest width. The body is more elongate, the carapace more prominent, and the frontal organs more sharply defined than in the preceding stage (figs. 11 and 12). The labrum is further narrowed posteriorly and the labium is now bilobed.

The maxillae and maxillipeds have lengthened and now bear two or three terminal setae on each branch.

The caudal furcae are further separated by a sulcus which has developed between them. With the addition of a pair of spines inserted medially, furcal spine count is 7+7.

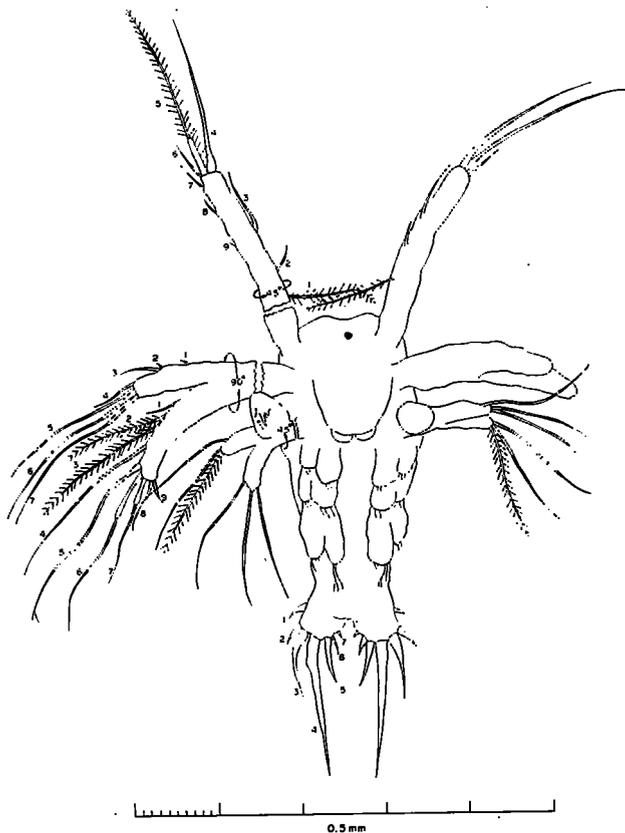


FIGURE 11.—Nauplius V, ventral view.

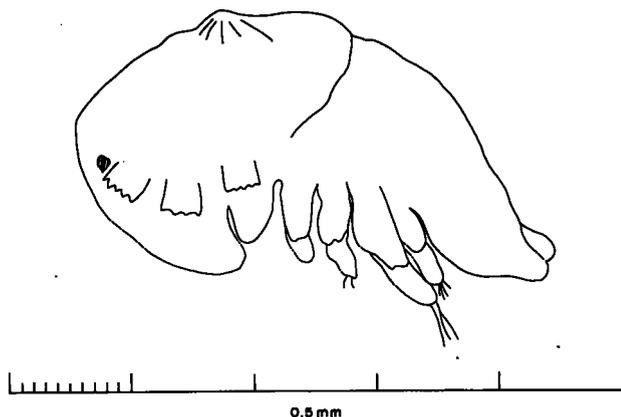


FIGURE 12.—Nauplius V, lateral view.

On each first antenna there are now three dorso-lateral setae as a result of the addition of setae 7 and 9.

On the endopod of each second antenna a small seta (seta 2) is present near the base of seta 3, and the small, terminal bud which was present in the last stage has lengthened to form seta 4. Each exopod gains an additional seta to make its total nine.

As in previous stages, setation of the mandibles is unchanged, but the endopods are frequently transparent. The rudimentary masticatory organ at the base of each mandible is further enlarged and is shaped somewhat like a strawberry. Transparent, toothed structures are faintly discernible on its posterior surface.

PROTOZOA I

Measured from the anterior margin of the carapace to the ends of the furcae, eight Protozoa I specimens averaged 0.69 mm. Six averaged 0.32 mm. in greatest carapace width and 0.36 mm. in carapace length (figs. 13, 14, and 15).

Although the Protozoa I does not move as rapidly as the Nauplius V, it is much stronger, swimming almost continuously with its ventral surface up. All appendages except the mandibles appear to aid in locomotion, and occasionally protozoa were observed to bend the abdomen beneath the cephalothorax and flip themselves when meeting an obstacle.

The carapace, which is somewhat flattened, fits loosely on the dorsal surface. The dorsal protuberance present in the nauplii persists but is not so prominent in this stage. The anterior edge of the carapace is divided into two lobes each of which

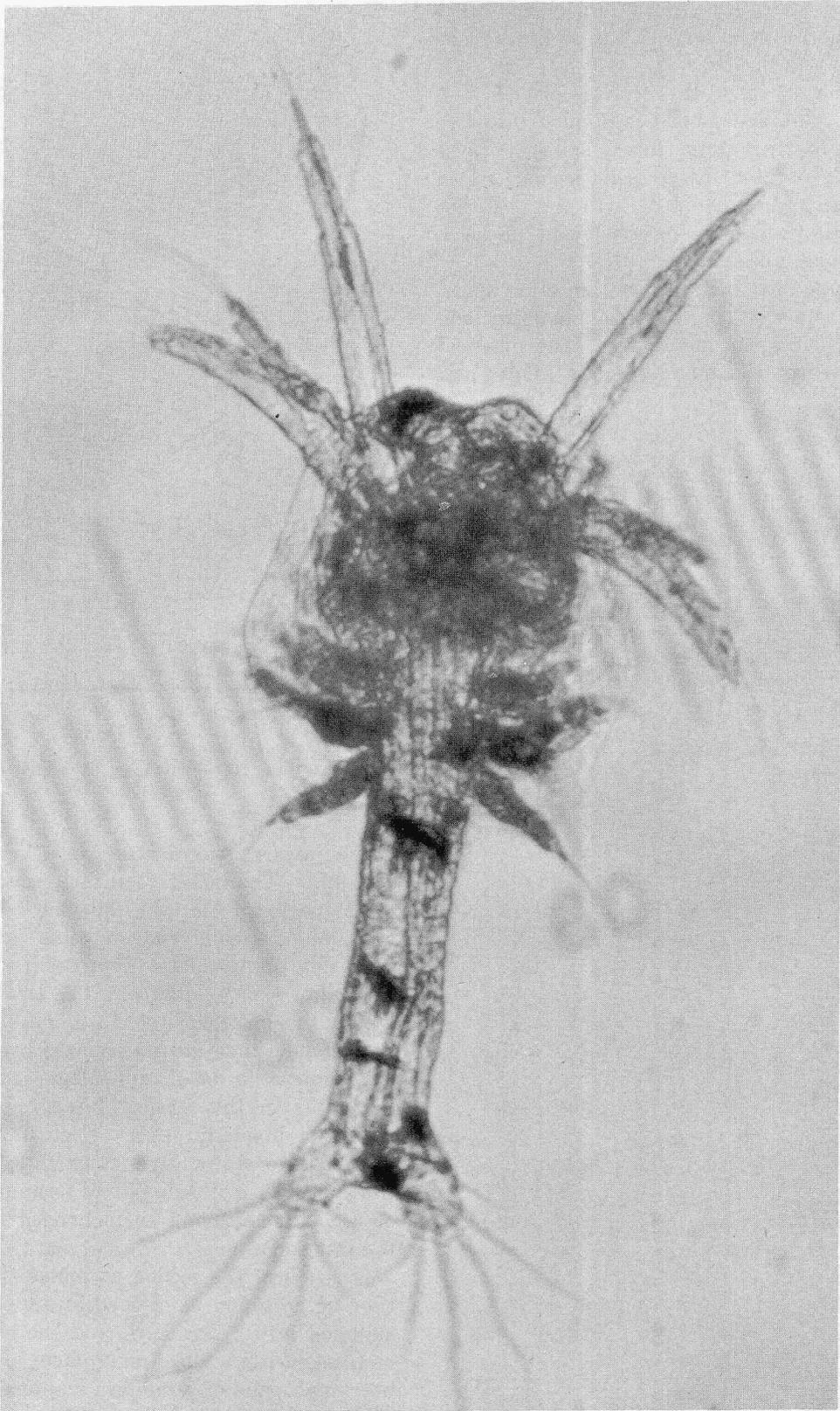


FIGURE 13.—Photomicrograph of Protozoa I, ventral view.

bears a well-developed frontal organ ventrally. The compound eyes as well as the ocellus can be seen beneath the carapace.

Behind the carapace the body is slender and segmented. The caudal end is divided into two lobes, each bearing seven furcal spines. These furcae are separated by a semicircular notch through which the anus opens. In the posterior portion of the body the intestine can be seen, flanked by long muscle fibers.

The labrum now has a stout, anterior spine, bears fine setae on its posterior margin, and partially obscures the mandibles. The masticatory processes of the mandibles are longer and

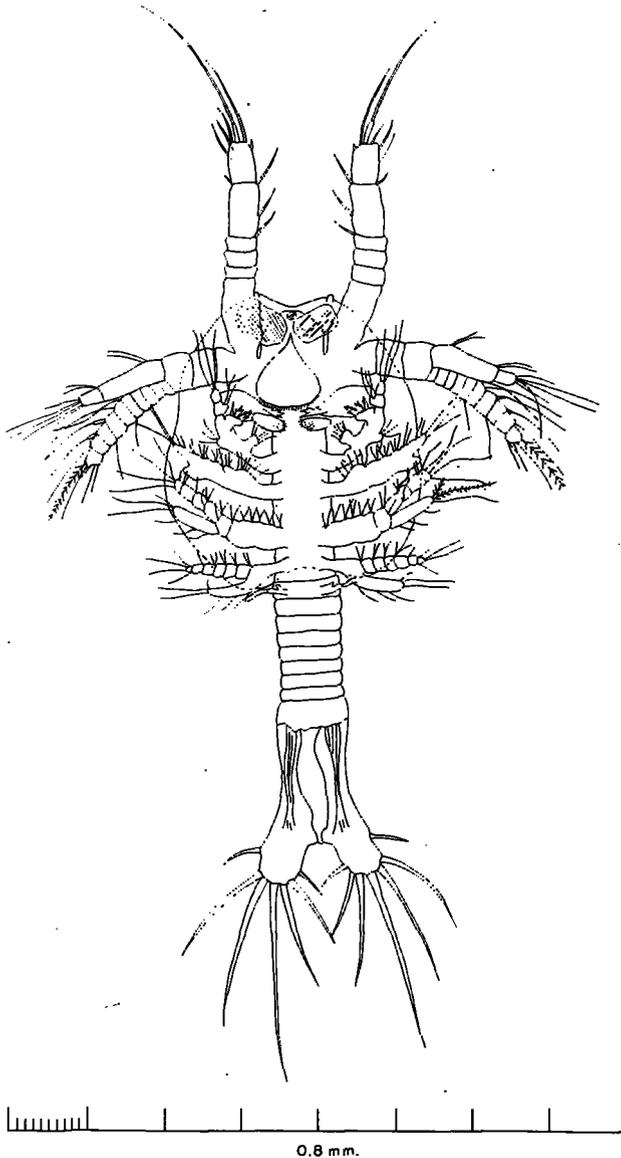


FIGURE 14.—Protozoa I, ventral view.

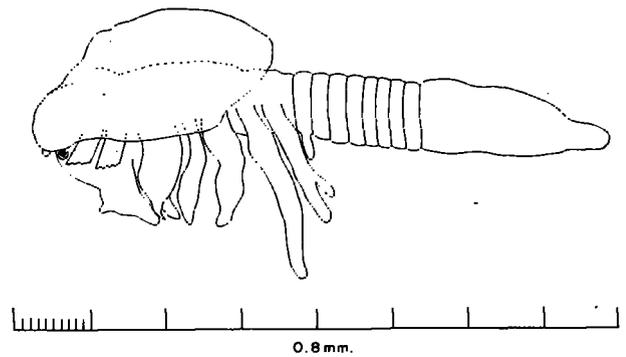


FIGURE 15.—Protozoa I, lateral view.

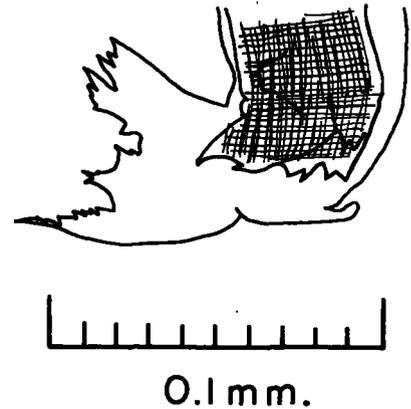


FIGURE 16.—Protozoa I, right mandible, posterior view.

curve inward, terminating in a ring of teeth (fig. 16). The larger teeth are prominent structures posterior to the labrum. Within each mandible a second ring of teeth is present. A small lobe directed laterally arises from the ventral surface of each mandible. The two lobes of the labium lie posterior to the mandibles and bear fine setae on their medial surfaces.

Segmentation of all appendages occurs for the first time in this stage, although segments are indistinct in many cases. Each first antenna is divided into six or seven segments. Except for the appearance of a small bud terminally, setation of each first antenna is unchanged from that of the last stage.

On each of the second antennae the basal portion, or protopod, is divided into 3 segments, the endopod into 2 segments, and the exopod into 9 or 10 segments. The first segment of the endopod bears two pairs of setae on its anteroventral margin: one pair proximally and the second distally.

The distal segment bears five terminal setae. The exopod of each second antenna bears five setae on its anteroventral margin, one each arising from the fifth, sixth, seventh, eighth, and ninth segments. Its 10th segment bears four terminal setae. The fifth and seventh segments also have a single seta on their posterodorsal surface.

The protopod of each first maxilla (fig. 17) is unsegmented but has two lobes on its anterior margin. The proximal lobe bears eight short, thick setae, and the distal lobe bears three stout setae, which are barbed terminally. The en-

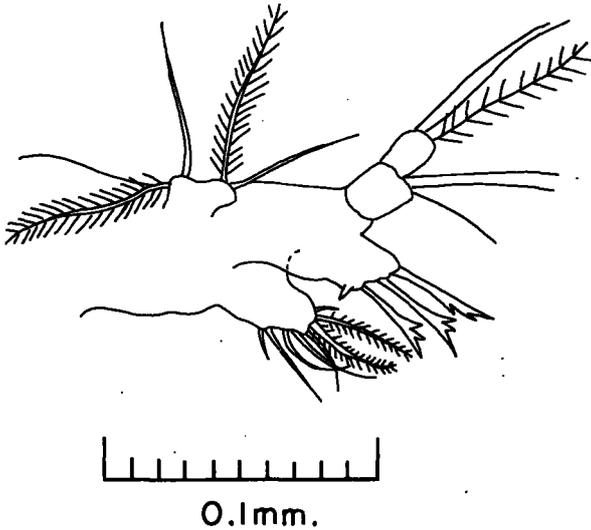


FIGURE 17.—Protozoa I, right first maxilla, posterior view.

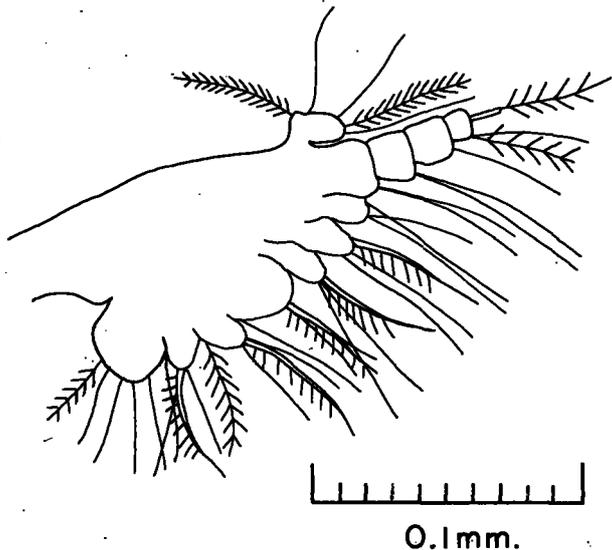


FIGURE 18.—Protozoa I, right second maxilla, posterior view.

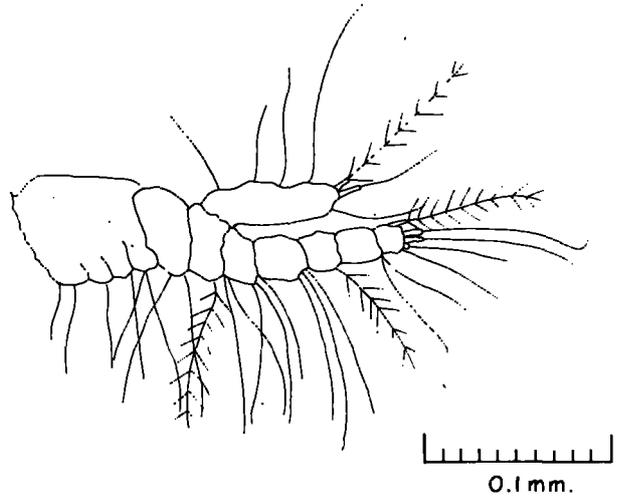


FIGURE 19.—Protozoa I, right first maxilliped, posterior view.

dopod is composed of two segments bearing three setae each. The exopods of the first maxillae are present as small, spherical knobs, each of which bears four setae.

The protopod of each second maxilla (fig. 18) shows no segmentation but has seven small lobes on its anterior margin. The first four lobes are sometimes coalesced to form one large lobe. The first or proximal lobe bears six setae while the remainder bear three or four. Two setae also arise from the distal end of the protopod. The endopod is composed of three segments: the proximal bearing two setae; the middle, one; and the distal, three. The exopod is a small knob which bears five setae.

The protopod of each first maxilliped (fig. 19) is composed of three segments. The proximal segment has four lobes on its anterior margin, each bearing one or two setae. The second and third segments of the protopod also bear one or two setae. Each endopod has five segments, the first four bear one to three setae on their anterior margins and the fifth possesses five terminal setae. The exopod of each first maxilliped is unsegmented and bears four lateral and three terminal setae.

The second maxillipeds (fig. 20) closely resemble the first maxillipeds. Their protopods consist of four segments, each of which bears one or two setae. Each endopod is composed of six segments with the first five segments bearing one or two setae on their anterior margins and the sixth bearing three terminal setae. The exopod of each

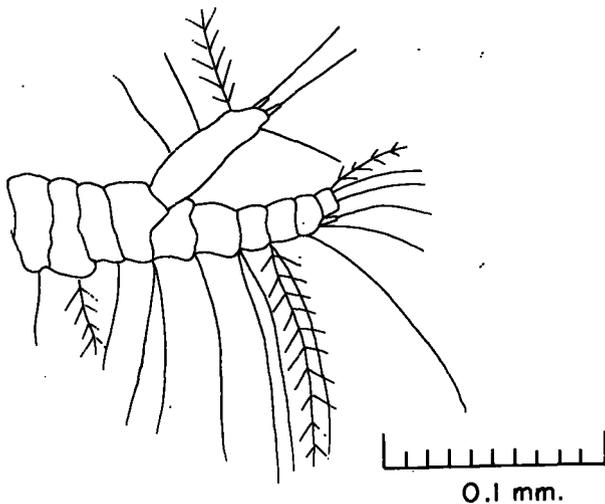


FIGURE 20.—Protozoa I, right second maxilliped posterior view.

second maxilliped is unsegmented and bears three posterolateral and three terminal setae.

Posterior to the second maxillipeds is a pair of small third maxillipeds. The exopods are considerably longer than the endopods and bear two terminal setae.

MORPHOLOGICAL VARIATION AMONG SPECIMENS WITHIN AN INSTAR

The development of these normally planktonic larvae was probably slower in the laboratory than in nature. For example, molting in some specimens continued for 15 minutes or more in the laboratory. In the sea, this process might be completed in much less time. It is possible, therefore, that the morphological variations discussed here were observable only because normal developmental rates were retarded.

Hudinaga (1942, p. 331) stated: "It may be said that in Crustacea the body-length increases only by moulting, but in some species there is a slight difference in the length immediately after one moult and before the next, an outstanding example of which is the zoea stage of *P. japonicus*." During our rearing trials individual nauplii were isolated in small containers and observed periodically. Slight elongation of some body parts was observed, but actual, periodic measurements of the moving larvae were not attempted. The spines and setae of all preserved specimens were measured to the nearest 0.01 mm. These measurements were examined to determine the extent of variation in morphology among specimens in the

same instar. The results showed: (1) Nauplius I. Fourteen specimens had one pair of furcal spines 0.04 to 0.05 mm. long and 10 specimens possessed one pair of furcal spines measuring 0.06 mm. The 10 specimens with larger furcal spines also had longer setae on all appendages. (2) Nauplius II. Ten specimens with furcal spines 0.06 to 0.08 mm. long had, in almost every case, longer setae than did 13 specimens with furcal spines 0.04 to 0.05 mm. in length. (3) Nauplius III. Three groups of specimens were distinguished (table 1); three with four pairs of furcal spines, four with three pairs, and two with two pairs. Specimens with fewer and shorter furcal spines also had shorter setae. Of interest was the fact that the furcal spines missing in the two groups having shorter setae were those spines which are added at this instar. (4) Nauplius IV. Four specimens with four pairs of furcal spines had, in most instances, shorter setae than the remaining five specimens with six pairs. (5) Nauplius V. Of seven specimens one had four pairs of furcal spines, one had five pairs, and five specimens had seven pairs. In general the specimens with fewer furcal spines had shorter setae.

Obviously, individual nauplii in the same instar differ considerably in their body dimensions. Several possible causes for these observed differences might be considered: (a) The nauplii with shorter and fewer furcal spines and setae may be malformed specimens which die before reaching the next instar. (b) The differences are the result of individual variation, some nauplii simply being smaller and less well developed than others. (c) These tiny larvae, covered with a thin cuticle, continue to develop and lengthen, during the period between molts.

Another cause for variation observed among individuals in the same stage of development lies in the molting process. Loss of the exoskeleton was observed to begin at the posterior end of the nauplius. The furcal spines and the posterior cuticle were shed first followed by the setae and exoskeleton of the mandibles, the second antennae, and the first antennae. In most cases, the body exoskeleton was lost in pieces. The molting of right and left appendages did not always occur simultaneously. Because molting of all parts was not instantaneous, a number of our specimens had only partially shed their exoskeletons. In one Nauplius IV specimen, for example, the right

TABLE 1.—*Nauplius III*, mean length of furcal spines and setae in specimens with different furcal spine counts
[0.01-mm. units]

Process	Furcal spine count		
	2+2	3+3	4+4
Furcal spine 1.....	(1)	(1)	>1.0
Furcal spine 2.....	(1)	1.0	2.0
Furcal spine 3.....	6.0	7.0	10.7
Furcal spine 4.....	>1.0	>1.0	1.0
First antenna:			
Seta 1.....	2.0	2.3	8.0
Seta 2.....	2.0	2.5	3.3
Seta 3.....	5.0	2.5	5.7
Seta 4.....	5.0	6.0	12.3
Seta 5.....	9.0	11.8	17.7
Seta 6.....	5.0	3.8	4.0
Seta 7.....	(2)	>1.5	>2.5
Second antenna:			
Endopod:			
Seta 1.....	>1.0	>1.0	>1.0
Seta 2.....	>1.0	1.5	>1.3
Seta 3.....	(2)	2.5	6.3
Seta 4.....	10.0	13.0	18.7
Seta 5.....	10.0	13.0	18.7
Exopod:			
Seta 1.....	5.0	7.0	12.0
Seta 2.....	5.0	11.8	17.3
Seta 3.....	6.0	12.3	17.3
Seta 4.....	10.0	13.0	22.0
Seta 5.....	6.0	10.8	15.7
Seta 6.....	>1.0	5.8	9.7
Seta 7.....	>1.0	>2.0	1.3
Mandibles:			
Endopod:			
Seta 1.....	8.0	9.2	14.0
Setae 2 and 3.....	11.0	11.0	15.0
Exopod:			
Setae 1, 2, and 3.....	11.0	11.8	15.7

¹ Not measured.
² Absent.

second antenna had molted, while the left second antenna retained the exoskeleton of the previous instar, thus the right had more setae than the left. Occasionally the exoskeleton of an appendage had loosened but was not completely shed at the time of preservation. Its new setae, which were visible beneath the old cast, were very small.

Listed below are variations from the described forms:

NAUPLIUS I

The slight depression posterior to the dorsal hump was not present on a few of the specimens studied.

The labrum varied in size from slight to very prominent.

Seta 1 on the anteroventral margin of each first antenna was absent in 2 of 25 specimens.

Seta 1 on the endopods of the second antennae was not present in 3 of 25 specimens.

NAUPLIUS II

Some specimens, preserved in the process of molting, exhibited appendage setation characteristic of Nauplius II while retaining the Nauplius I setation on the corresponding appendage of the opposite side. Frequently, the cast of an append-

age had only partially slipped off and obscured the new setae beneath it.

Addition of setules to the setae varied in individual specimens and among the different specimens. That is, some specimens had plumose setae on one appendage while corresponding setae on the opposite appendage or on another specimen lacked setules.

The shanks present at the bases of setae 4 and 5 on the exopods of the second antennae were also found randomly on all longer setae.

The terminus of seta 4 on the exopod of each second antenna was split in occasional specimens of Nauplius II and later stages. This seta is always the longest seta on the exopod although its number may change.

NAUPLIUS III

In three specimens a small median spine between the furcae was noted.

On two specimens having three pairs of furcal spines, seta 7 on the exopods of the second antennae was absent. Variation in the number of furcal spines has previously been discussed.

NAUPLIUS IV

Four individuals possessed four pairs of furcal spines, five had six pairs, and one specimen was too badly damaged to determine the spine count.

Seta 8 on the exopods of the second antennae was absent in two of six specimens which were otherwise in good condition.

NAUPLIUS V

Seta 2 on the endopods of the second antennae was missing in three of seven specimens.

PROTOZOA I

No significant morphological differences were noted among the eight specimens examined.

SUMMARY

There are five naupliar stages during the early larval development of the seabob. With each molt the larva increases in length and becomes more advanced in its morphology. Differences in various body structures among specimens in the same instar are discussed. A characteristic which is usually sufficient to separate naupliar stages is the addition of one seta on the exopods of the second antennae with each molt. This and other characteristics are summarized in table 2.

TABLE 2.—Counts of furcal spines and setae

Stage	Furcal spines	Setae on—				
		First antenna	Second antenna		Mandible	
			Endopod	Exopod	Endopod	Exopod
Nauplius I.....	1+1	6	4	5	3	3
Nauplius II.....	1+1	7	4	6	3	3
Nauplius III.....	4+4	7	5	7	3	3
Nauplius IV.....	6+6	7	6	8	3	3
Nauplius V.....	7+7	9	7	9	3	3
Protozoa I.....	7+7	9	9	11	-----	-----

LITERATURE CITED

DOBKIN, SHELDON

1961. Early developmental stages of pink shrimp, *Penaeus duorarum* from Florida waters. U.S. Fish and Wildlife Service, Fishery Bulletin 190, vol. 61, pp. 321-349.

HUDINAGA, MOTOSAKU

1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Japanese Journal of Zoology, vol. 10, no. 2, pp. 305-393, 46 plates. Tokyo.

APPENDIX 1

NOTES ON REARING

Trial 1

The first seabob to spawn viable eggs was caught October 7, 1959, with a 10-foot otter trawl 6 miles northeast of the Galveston Jetties in a depth of 5 fathoms. This female was returned to the laboratory and placed in a plastic barrel filled with sea water filtered through a plankton net. Thirteen hours later, eggs were found in the container. The eggs were pipetted from the container bottom and distributed among seven 4-liter beakers filled with water from the spawning container. These beakers were sampled for larvae periodically during the next 110 hours.

Hatching began shortly after introduction of the eggs into the beakers and continued for 2 days. As development proceeded, specimens of each instar were examined and preserved for future study. Water temperatures in the beakers ranged from 19.6° to 25.0° C. during the trial, and salinity measured 29.5‰. Mortality in all instars proved high, and no more than 40 specimens reached the Protozoa I stage.

At the conclusion of this trial, preliminary descriptions of each instar were begun. It soon became apparent, however, that too few specimens of Nauplius III and IV in good condition were available to complete the figures and descriptions.

Trials 2 to 6

Through the spring, summer, and fall of 1960 repeated attempts to rear seabob larvae failed. On five different occasions gravid females were captured and returned to the laboratory. Some aborted their eggs in gelatinous masses, while the eggs of others were round and smooth but proved

nonviable. Sometimes viable eggs were spawned and appeared to develop normally for a time, only to stop for no apparent reason. Destruction of the eggs by micro-organisms, chiefly bacteria and ciliates, frequently caused hatching failures. Entanglement of the larvae in detritus also seriously hindered the rearing trials.

After each failure, efforts to improve conditions in the rearing containers were made. These included: addition of antibiotics, irradiation with ultraviolet light, filtration, centrifuging, and preheating the medium to rid it of micro-organisms. Artificial sea water was tried as a medium also. Despite these efforts, all rearing trials failed during 1960.

Trial 7

On April 25, 1961, 2 dozen gravid females, collected from 2 to 3 fathoms northeast of the Galveston Jetties, were returned to the recently completed circulating sea-water laboratory. Here they were distributed among five small glass aquaria and three circular, wooden tanks, 4 feet in diameter and 3 feet deep. Water circulating in the aquaria and two of the tanks was filtered through glass wool, then through a cellulose filter, and finally irradiated with ultraviolet. The third wooden tank received sea water filtered through an 18-inch layer of coarse sand. Water temperature ranged from 23.0° to 24.0° C., and salinity was 22.6‰.

Spawning took place in all the containers within 6 hours after introduction of the females. Eggs were siphoned from the spawning aquaria, distributed among containers in which the treated

water was circulated, and observed continuously. Hatching began approximately 10 hours after spawning and continued for 41 hours. Although none of the resulting larvae reached the protozoa stage during this trial, the additional naupliar specimens obtained permitted completion of the early larvae descriptions.

The following table, constructed from notes made during the two successful trials, indicates intervals between molts.

TABLE A-1.—*Chronological development of larvae*

	Hours after spawning	
	Trial 1	Trial 7
Nauplii well-developed and moving sporadically inside egg.....	11	11
Nauplius I first found.....	11½	12
Nauplius II.....	17	25
Nauplius III.....	51	28
Nauplius IV.....	55	44
Nauplius V.....	57	-----
Protozoa I.....	58	-----
Hatching ceased.....	32	41

ABUNDANCE, AGE, AND FECUNDITY OF SHAD, YORK RIVER, VA., 1953-59

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ABSTRACT

A study of the American shad fishery of the York River, Va. during 1959 showed an estimated total catch of 463,000 pounds, a fishing rate of 55.2 percent, and a total population of 839,000 pounds. Additional estimates of catch and effort were used to calculate fishing rate and population size for each year 1953

through 1958. Analyses of scales showed that most shad spawn at 3, 4, and 5 years of age and approximately 23 percent of the fish caught during the 1957-59 seasons had spawned the previous year. The number of ova produced by York River shad ranged from 169,000 to 436,000 per fish.

The commercial yield of American shad (*Alosa sapidissima*) on the Atlantic coast declined from a peak of 50 million pounds in 1896 to 8 million pounds in 1950. In 1950 the Bureau of Commercial Fisheries, acting as the primary research agency of the Atlantic States Marine Fisheries Commission, began an investigation of the fishery to determine causes for the decline, conditions favoring recovery, and management measures necessary to obtain maximum continuing yields.

Since funds and personnel were not sufficient for a study of all shad producing streams of the Atlantic coast, it was necessary to limit the investigation to certain areas each year. This report concerns the shad population of the York River, Va. In this study the York, which includes the Pamunkey and Mattaponi Rivers, was termed the York River system.

During the spring spawning run of 1959, personnel of the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., in cooperation with the Virginia Institute of Marine Science, Gloucester Point, Va., conducted an investigation of the fishery to estimate total catch, fishing rate,

total population entering the river for each year in which catch and effort data were available, and to obtain certain life history information.

LIFE HISTORY

American shad are the largest members of the herring family in the United States. They are anadromous, spending most of their life in the sea, but ascending coastal rivers to spawn. On the Atlantic coast, shad range from the St. Lawrence River, Canada, to the St. Johns River, Fla. Spawning migrations begin in Southern rivers as early as November and progressively later in Northern rivers. The number of eggs produced by females sampled from Atlantic coast rivers ranges from 116,400 to 659,000 (Lehman, 1953; Walburg, 1960). The young spend the first summer of life in the rivers and usually migrate to sea in the fall of the same year, at which time they are from 3 to 6 inches in length. In 3 to 6 years, they reach sexual maturity and return to the stream of origin to spawn.

Adult shad enter the York River as early as January, and the run usually continues until mid-May. It is during this time that they become available to the fishery. The bulk of the catch is usually made in a 6-week period from early March until mid-April. Massmann and Pacheco

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[Contribution No. 130. Virginia Institute of Marine Science, Gloucester Point, Va.]

(1957), in a study of the relationship of water temperature and shad catch in Virginia, showed that the greatest catches were made at water temperatures ranging from 45° to 59° F., and that below 40° F. very few shad were caught. The major spawning areas in the Pamunkey River are 20 to 25 miles above West Point and in the Mattaponi River 15 to 20 miles above West Point (Massmann, 1952). York River shad normally do not die after spawning, and if they survive natural and fishing hazards, they return to spawn in successive years (Talbot and Sykes, 1958).

DESCRIPTION OF RIVER AND SHAD FISHERY

The York River is formed by the union of the Pamunkey and Mattaponi at West Point, Va. (fig. 1). It flows southeasterly for a distance of 28 miles and empties into Chesapeake Bay at Tue Point. In this study an imaginary line drawn between Tue Point and Guinea Marshes marks the mouth of the river. The Pamunkey is formed by the junction of North Anna and South Anna Rivers in central Virginia and flows approximately 100 miles to its union with the Mattaponi. The Mattaponi is formed by the Matta, the Po, and

the Ni Rivers in northeastern Virginia and flows approximately 120 miles to unite with the Pamunkey. Tidal waters extend about 45 miles up the Pamunkey and 30 miles up the Mattaponi. The change from brackish to fresh water occurs from 5 to 10 miles above West Point in each river.

Stake gill, drift gill, pound, and fyke nets, and haul seines were the gears employed in the fishery, named in order of their importance as determined by pounds of fish taken. The locality and miles of river fished by each gear are shown in table 1. Stake gill nets fished in the York were suspended from poles, spaced about 20 feet apart, driven into the river bottom. These nets were fished continuously during the shad season and were lifted on high and low tides. Pound nets, haul seines, and fyke nets, also employed in the York, were fished from early spring until fall. After the shad season these gears were fished for other species. Drift gill nets employed in the Mattaponi and Pamunkey were fished during periods of high and low slack waters, which permitted about 3 hours fishing on each tide. Regulations established by the Virginia Commission of Fisheries licensed stake gill nets by 600-foot rows, limited the length of drift gill nets to 600 feet, and permitted the taking of shad from inlets and rivers during the period from October 16 to May 25. Because of navigational difficulties from the mouth of the river to West Point, the location fished by stationary gears was designated by the U.S. Army Corps of Engineers so that shipping channels were unobstructed.

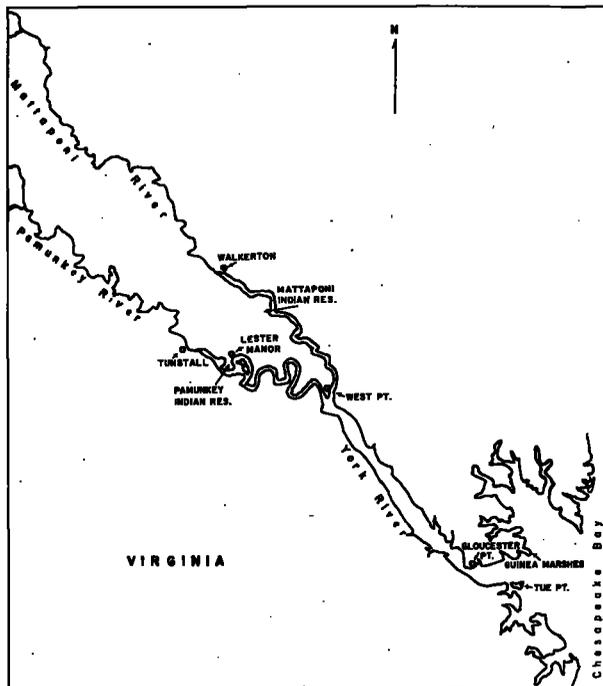


FIGURE 1.—York River system, Virginia.

TABLE 1.—Water area and location of shad gear fished, York River system, 1959

Water area	Gear	Miles of river	Location of area
York River.....	Pound net....	6	Mouth of river to Gloucester Point.
York River.....	Haul seine....	6	Mouth of river to Gloucester Point.
York River.....	Fyke net.....	20	Gloucester Point to West Point.
York River.....	Stake gill net..	20	Gloucester Point to West Point.
Pamunkey River...	Drift gill net..	26	West Point to Tunstall.
Mattaponi River...	Drift gill net..	21	West Point to Walkerton.

STATISTICS OF THE FISHERY, 1929-59

Estimated shad catches in the York River system for years 1929 through 1959 are shown in figure 2. The annual yield was at a low level during the years 1930 through 1943, with the

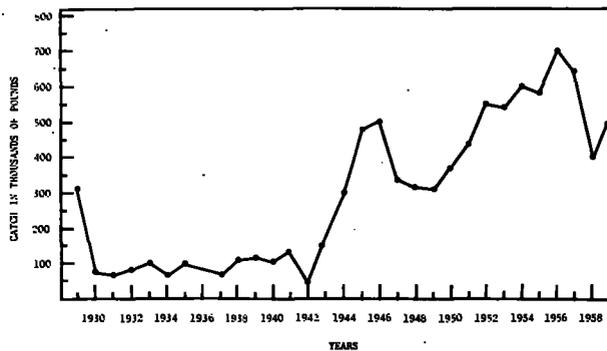


FIGURE 2.—Estimated shad catch, York River system, 1929-59.

least production of 23,800 pounds in 1936. After 1943 the yield increased rapidly and was approximately one-half million pounds by 1946. Then in the following 3 years the catch declined to less than one-third million pounds, after which it again increased with a peak production of more than two-thirds million pounds in 1956. The 1959 yield was more than that of 1958, but was less than the catch for any of the years from 1953 through 1957.

Catch statistics for the years 1929 through 1952 were compiled by the Branch of Statistics of the Bureau of Commercial Fisheries,³ those for 1953 through 1958 were estimated from logbook records collected by the Virginia Institute of Marine Science, and the 1959 data were obtained from the present study.

To obtain the 1959 statistics a letter explaining the study was mailed prior to the start of the season to each shad fisherman licensed on the York River system during 1958. A logbook was enclosed, and each fisherman was asked to record his catch and effort each day. Biologists contacted fishermen throughout the season to learn the amount of each type of gear fished, to collect tags recovered from the tagging study conducted simultaneously with the statistical study, to encourage the recording of catch and effort data, and to help with the logbook records. At the end of the season, all fishermen were contacted personally or by letter for logbook and tag returns. Catch and effort data were obtained for all pound-net, haul-seine, and fyke-net fishermen; 94 percent of the stake gill-net fishermen; and 56 percent of the drift gill-net fishermen. Total

catch and effort for the gill-net fisheries were estimated from information obtained from the logbooks.

In 1959 the shad catch was reported in pounds and the effort recorded in number of nets fished each day. Number of nets fished each day was converted to net days, i.e., a pound net, haul seine, or fyke net-day was defined as one net fished for 1 day, and a stake and drift gill net-day was defined as 100 linear yards of net fished for 1 day. The estimated total catch and effort for all gears was 463,124 pounds in 24,112 net-days (table 2). Gill nets accounted for 94 percent of the total catch and 84 percent of the total effort.

TABLE 2.—Estimated total catch and effort of shad fishery, York River system, 1959

Gear	Nets fished	Effort	Catch		
			Males	Females	Total
	<i>Number</i>	<i>Net-days</i>	<i>Pounds</i>	<i>Pounds</i>	<i>Pounds</i>
Pound nets.....	20	1,204	6,679	8,809	15,488
Haul seines.....	2	20	700	800	1,500
Fyke nets.....	64	2,575	6,581	4,114	10,705
Stake gill nets.....	5,003	11,308	58,975	164,209	223,184
Drift gill nets.....	524	9,005	98,247	114,000	212,247
Total.....	5,613	24,112	171,192	291,932	463,124

Logbook data, collected each season from 1953 to 1958 by the Virginia Institute of Marine Science, were made available for this study. Analysis of the logbook data, kept by the same fishermen each year, accounted for approximately 25 percent of the total catch and effort in 1959. Catch per unit of effort for the major gears remained relatively constant from 1953 to 1959. Data for the years 1953 through 1958 were therefore adjusted, based on the results of the 1959 study. The estimated catch and effort by gear for 1953 through 1959 are given in table 3.

TAGGING STUDY, 1959

During the 1959 season, a tagging and recovery program was conducted to estimate the rate of exploitation and the size of the shad population. Fish for marking were obtained from pound nets located near the mouth of the river in the vicinity of Tue Point. Tagging began on March 9 and was discontinued on May 3 when the run terminated. During this period 842 shad were marked with streamer tags, similar to those used by Davis (1959). The tag was a red plastic disk, with an identification number on one side

³ Unpublished data. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.

TABLE 3.—Estimated shad catch and effort by gear, York River system, 1953-59

Year	Pound net		Haul seine		Fyke net		Stake gill net		Drift gill net		Total catch Thousands of pounds
	Effort	Catch	Effort	Catch	Effort	Catch	Effort	Catch	Effort	Catch	
	Net-days	Pounds	Net-days	Pounds	Net-days	Pounds	Net-days	Pounds	Net-days	Pounds	
1953	46	4,544	23	17,764	6,102	16,451	12,614	231,727	9,801	282,069	552
1954	138	4,544	69	13,525	3,821	20,911	8,980	300,139	9,064	262,709	602
1955	49	3,416	25	8,115	3,274	9,639	11,509	251,484	8,005	264,923	538
1956	79	5,404	40	8,115	5,372	14,483	10,843	398,114	7,706	290,392	716
1957	75	4,866	38	7,304	4,339	15,393	10,060	399,844	6,845	211,033	638
1958	77	4,555	39	5,000	4,247	14,500	8,777	215,289	6,328	146,772	386
1959	1,204	15,488	20	1,500	2,575	10,705	11,308	223,184	9,005	212,247	463

and return address and reward notice on the other, to which a loop of nylon twine was tied. The nylon loop was fastened under the origin of the dorsal fin, which allowed the disk to trail immediately behind the fin, not interfering appreciably with the normal activity of the fish.

Of the total number of fish tagged, 118 were recaptured from areas outside the York River system. Of these, 105 were recaptured in the Chesapeake Bay system, 4 in North Carolina, 4 off the New England coast, 3 in the Hudson River, and 2 tags were returned from fish markets in Philadelphia, Pa. Approximately 89 percent of the outside returns were recaptured in the Chesapeake Bay system. On the basis of previous studies in the bay by Walburg (1955) and Walburg and Sykes (1957), an outside fishing rate of 50 percent was estimated. Therefore, 236 shad tagged at the mouth of York River were considered as en route to other river systems and were subtracted from the number tagged. Using criteria established by Talbot and Sykes (1958), one tagged fish recaptured in Chesapeake Bay on June 8 was not included since it was not known whether this fish had spawned in the York. This left 605 tagged fish which entered the York River for the purpose of spawning. Of this total, 334 were recaptured: 173 in the York, 104 in the Pamunkey, and 57 in the Mattaponi.

To obtain valid estimates from our tagging program certain factors, which may be sources of error, must be examined and their consequences satisfied (Ricker, 1958).

(1) *Differential mortality.*—Extra mortality among the tagged fish, either as a direct result of the tag or indirectly from effects of exertion by the fish during capture and handling incidental to the marking operation, may result in a biased fishing rate and population estimate. Sykes (1951) successfully handled and moved adult fish

for distances up to 95 miles, and they remained alive and active for some time after transfer. This was considered as adequate demonstration that shad can survive rigorous handling. Atkinson (1951) handled and held adult shad in experimental ponds for several weeks without appreciable mortality. During the present experiment, only fish in apparent good physical condition and those unabraded in the process of capture were marked. Every precaution was taken to prevent damage to the fish which could result in extra mortality from handling and marking.

(2) *Loss of tags by detachment.*—The tag and attachments are completely durable. Approximately 25 percent of the catches were examined for scars that would be left from detachment, and no evidence was found of nonpermanent attachment. No unattached tags were reported taken in the nets. Therefore, loss of tags by detachment was considered negligible.

(3) *Tagged fish more, or less, vulnerable to fishing than untagged fish.*—If tags made shad more vulnerable to fishing, a higher proportion of tagged to untagged fish would occur in the catch of the lower fishery than at locations further upstream. The proportion of tagged to untagged fish in the lower river catch was no greater than that found further upstream, and the rate of capture of tagged fish was approximately the same as that for untagged fish by each gear at the different locations. Pound nets and haul seines in the lower York took 3.7 percent of the total catch and 3.6 of the tagged fish recaptured. Fyke and stake gill nets employed in the upper York took 50.5 percent of the total catch and 48.2 percent of the tagged fish recaptured, and drift gill nets operated in the tributaries took 45.8 percent of the total catch and 48.2 percent of the tagged fish recaptured.

The point of insertion of the tag and type streamer used did not make the tagged fish more vulnerable to gill nets than untagged fish by reason of the tag entangling in the net. For the first 5 weeks the weekly rate of recapture of tagged fish and untagged fish indicated no difference in behavior of the fish; i.e., in the first week 6.9 percent of the recaptures of tagged fish was made and 5.0 percent of the catch was made; in the second week the rate was 10.0 and 10.0; in the third week 15.0 and 15.1; in the fourth week 20.0 and 20.0; and in the fifth week 24.4 and 25.0.

Length measurements of shad caught in previous seasons indicated that fish more than 14.3 inches fork length were liable to capture by all types of gear fished in the York system; therefore, no fish less than this length were tagged. Fish less than this length were of no market value and were released or eliminated from the catch.

A chi-square test between catch and number of tags recovered by gear type showed that no tag selectivity occurred within the size range tagged

$$(\chi^2=2.16; P=0.71).$$

(4) *Nonreturn of tags.*—Each fisherman was contacted prior to the season to acquaint him with the tagging program. Then four biologists canvassed the fishery daily throughout the entire season for tag returns. At the end of the season each fisherman was contacted to collect the recovered tags. The number of recaptured tags not recovered probably would not appreciably bias the estimates.

(5) *Nonrandom distribution of tagged fish.*—Marked fish were randomly distributed throughout the population being sampled by tagging uniformly throughout the season from the first gear the fish encounter in the river, so that, as nearly as possible, tags were affixed in proportion to the number of shad migrating upstream. Close agreement of the ratio of tagged to untagged fish taken in the tributaries (spawning grounds) provided evidence that tagging was random with respect to the destination of the shad.

Based on the tagging study the calculated fishing rate was 55.2 percent and the estimated population size 838,892 pounds. To determine the total population of shad entering the river in 1959, Chapman's (1948) formula $N = \frac{nt}{s}$ was used, where

N =total population, n =total catch (463,124 pounds), t =number of fish tagged (605), and s =number of tagged fish recaptured (334). Escapement from the fishery was 375,768 pounds. The limits within which the population estimate fell with 95 percent confidence were 900,000 and 800,000 pounds (Chapman, 1948).

GEAR EFFICIENCY AND STANDARDIZATION OF EFFORT

To determine total fishing effort in standard units required to make the 1959 shad catch, the fishing efficiency of the various gears must be determined. Fishing efficiency was defined as the ability of one unit of effort to remove a certain fraction of the available population in a specified interval of time. The method used to determine fishing efficiency was similar to that used by Talbot (1954), in which fishing gears fish different areas. As previously noted, however, pound nets and haul seines fished the lower river, stake gill and fyke nets fished the central section of the river, and drift gill nets were fished upriver. Before the efficiency of gears fished in different areas could be determined, it was necessary to combine the effort of those gears fishing in the same area.

The unweighted average catch per unit of effort by haul seines 1953 through 1959 was found to be 4.60 times that of pound nets, and the unweighted average catch per unit of effort by fyke nets 1953 through 1959 was 0.12 times that of stake gill nets. Haul-seine effort was converted to pound-net effort by multiplying haul-seine effort (table 3) by 4.60. Fyke-net effort was converted to stake gill-net effort by multiplying fyke-net effort (table 3) by 0.12. The effort and catch of these gears as combined will henceforth be included under pound nets and stake gill nets as given in table 4. We now have three standardized gears, each fishing a different area of river.

TABLE 4.—Estimated catch and effort, York River system, 1953-59

Year	Pound nets		Stake gill nets		Drift gill nets		Total	
	Effort	Catch	Effort	Catch	Effort	Catch	Effort	Catch
	<i>Net-days</i>	<i>Pounds</i>	<i>Net-days</i>	<i>Pounds</i>	<i>Net-days</i>	<i>Pounds</i>	<i>Net-days</i>	<i>Thousands of pounds</i>
1953---	152	22,308	13,346	248,178	9,801	282,069	23,299	552
1954---	455	18,069	9,438	321,050	9,064	262,709	18,957	602
1955---	164	11,531	11,902	261,123	8,005	264,923	20,071	538
1956---	263	13,519	11,488	412,597	7,706	290,392	19,457	716
1957---	249	12,170	10,581	415,237	6,845	211,033	17,675	638
1958---	256	9,555	9,287	229,789	6,328	146,772	15,871	386
1959---	1,296	16,988	11,617	233,889	9,005	212,247	21,918	463

The fishing efficiency of each gear, designated as p , was determined using Fredin's (1954) formula $q^n N = E$,⁴ from which we derive

$$\log q = \frac{\log E/N}{n}$$

where $q = 1 - p$, E = escapement from a fishery, N = size of run available to a fishery, and n = units of effort in net-days. From our tagging and recovery program, the estimated size of run (N) available to pound nets was 838,892 pounds. The catch (c) was 16,988 pounds; hence, the escapement (E) from these nets was 821,904 pounds. The units of effort (n) were 1,296. Solving the above equation, the q value obtained was 0.999984. Since $p = 1 - q$, the fishing efficiency of pound nets was 0.000016. Shad that escaped the pound nets were available to the stake gill nets. The fish available to this gear were 821,904 pounds, of which 233,889 pounds were removed by 11,617 units of effort. Solving the equation, the q value obtained was 0.999971, and therefore $p = 0.000029$. Fish that escaped both pound and stake gill nets were available to the drift gill nets. The shad available to these nets amounted to 588,015 pounds, of which 212,247 pounds were removed by 9,005 units of effort. Solving the equation for this gear, the q value obtained was 0.999950, and therefore $p = 0.000050$.

After a measure of the fishing efficiency of each gear was determined, it was possible to convert fishing effort in net-days to standard-fishing-unit days (Talbot, 1954). A standard-fishing-unit (s.f.u.) day was defined as 100 linear yards of drift gill net fished for 1 day. The fishing efficiency

of the pound net and stake gill net was 0.32 and 0.58 that of the drift gill net. This was determined by dividing the fishing efficiency of the pound and stake gill net by that of the drift gill net. Fishing effort of pound nets and stake gill nets was converted to standard-fishing-units by multiplying the effort of each net in net-days by these conversion factors. Total catch, effort, and catch per unit of effort are listed in table 5.

ESTIMATE OF POPULATION SIZE, 1953-59

The relative population of shad entering the river can be estimated for any year in which catch and effort statistics are available provided: (1) fishing effort is uniform throughout the season, (2) fishing efficiency remains constant within and between seasons, and (3) the migration pattern of the fish is similar each year (Ricker, 1940).

Available records indicated that fishing was carried out essentially in the same areas using the same types of gear as when the fishery was first investigated in 1953. The main part of the run lasted about 6 weeks, and fishermen fished every day possible. Fishing effort and efficiency, therefore, tended to be uniform throughout the season and between seasons. Water level, turbidity, or water temperature may have affected migration routes within the river for short periods of time, but not necessarily over the entire season. Even though the length of runs and time of fish passage through the fishing areas may have varied from year to year, there was no indication that the York River shad, once in the river, migrated differently in different seasons. Based on these assertions, it was assumed that the above provisions given by Ricker were satisfied for this fishery.

The population for each year 1953-59 was estimated by Talbot's (1954) formula:

$$N = \frac{C}{1 - q^n}$$

where C = catch, $q = 1 - p$, and n = fishing effort in standard-fishing-unit days. The estimated population for these years is listed in table 6. Fishing rate ranged from 58.3 percent in 1953 to 44.4 percent in 1958. The population fluctuated between 1.4 million pounds in 1956 and 0.8 million pounds in 1959. Escapement reached a peak of 0.7 million pounds in 1957 compared to a low of 0.4 million pounds in 1959.

TABLE 5.—Estimated effort in standard-fishing-unit (s.f.u.) days by gear, York River system, 1953-59

Year	Effort in s.f.u. days				Total catch	Catch per s.f.u. day
	Pound net	Stake gill net	Drift gill net	Total		
1953	49	7,741	9,801	17,591	552	31.4
1954	146	5,474	9,064	14,684	602	41.0
1955	52	6,903	8,005	14,960	538	36.0
1956	84	6,663	7,706	14,453	716	49.5
1957	80	6,137	6,845	13,062	638	48.8
1958	82	5,386	6,328	11,796	386	32.7
1959	415	6,738	9,305	16,158	463	28.6

⁴ Modification of Beverton and Holt's (1957) model for estimating relative fishing power of vessels and standardization of commercial statistics of fishing effort.

TABLE 6.—Estimated shad population parameters, York River system, 1953-59

Year	Catch	Effort	Fishing rate	Total population	Escape-ment
	<i>Thou- sands of pounds</i>	<i>s. f. u. days</i>	<i>Percent</i>	<i>Thou- sands of pounds</i>	<i>Thou- sands of pounds</i>
1953	552	17,591	58.3	947	395
1954	602	14,684	51.8	1,162	560
1955	538	14,960	52.5	1,025	487
1956	716	14,453	51.3	1,396	680
1957	638	13,062	47.8	1,335	697
1958	386	11,796	44.4	869	483
1959	463	16,158	55.2	839	376

AGE COMPOSITION

Each season 1957 through 1959 scales were collected from fish taken in stake and drift gill nets. Plastic impressions were made of two symmetrical scales from each fish, and age was determined using the method described by Cating (1953).

The scales were read for age at capture, age at first spawning, and number of times previously spawned (table 7). Shad entering the river for the first time were predominately 3- and 4-year-old males and 4- and 5-year-old females. Approximately 23 percent of the fish in the samples (14.8 percent of the females and 37.6 percent of the males) had spawned the previous year. The

TABLE 7.—Age composition of shad, York River system, 1957-59

Group	1957		1958		1959	
	Females	Males	Females	Males	Females	Males
Total age at capture:						
2 years	2	3	0	0	0	0
3 years	7	21	5	23	19	35
4 years	71	62	63	73	398	190
5 years	77	25	80	34	154	99
6 years	15	3	27	2	25	21
7 years	2	2	9	1	3	4
8 years	0	0	0	0	0	1
Total	174	115	184	133	599	350
Age at first spawning:						
2 years	2	3	0	0	0	0
3 years	14	35	12	42	32	128
4 years	89	65	83	77	447	211
5 years	67	12	78	14	112	11
6 years	2	0	11	0	8	0
Total	174	115	184	133	599	350
Number of times previously spawned:						
0	137	88	152	92	526	193
1 time	29	18	21	24	58	83
2 times	5	8	7	15	15	65
3 times	3	0	3	2	0	5
4 times	0	1	1	0	0	4
Total	174	115	184	133	599	350
Total	289		317		949	

small percentage of fish returning to spawn the second or more times is probably due to exploitation outside the river and to ocean mortality. In 1952 Walburg and Sykes (1957) found that 27 percent of the James River shad and 17 percent of the Potomac River shad had spawned previously.

The size by sex was determined. Mean weight was 2.3 pounds for males and 3.2 pounds for females. Fork length ranged from 12.6 to 17.3 inches for males and 14.0 to 20.0 inches for females.

OVA PRODUCTION

Ova production was determined by sampling the ovaries from 18 females captured during April 1959. Fish were taken from stake gill nets located in the lower section of the river approximately 50 miles below the spawning ground. Fish were chosen selectively so that different size and age groups were represented. They ranged from 14.9 to 19.0 inches in fork length, 2.1 to 5.0 pounds in weight, and 4 to 7 years in age. Ova estimates were made using the method described by Lehman (1953) and modified by Davis (1957). Ova counts ranged from 169,000 to 436,000 (table 8).

TABLE 8.—Estimated ova production of 18 female shad, York River, 1959

Specimen No.	Fork length	Total weight	Weight of ovaries	Mean number of ova	Estimated total ova
	<i>Inches</i>	<i>Ounces</i>	<i>Grams</i>	<i>Per gram</i>	<i>Thousands</i>
1	14.9	34	120.5	2,090	252
2	15.2	37	133.2	1,696	228
3	15.4	43	141.4	1,488	210
4	15.7	39	217.7	778	169
5	15.8	39	146.1	1,412	206
6	16.0	42	126.0	1,542	194
7	16.0	44	155.4	1,956	304
8	16.8	48	214.0	966	207
9	16.8	53	164.4	1,698	279
10	17.0	52	224.6	1,322	297
11	17.3	59	210.4	1,169	246
12	17.5	56	164.4	1,540	253
13	17.9	64	213.1	1,977	421
14	18.2	65	233.3	1,675	391
15	18.3	67	280.8	1,318	370
16	18.5	73	303.5	1,436	436
17	18.7	62	220.3	1,686	380
18	19.0	80	391.7	914	358

The relation between ova production and length, or weight, or age of the York River shad is shown in figure 3. Linear regressions showed that there was an increase in ova production with increase in each of these variables within the size and age range sampled. Ova production was somewhat more highly correlated with weight ($r=0.820$) than with length ($r=0.795$) or with age ($r=0.740$).

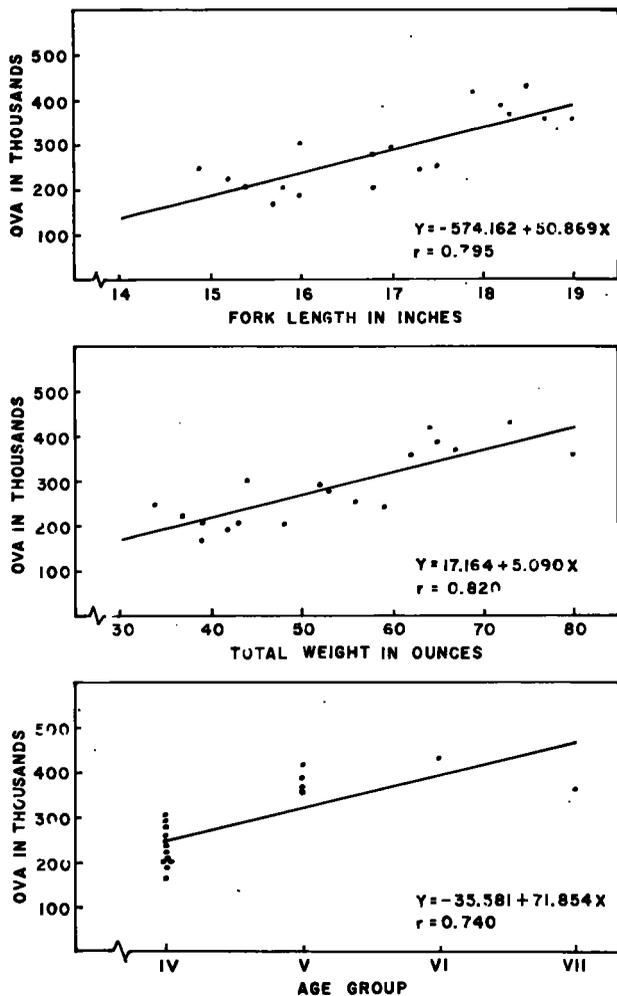


FIGURE 3.—Relation between ova production and length, weight, and age in female shad, York River, 1959.

SUMMARY AND CONCLUSIONS

The Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., in cooperation with the Virginia Institute of Marine Science, Gloucester Point, Va., conducted a study on the shad population of the York River system in 1959 as part of an investigation of the Atlantic coast shad fishery. This river system includes the York, Pamunkey, and Mattaponi Rivers. The purposes were to determine total catch, fishing rate, population entering the river system for each year in which catch and effort data were available, and certain life history information.

Estimated total catch in 1959 was 463,000 pounds, of which gill nets accounted for 94 percent. The fishing rate was estimated to be 55.2 percent,

estimated population 839,000 pounds, and spawning escapement 376,000 pounds. Ninety-five percent confidence limits on the population estimate were 900,000 and 800,000 pounds. With catch and effort statistics available for the years 1953 through 1958, it was possible to estimate population size, fishing rate, and spawning escapement for each of these years, based on information obtained during the 1959 study. Estimates showed that the commercial yield reached a peak of 716,000 pounds in 1956 and a low of 386,000 pounds in 1958; fishing rate ranged from 44.4 percent in 1958 to 58.3 percent in 1953; population reached a peak 1.4 million pounds in 1956 compared to a low of 0.8 million pounds in 1959; and escapement reached an estimated high of 0.7 million pounds in 1957 compared to a low of 0.4 million pounds in 1959.

Shad that entered the York River for the first time were predominantly 3- and 4-year-old males and 4- and 5-year-old females. Twenty-three percent of the catch had spawned the previous year. Ova production ranged from 169,000 to 436,000, and linear regressions showed an increase in number of eggs with an increase in weight, length, and age of the fish.

In this investigation, a method was presented to estimate the shad population of the York River system, provided catch and effort statistics are collected each year. Population estimates were calculated on this shad fishery for seven consecutive years. The value of this study for scientific management of the fishery will not be realized, however, until population estimates have been obtained for an additional number of years.

ACKNOWLEDGMENTS

We wish to acknowledge the cooperation of the York River shad fishermen and fish dealers, and personnel of the Virginia Commission of Fisheries who helped with the investigation.

LITERATURE CITED

- ATKINSON, CLINTON E.
1951. Feeding habits of adult shad (*Alosa sapidissima*) in fresh water. *Ecology*, vol. 32, no. 3, pp. 556-557.
- BEVERTON, R. J. H., and S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fisheries and Food Fishery Investigations, Series II, vol. 19, Ministry of Agriculture, 533 pp.

- CATING, JAMES P.
1953. Determining age of Atlantic shad from their scales. U.S. Fish and Wildlife Service, Fishery Bulletin 85, vol. 54, pp. 187-199.
- CHAPMAN, D. G.
1948. Problems in enumeration of populations of spawning sockeye salmon. 2. A mathematical study of confidence limits of salmon populations calculated from sample tag ratios. International Pacific Salmon Fisheries Commission, Bulletin 2, pp. 69-85.
- DAVIS, WILLIAM S.
1957. Ova production of American shad in Atlantic coast rivers. U.S. Fish and Wildlife Service, Research Report 49, 5 pp.
1959. Field tests of Petersen, streamer, and spaghetti tags on striped bass, *Morone saxatilis* (Walbaum). American Fisheries Society, Transactions, vol. 88, no. 4, pp. 319-329.
- FREDIN, REYNOLD A.
1954. Causes of fluctuations in abundance of Connecticut River shad. U.S. Fish and Wildlife Service, Fishery Bulletin 88, vol. 54, pp. 247-259.
- LEHMAN, BURTON A.
1953. Fecundity of Hudson River shad. U.S. Fish and Wildlife Service, Research Report 33, 8 pp.
- MASSMANN, WILLIAM H.
1952. Characteristics of spawning areas of shad, *Alosa sapidissima* (Wilson), in some Virginia streams. American Fisheries Society, Transactions, vol. 81 (1951), pp. 78-93.
- MASSMANN, WILLIAM H., and ANTHONY L. PACHECO.
1957. Shad catches and water temperatures in Virginia. Journal of Wildlife Management, vol. 21, no. 3, pp. 351-352.
- RICKER, W. E.
1940. Relation of "catch per unit effort" to abundance and rate of exploitation. Fisheries Research Board of Canada, Journal, vol. 5, pp. 43-70.
1958. Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin No. 119, Queen's Printer and Controller of Stationery, Ottawa, 300 pp.
- SYKES, JAMES E.
1951. The transfer of adult shad. Progressive Fish-Culturist, U.S. Fish and Wildlife Service, vol. 13, no. 1, pp. 45-46.
- TALBOT, GERALD B.
1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish and Wildlife Service, Fishery Bulletin 101, vol. 56 (1956), pp. 373-413.
- TALBOT, GERALD B., and JAMES E. SYKES.
1958. Atlantic coast migrations of American shad. U.S. Fish and Wildlife Service, Fishery Bulletin 142, vol. 58, pp. 473-490.
- WALBURG, CHARLES H.
1955. Relative abundance of Maryland shad, 1944-52. U.S. Fish and Wildlife Service, Research Report 38, 17 pp.
1960. Abundance and life history of shad, St. Johns River, Florida. U.S. Fish and Wildlife Service, Fishery Bulletin 177, vol. 60, pp. 487-501.
- WALBURG, CHARLES H., and JAMES E. SYKES.
1957. Shad fishery of Chesapeake Bay with special emphasis on the fishery of Virginia. U.S. Fish and Wildlife Service, Research Report 48, 26 pp.

COD GROUPS IN THE NEW ENGLAND AREA

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ABSTRACT

Indications from previous tagging experiments since 1897 result from tagging 2,794 cod by the author from 1955 to 1959, and evidence from other sources indicate four groups of cod in the New England area: (1) The cod of the offshore banks, (2) the cod of the Gulf of Maine, (3) the cod of southern New England and the

South Channel, and (4) the New Jersey coastal cod which spend the summer in southern New England.

It is suggested that the first three groups are stocks not genetically separate, while the New Jersey fish are a genetic subpopulation. Within all of these groups, except the last, there is a tendency for the larger fish to move permanently to the north and east.

Although cod, *Gadus morhua* L., are widely distributed on both sides of the North Atlantic, no cod marked on the European coast has ever been recovered on the coast of North America, nor vice versa. Many cod tagged at Iceland (fig. 1) have been recaptured at West Greenland, but there are only one or two records of fish tagged at Iceland recaptured as far west as Newfoundland waters. Many years of marking experiments by Europeans and North Americans, supported by studies of meristic characters (Schmidt, 1930), have conclusively demonstrated the lack of interchange between European cod and those of the North American coast.

Concentrating, then, on the cod of the western Atlantic, there have been a considerable number of important studies which serve to point out the separation of various groups found here.

Templeman (1953) considers the cod of Labrador separate from those of West Greenland, basing his conclusions chiefly on vertebral counts. In a consideration of growth rates, age at sexual maturity, and parasite infestation, he concludes further that the Labrador cod are distinct from the Newfoundland and Grand Bank fish. He points out (p. 64) that, "Apart from fish tagged

on St. Pierre Bank it is very unusual for any fish tagged in Newfoundland to cross the Laurentian Channel to the Nova Scotia Banks or to the southern side of the Gulf of St. Lawrence."

Martin (1953), in discussing the major ground-fish stocks of Subdivision 4 of the Convention Area of the International Commission for the Northwest Atlantic Fisheries (roughly the Nova Scotian and Gulf of St. Lawrence regions), states (p. 57), "The deep-water Fundian Channel between Georges and Browns Banks and the still deeper Laurentian Channel between St. Pierre Bank and Banquereau are barriers to the movement of cod. Except for occasional movements of individual cod across these channels we may consider that the cod populations along the Nova Scotian coast, in the western Gulf of St. Lawrence, and on the Nova Scotian offshore banks are resident in Subarea 4." As to western Nova Scotia, he reports that, "Resident populations show restricted movement and do not mix with eastern or offshore cod."

The data published by McKenzie (1956) show that from about 20,000 cod tagged along the Nova Scotia and Gulf of St. Lawrence coasts and offshore banks from 1926 to 1940, there were many hundreds of returns east of longitude 65° W.

NOTE.—Approved for publication July 24, 1962.

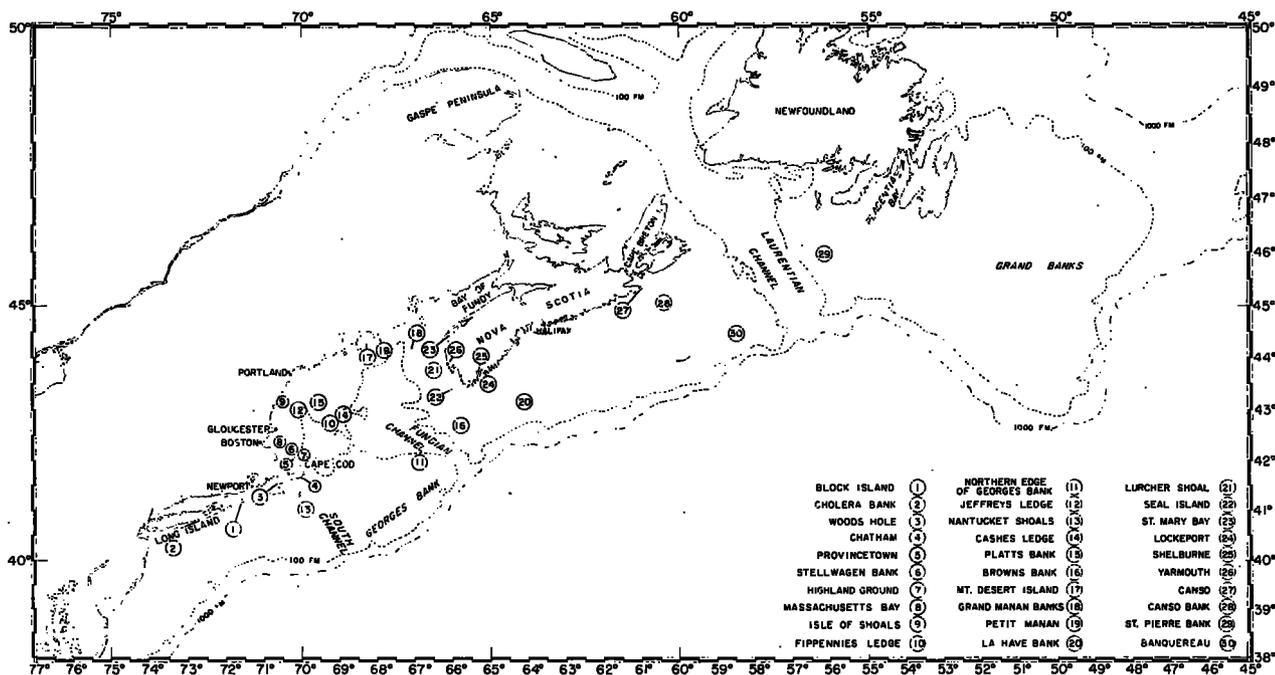


FIGURE 1.—The western North Atlantic area.

However, only about a dozen came from west of 65°, that is from New England waters as considered here.

For purposes of this study, New England waters have been rather liberally defined as those parts of the Atlantic Ocean north of latitude 40° N. and west of longitude 65° W. With this and the results above in mind, it is evident that the New England cod are generally distinct from American cod living to the north and east and may be treated as one or more discrete ecological units. The only exception is the southern stock of cod which infiltrates the New England area in summer (Wise, 1958).

This report presents the results of recent (since 1955) marking experiments in New England waters, taking into consideration, however, the results of previous experiments and other evidence where applicable, to provide the best description possible of the relations of the cod groups in the New England area. (The words "group" and "stock" are used here as defined by Marr (1957).)

PREVIOUS TAGGING EXPERIMENTS

Although cod had been tagged in the north-eastern Atlantic as early as 1888, it was not until 1897 that any were marked on the American side.

During the 1920's and early 1930's, under the stimulus of the newly formed North American Council on Fishery Investigations, considerable numbers were marked in New England waters by Canadian and United States biologists. A few publications were issued as a result of this work, but unfortunately many of the experiments were never reported in detail in any permanent form, and the original records are either lost or destroyed. Many of the summary reports are ambiguous and contradictory, particularly as regards the number of fish tagged and recaptured, and the exact locations of tagging and recapture. I have consulted some of the men who engaged in these operations, but after nearly 40 years their memories of dates, places, and numbers are understandably imprecise. Insofar as possible, the following summary, based, unless otherwise stated, on Higgins (1929, 1930, 1931a, 1931b, 1932, 1933, 1934, 1936), Rich (1925, 1926), Schroeder (1928, 1930), and the reports of the North American Council (1932, 1935), presents the most complete reconstruction of all experiments previous to December 1955 in New England waters. The results and conclusions drawn from them, the development and evolution of tags and methods, were also reconstructed from the same sources, and the latter is presented as a separate section.

**TAGGING EXPERIMENTS AND RESULTS
FROM 1897 TO 1955**

Table 1 shows in summary form all tagging previous to 1955. Obviously these experiments were of vastly different scopes, and the results in terms of returns were extremely variable, both in numbers and percentage, from a fraction of 1 percent to numbers approaching one-half of the fish returned, for instance, the 1953 Canadian experiment yielding more than 40 percent by the spring of 1955.

In retrospect, however, they may be grouped with their results in the following way:

1. Southern Nova Scotia and Browns Bank. On the basis of the Canadian work from 1924 to 1927, McKenzie (1934, 1956) concluded that the fish around Shelburne were essentially stationary, while those at Seal Island showed a movement eastward during summer and returned in winter. The U.S. tagging on Browns Bank in 1927 was not successful; the Canadian work from 1926 to 1930, in the Bay of Fundy, was never reported in detail, nor was the U.S. work on Browns in 1928 and 1930. Inshore tagging in 1938 and 1939 yielded less than 20 returns, most of these nearby, but 1 from Georges Bank.

Most of the large numbers of cod reported recaptured by McCracken (1956) from his work off Lockeport, Nova Scotia, in the summer of 1953 were taken more or less locally, a few from the banks directly offshore, about 20 well to the northeast, and 7 from Georges Bank and vicinity.

2. Gulf of Maine. From 1923 to 1932, the U.S. Bureau of Fisheries marked fish in the Gulf of Maine, with a concentration of the work around Mount Desert Island and on Platts Bank. Although good numbers of fish were marked, probably more than 6,000, and the percentages of returns up to about 20 percent in some cases, no report was ever published in detail, and the only available summary occurs in the Proceedings of the North American Council on Fishery Investigations (1932, p. 12), that there was "very little intermingling between the more southern population and the cod of the gulf of Maine, of Georges bank and of Nova Scotia. . . . In general the fish of the Mt. Desert ground have been found, by recapture, to remain chiefly stationary in the locality, the few recorded journeys . . . being nearly all eastward"

3. Georges Bank. The U.S. Bureau of Fisheries marked cod on Georges Bank from 1926 intermit-

TABLE 1.—Summary of all cod tagging experiments in New England waters previous to 1955

[See text for sources not given here]

Year	Area	Number tagged	By whom tagged
1897-1901 (winters)	Woods Hole and vicinity	4,019	H. M. Smith. ¹
1923 (April-October)	Stellwagen Bank	12	W. C. Schroeder.
1924	Mouth of Bay of Fundy	56	Canadian biologists.
1924 (July-October)	Massachusetts Bay	218	W. C. Schroeder.
	Platts Bank		
	Mount Desert Island	1,611	W. C. Schroeder.
1925	Petit Manan, Maine to Southern Mass		
	Mount Desert Island (April-May)		
	Platts Bank (June-July)		
1926 (August)	Georges Bank	1,016	W. C. Schroeder.
1925-1928 (winters)	Woods Hole	1,859	W. C. Schroeder. ²
1923-1929	Southern New England	23,555	W. C. Schroeder. ²
	Cholera Bank		
	Southern New Jersey	884	
1926 (summer)	Shelburne, Nova Scotia	4,011	Biological Board of Canada.
	Yarmouth, Nova Scotia	28	
1927 (June)	Seal Island, Nova Scotia	1,840	Biological Board of Canada. ²
	Georges Bank	477	
1927	Browns Bank	904	U.S. Bureau of Fisheries.
	Platts Bank (April-October)	79	
	Cashes Ledge (September-October)	321	
1928	Massachusetts coast, north of Cape Cod, off New Hampshire and Maine, on or near Browns and Georges Banks.	1,285	U.S. Bureau of Fisheries.
1926-1930	Bay of Fundy	61	Biological Board of Canada. ²
1930 (April-October)	Mount Desert, Georges Bank, Browns Bank, Cashes Ledge, Platts Bank, Nantucket Shoals.		U.S. Bureau of Fisheries.
1931	Mount Desert	1,199	U.S. Bureau of Fisheries.
	Woods Hole (January)	340	
	Nantucket Shoals (August)	172	
1932	Mount Desert	1,481	U.S. Bureau of Fisheries.
	Woods Hole (January)	304	
1938	Mouth of Bay of Fundy	13	Biological Board of Canada. ²
1939 (April)	St. Mary Bay	83	Biological Board of Canada. ²
1953 (summer)	Lockeport, Nova Scotia	1,804	Fisheries Research Board of Canada. ⁴

¹ Smith, 1902.

² Schroeder, 1930, which includes some 1,184 fish tagged to the south of the area.

³ McKenzie, 1934, 1956.

⁴ McCracken, 1956.

tently to 1930, probably something on the order of 2,000 fish in all, but the records show only 6 recaptures, 3 of them on the bank.

4. Woods Hole. Smith (1902) and Schroeder (1930) report basically similar results from releasing with marks during the winters of 1897-1901 and 1925-28, nearly 6,000 of the cod which had been held at Woods Hole as a source of eggs and milt for the hatchery in operation during that period. Most were recaptured locally, some to the north and east, and some as far south as southern New Jersey. Schroeder incorporated the results of this work in his conclusions about the cod of southern New England (see below). The results of the 1931 and 1932 work were never published.

5. Nantucket Shoals and southward. Schroeder (1930) reports in considerable detail on the tagging from 1923 to 1929 of nearly 25,000 fish, mostly on Nantucket Shoals, and also as far south as southern New Jersey. His most important conclusions from these experiments, taken together with length frequency studies and sclerite counts of the scales were:

(a) The stock of cod living on Nantucket Shoals is for the most part distinct from that living to the north and east of southern Massachusetts.

(b) A large part of this stock makes a fall migration to the Rhode Island-North Carolina region, where many spawn and most remain until spring (see Wise (1958) for another interpretation of this movement).

(c) Part of the cod living on Nantucket Shoals emigrate eastward to the Chatham-South Channel region during certain summers.

(d) The stock on Nantucket Shoals is recruited from younger fish from other regions, most of them from offshore grounds. When they reach about 75 cm. in length, they tend to move off the shoals, perhaps to the offshore banks.

TAGS AND METHODS

Smith (1902) used numbered pieces of sheet copper about three-fourths of an inch by one-fourth of an inch, with a hole in one end through which a fine copper wire was passed. These tags were fastened at various places on the fish, but mostly the upper part of the caudal fin, near the peduncle. About 3.5 percent of the cod were recaptured.

Later, Bureau of Fisheries investigators used a metal tag similar to a cattle ear tag, and in the

beginning attached it exclusively to the upper part of the caudal peduncle by means of special clamping pliers. Various metals were used experimentally: silver, aluminum, copper, silver-plated copper, but monel was finally chosen as best. The vast majority of all cod marked between 1901 and the termination of the experiments in 1932 were marked with this tag and in this manner.

It was estimated early in the work, however, that as high as 60 percent of these tags were shed by the fish within the first year. Later the estimate was revised upward, based partially on recaptures by research vessels of fish which bore unmistakable marks of having been tagged. Beginning in October 1927, some fish of 75 cm. or less were marked with the same tag clamped on the lower jaw between the dentary and articular bones, in the hope that these tags would not be so easily lost. Fish thus marked, however, yielded no higher percentage of return, and in 1928 this method was abandoned.

Some tags made of duralumin, a hard alloy of aluminum, were used after 1929, since it was felt that this metal had all the virtues of monel without its weight.

In 1930, a pair of celluloid discs, resembling the Scottish plaice mark, was used with considerable promise. Half of the cod released at Woods Hole in 1932 were marked with celluloid discs on the tail and half on the opercle; within 11 months 8.5 percent of the opercle-tagged cod had been recaptured vs. 5.3 percent of the caudally tagged. In the same year, experiments were carried out with celluloid strips inserted into the coelom during the Mount Desert experiments. These showed some promise of being more permanent than anything used previously, but the U.S. cod investigations were not carried out long enough thereafter to establish conclusive results.

All of the Canadian work from 1924 through 1939 was done with the monel tag described above. In McCracken's (1956) tagging, he used this tag and also used red and white Petersen discs (one of each color) attached on stainless steel wire through the back of the fish, yellow discs attached similarly, and Lea hydrostatic tags on a stainless wire loop through the back. The red and white discs gave by far the best returns, more than 60 percent, the yellow discs over 50 percent. The hydrostatic and strap tags were a poor third and

fourth, with just above 30 percent each, vs. an overall average of more than 40 percent.

RECENT TAGGING EXPERIMENTS

While marking experiments from 1955 through 1959, like all such work, were somewhat opportunistic, depending on weather, availability of fish for tagging, availability of research and commercial vessel time, etc., in retrospect the coverage of the New England area was reasonably good. The experiments fall naturally into three geographic groups, offshore banks, Gulf of Maine, and off southern New England. Table 2 gives a summary of the time and place of each of the experiments in this series, together with the number of fish tagged and the number and percentage returned. The percentages returned should be taken here as only the grossest indication of

TABLE 2.—Summary of cod tagging experiments, 1955–1959

Place and time	Number tagged	Number returned	Percent returned
OFFSHORE BANKS			
Georges Bank:			
Dec. 1956.....	113	8	7.1
Mar.-Apr. 1957.....	434	66	15.2
Oct. 1957.....	51	2	3.9
Total.....	598	76	12.7
Browns Bank:			
Mar. 1957.....	149	48	32.2
Oct. 1957.....	76	11	14.5
Total.....	225	59	26.3
GULF OF MAINE			
Cashes Ledge:			
June-July 1956.....	114	11	9.6
Nov. 1957.....	50	5	10.0
Jeffreys Ledge:			
July 1956.....	20	3	15.0
Apr. 1959.....	4	0	0
Thatchers Island:			
July 1956.....	2	0	0
Lurcher Shoal:			
Oct. 1957.....	7	1	14.3
Grand Manan Banks:			
Oct.-Nov. 1957.....	232	7	3.0
Fippennies Ledge:			
Nov. 1957.....	7	0	0
Total.....	436	27	6.2
SOUTHERN NEW ENGLAND			
Newport, R.I.:			
Dec. 1955.....	59	7	11.9
Chatham, Mass.:			
Feb.-Mar. 1957.....	1,020	253	24.8
South Channel:			
Oct. 1957.....	177	13	7.3
Highland Ground:			
Oct. 1957.....	237	27	11.4
Nov. 1958.....	42	4	9.5
Total.....	1,535	304	19.8
Grand total.....	2,794	466	16.7

¹ Actually 248 fish (253 returns) as 4 were caught after tagging, released and caught again, of which 1 was caught, released, and caught again.

the success of a particular operation; the factors affecting these percentages have been taken up in some detail elsewhere¹ and will be considered briefly here.

THE TAGS

The Lea tag has been described by Rounsefell and Everhart (1953). It consists basically of a small plastic tube, stopped at each end. Inside the tube, which is waterproof, directions for the finder are printed on a roll of thin paper. Although this tag is often fastened to the dorsal musculature of the fish with a wire bridle, in this work the tags were affixed to a monel chain which was in turn fastened to a plastic tab inserted in the coelom as described by Wise (1958).

Rounsefell and Everhart also give a good description of the Petersen tag and its development. The discs used in these experiments were of the type they describe as developed by Nesbit, and were bright yellow. The method of attachment was one worked out by scientists of the St. Andrews Biological Station of the Fishery Research Board of Canada, i.e., on stainless-steel wire through the dorsal musculature. A No. 12 hypodermic needle on a pin vise handle was passed through the muscles just in front of the first dorsal fin and the first interspinous bone. The stainless-steel wire bearing the numbered disc was then pushed through the bore of the needle, the needle withdrawn, another disc placed over the free end of the wire, and the wire cut to length and knotted to hold the two discs firmly in place. This method differs from the one most often used by the Canadians in that they place the tag between the first and second dorsal fins, with the wire passing between the interspinous bones.

A very few cod in these experiments were marked with plastic "spaghetti" tags through the dorsal musculature.

HANDLING METHODS

When tagging cod from a trap, the fish were removed by hand or by dip net from the pocket of the trap, as it was dried up, to a small floating live-car. These fish were taken one at a time

¹ Wise, J. P. Factors affecting number and quality of returns from tagging cod with different tags and using different methods of capture in ICNAF Divisions 4X and 5Y in 1957. International Commission for the Northwest Atlantic Fisheries, North Atlantic Fish Marking Symposium. (In press.)

from the live-car, tagged and measured, and released.

During long line operations, either from research or commercial vessels, fish which appeared not to have been seriously wounded by the hook or the other parts of the long line were gently released from the hook, immediately tagged and measured, and released.

The procedure used while otter trawling was quite different. The trawl net was towed on the bottom for periods of time varying from perhaps 20 minutes to an hour and a half; the time varied inversely with the abundance of fish. The objective was to obtain a reasonable number of fish which had been in the trawl for the shortest possible time.

At the end of the tow, the otter trawl was hauled back, the cod end hoisted aboard, and its contents dumped on deck. As quickly as possible the fish which appeared to be alive and in good condition were taken up from the deck by hand and placed in large wooden tanks of running sea water. The obviously dead or dying fish were culled from the tank, and sometimes when another tank was available the more promising specimens were transferred to a second tank. A measuring board was set up on the edge of the holding tank and fish were dip-netted as needed for tagging. Although some workers feel that it is profitable, where possible, to hold tagged fish in tanks for further culling of weak or dying individuals, this procedure was not followed in any of these operations.

Measurements were recorded usually to the nearest millimeter when the fish were less than 900 mm. in length, and to the nearest centimeter when the fish were larger. Because of haste or confusion, some fish were released before being measured. This happened perhaps 1 percent of the time.

RECOVERY METHODS

The message enclosed in the Lea tags and stamped on one of the pair of Petersen discs states that there is a reward for the return of the tag and gives the laboratory address. Although the tags are often returned directly by mail and the reward and information sent via return mail, agents of the laboratory stationed in New England ports have been empowered to pay the reward, a dollar, on the spot and to collect the pertinent information. In the same fashion, agents of the

Fishery Research Board of Canada working under a reciprocal agreement have collected tags and the Board has paid the reward. Since May 1958, agents of the Fish and Wildlife Service have paid an additional dollar when the fish was returned with the tag. These arrangements have undoubtedly fostered getting a good percentage of the tags recovered actually returned to the laboratory, more than if the initiative for sending them in were left entirely to the fishermen. In addition, having the tags and often the fish received by trained technicians has improved the accuracy of the information received, particularly concerning the length of the fish and its reaction to the tags.

These recovery methods, not available to earlier investigators, doubtless account for some of the improvement in returns over past experiments; how much would be difficult to estimate. On the other hand, previous workers, particularly Schroeder, fished deliberately with research vessels for tagged fish and caught some. This was not done in the recent experiments.

RESULTS

The details of the recent experiments, with exact locations and dates of tagging operations and recaptures are available for examination at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Mass. Below is a summary of the results, grouped as the experiments are in table 2. The figures show the locations of recaptures, plotted usually by 26-week (half-year) periods, in rectangles of 30 minutes of latitude by 30 minutes of longitude. Experiments which yielded no returns and tags returned with insufficient information were not considered in this summary.

Recaptures from Tagging on Offshore Banks

1. Georges Bank, December 1956 (fig. 2). Only eight of the cod tagged were recaptured, all of them on Georges Bank and all within a year. No seasonal pattern is discernible in the recaptures.

2. Georges Bank, March-April 1957 (fig. 3 (a), (b), (c), (d)). Through the summer and early autumn, 20 were recaptured on Georges, 16 on Browns and along the Nova Scotia shore as far east as Halifax County (fig. 3(a)). The position given in the upper left corner of this and subsequent figures gives the location of a return outside the area of the chart. During the winter, from

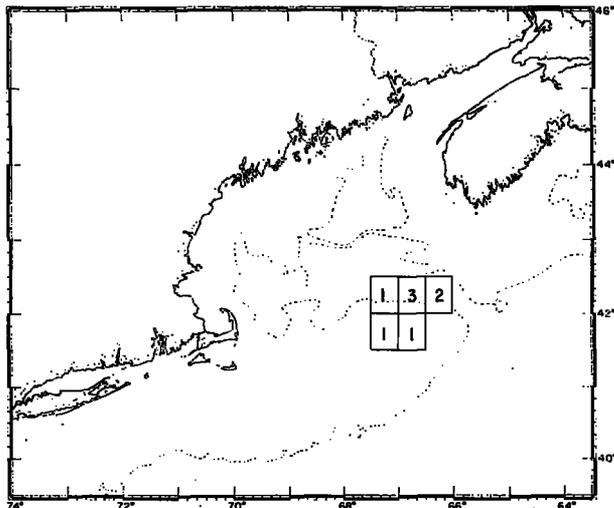


FIGURE 2.—Returns from tagging cod on Georges Bank, December 1956.

October until the next March (1958), 14 were returned from Georges Bank and 1 each from the south and the northeast (fig. 3(b)). The next summer, three were returned from Browns Bank and Nova Scotia (fig. 3(c)). During the winter and spring, three more were taken on Georges and two on Browns. In May and June, two were caught on the Nova Scotia shore (fig. 3(d)).

3. Georges Bank, October 1957. Only two fish were recaptured, and these were near where they had been tagged.

4. Browns Bank, March 1957. Through the summer and early autumn, 13 were captured on or near Browns and the near Nova Scotia shore, 3 from Georges, 3 from northern Nova Scotia, and 1 from the north shore of the Gaspé Peninsula (fig. 4(a)). During the winter and through the next summer (1958), 19 were taken on the Nova Scotia banks and inshore, and 1 on Georges (fig. 4(b), 4(c)). Only a single fish was recaptured, on or near Browns, until the next spring (1959) when three were caught in the same region and one on Georges. The following spring (1960), two were caught in the Browns-Nova Scotia area (fig. 4(d)).

5. Browns Bank, October 1957 (fig. 5). Until the next April (1958) three were taken on Browns. From May through August two more were taken on Browns and three on Georges. During the next summer (1959), one was returned from Browns, and the following spring (1960) one each on Browns and Georges.

Recaptures from Tagging in the Gulf of Maine

1. Cashes Ledge, June–July 1956. Through the next spring (1957) 11 were caught in the Gulf of Maine and near the Massachusetts coast.

2. Cashes Ledge, November 1957. In June (1958) a fish was returned from Georges Bank. Later that year, single individuals were taken in the Gulf of Maine and near Provincetown, and during the following winter (1959), one fish was returned from Georges.

3. Jeffreys Ledge, July 1956 and April 1959. The only returns were from the 1956 tagging. Two were taken near the tagging location, and the next year (1957) one was caught off Rhode Island.

4. Lurcher Shoal, October 1957. One return, near the tagging location.

5. Grand Manan Banks, October–November 1957. Six returns, through March 1960, scattered from the tagging area to the Gulf of Maine and Georges and Browns Banks.

Recaptures From Tagging off Southern New England

1. Newport, R.I., December 1955 (fig. 6). Until February, 1957, 6 were taken off southern New England and Long Island. The summer following the tagging, a single fish was captured on western Georges Bank.

2. Chatham, Mass., February and March 1957 (fig. 7 (a), (b), (c), (d)). Within the first 6 months 122 recaptures were made in or very near the area (see footnote, table 2). Sixteen were taken north of the tagging area, in the Gulf of Maine, along the Maine coast, and as far as the Nova Scotia shore. Five were recaptured on eastern Georges Bank, and one on western Georges (fig. 7(a)). By March (1958), 19 more were taken in or near the tagging area, 3 just north of it, 1 on Georges Bank, 13 to the south and west as far as northern New Jersey (fig. 7(b)). From February through August (1958), 34 were taken in or near tagging area, 19 to the north as far as the Nova Scotia shore, 4 as far south as northern New Jersey, and and 1 on Georges Bank (fig. 7(c)). In August (1958) two were caught in the tagging area or just north of it, and another in January (1959). Later in 1959 another was taken in the Gulf of Maine (fig. 7(c)). The following summer (1960) two curious reports were sent in: a tag found on the beach in the Bay of Fundy and a similar return from Placentia Bay, Newfoundland.

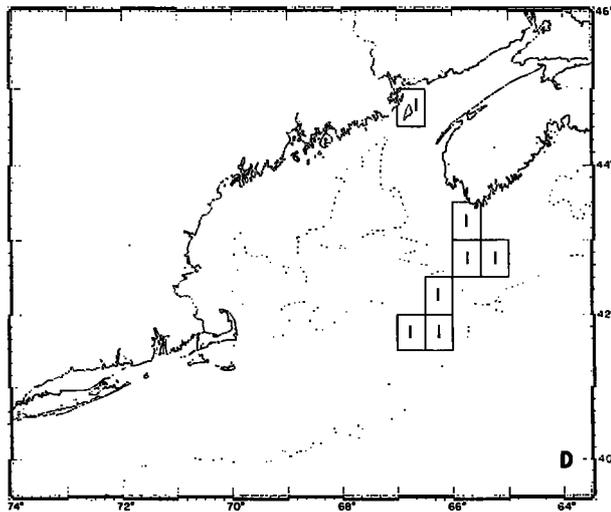
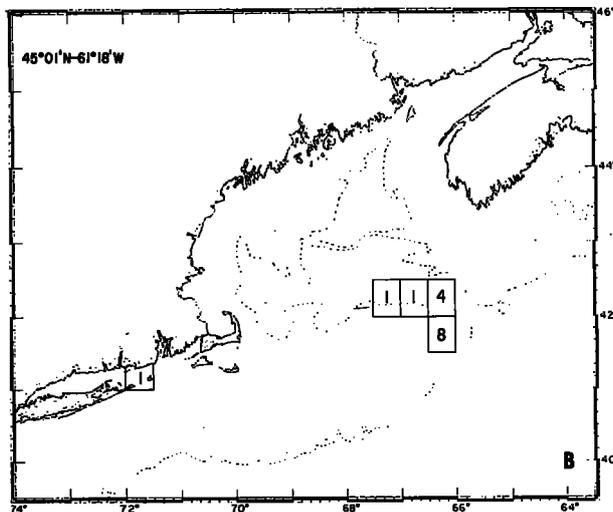
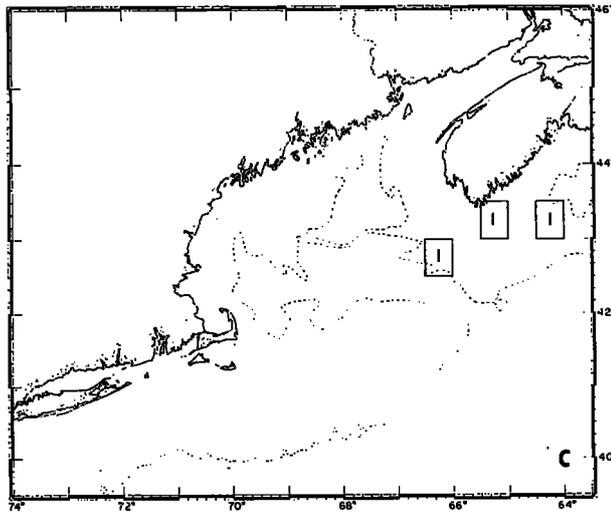
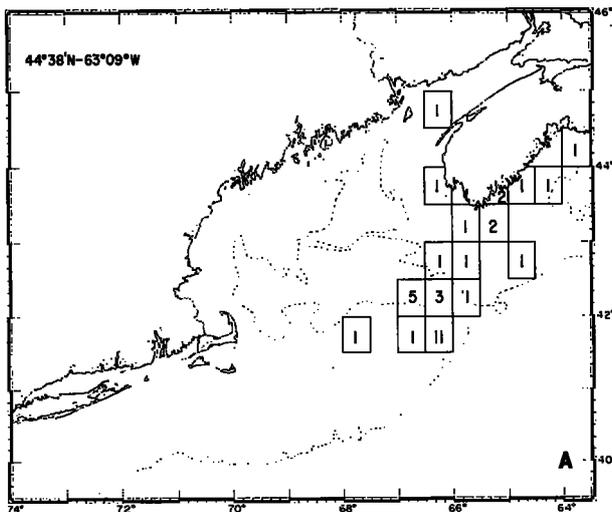


FIGURE 3.—Returns from tagging cod on Georges Bank, March–April 1957. (a) Within 26 weeks, (b) from 27 to 52 weeks, (c) from 53 to 78 weeks, (d) from 79 to 116 weeks.

3. South Channel, October 1957 (fig. 8 (a), (b), (c)). (Figure 8 also shows the returns from the Highland Ground experiment of 1957.) Five fish were caught in or near the tagging area in the first year. During that same period, two were taken off Rhode Island, three in the Gulf of Maine, one just north of the tagging area, and one on Georges Bank (fig. 8 (a), (b)). Two years later, in July 1960, one was caught north of the tagging area.

4. Highland Ground, October 1957 (fig. 8 (a), (b), (c)). By February (1958), 9 fish had been recaptured in the general area of tagging and 1 to the south and west (fig. 8(a)). By September,

four were taken near the area and two to the north of it (fig. 8(b)). By July (1959), four more were taken near the area, and one to the south (fig. 8(c)).

5. Highland Ground, November 1958. Only four fish were recaptured, three of them in or near the area and one in the Gulf of Maine.

Factors Affecting these Results

During 1957, cod captured both by otter trawling and long lining were marked with both the Petersen disc through the dorsal muscles and with the modified Lea tag. Except on Browns Bank in March and at Chatham, Mass., alternate

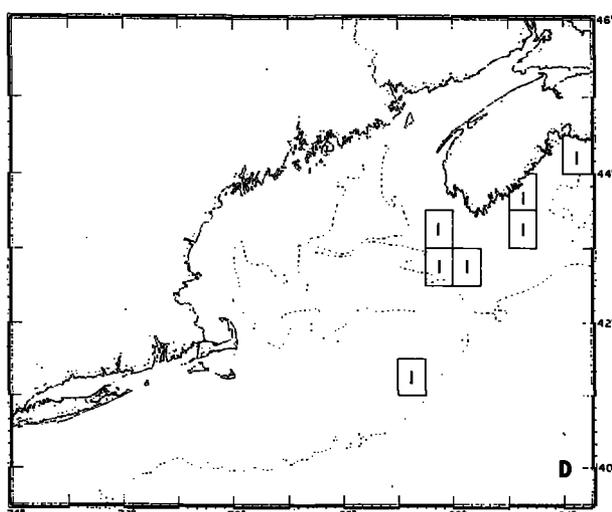
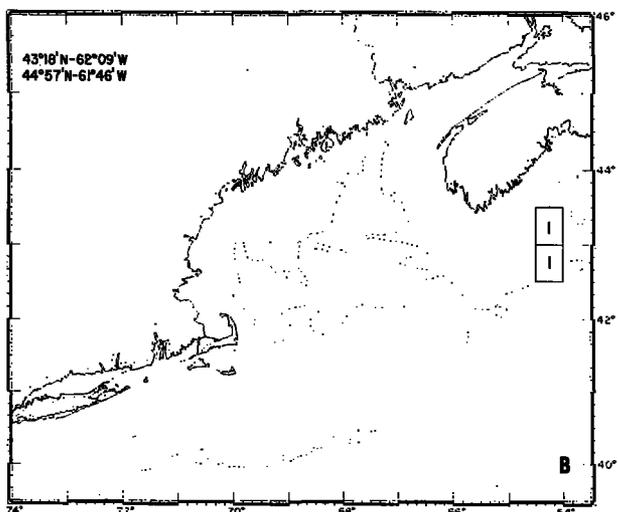
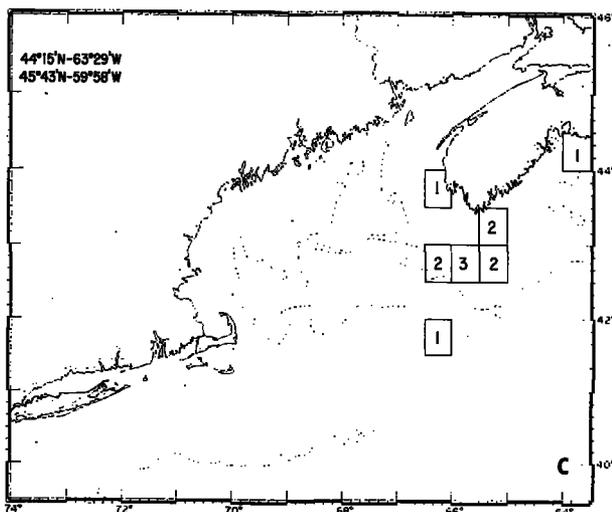
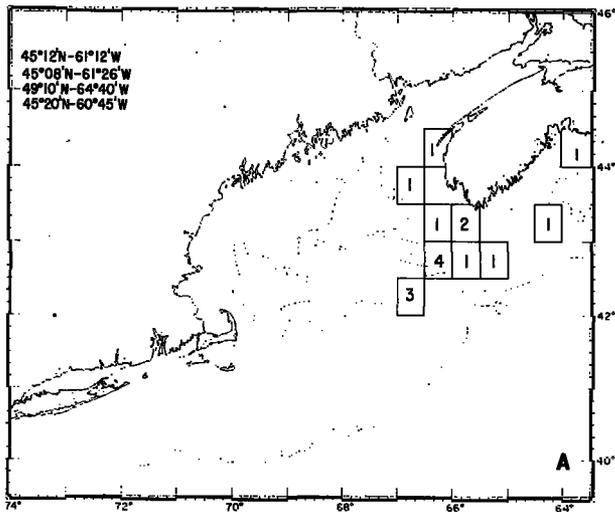


FIGURE 4.—Returns from tagging cod on Browns Bank, March 1957. (a) Within 26 weeks, (b) from 27 to 52 weeks (c) from 53 to 78 weeks, (d) from 79 to 163 weeks.

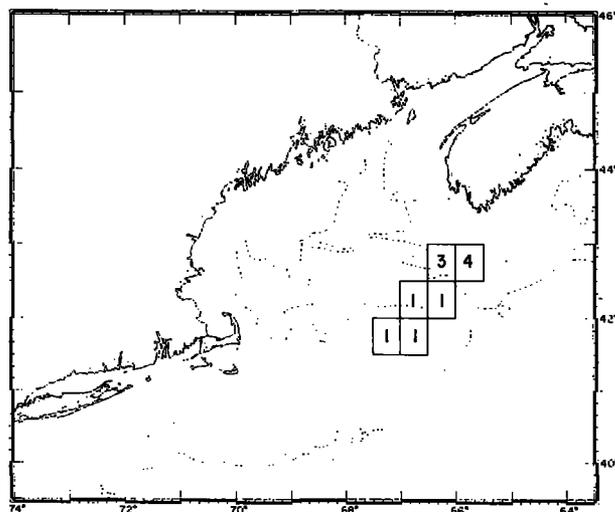


FIGURE 5.—Returns from tagging cod on Browns Bank, October 1957.

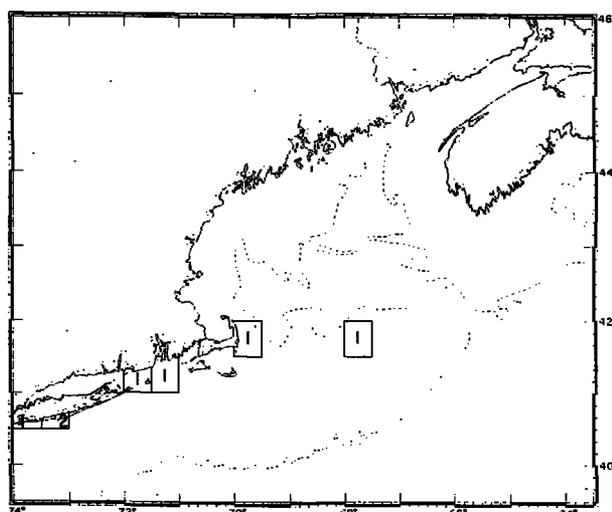


FIGURE 6.—Returns from tagging cod at Newport, R.I., December 1955.

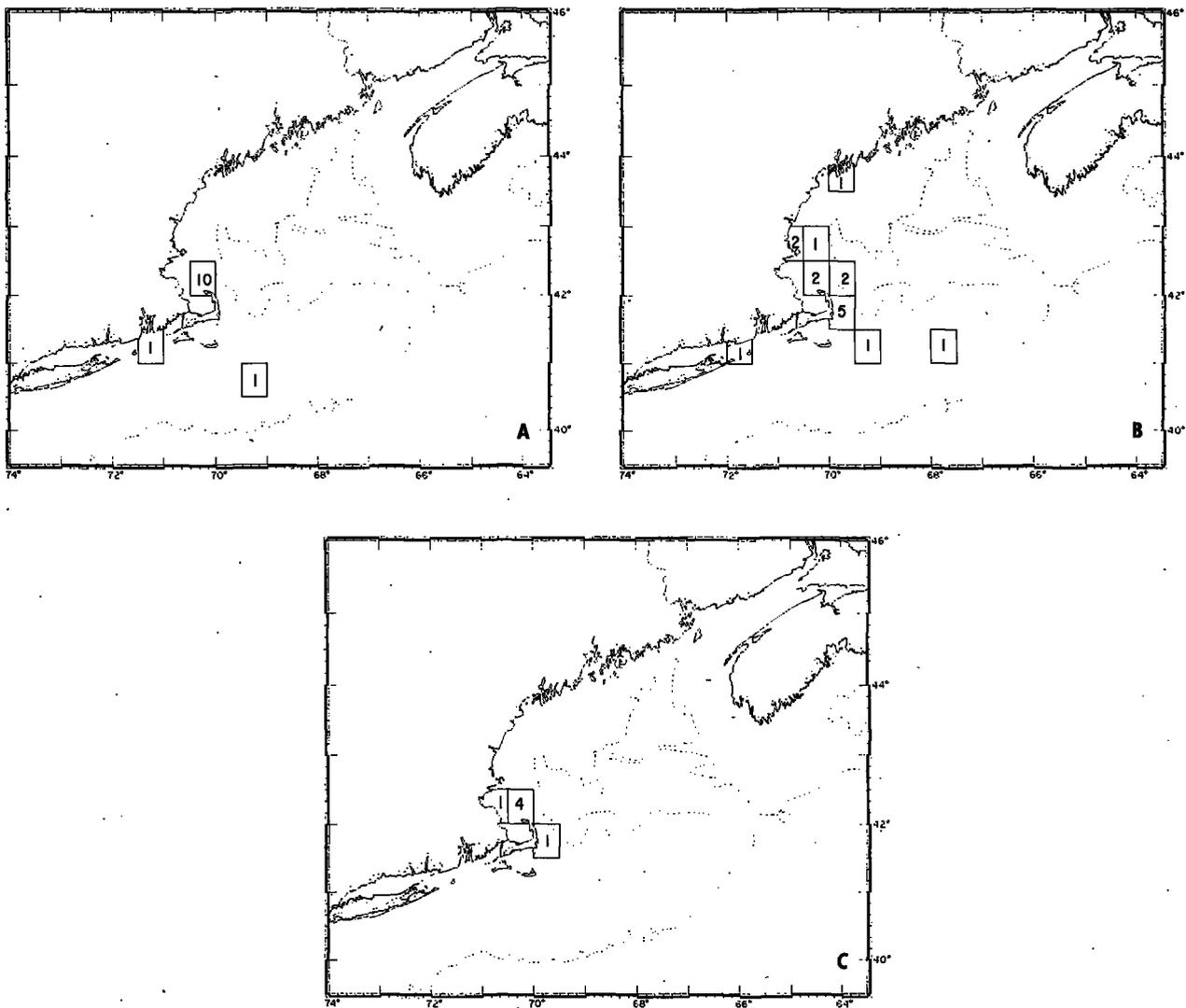


FIGURE 8.—Returns from tagging cod in the South Channel and on the Highland Ground, October 1957. (a) Within 26 weeks, (b) from 27 to 52 weeks, (c) from 53 to 144 weeks.

ments, the effects are minor. It is only if these data should be applied to estimation of population parameters that these variables would become important.

OTHER EVIDENCE OF DISCRETENESS OF GROUPS

THE COMMERCIAL LANDINGS

Although information about groups of fish derived from commercial landings must be interpreted with caution, because of the selectivity of various fishing gears and the culling practices of fishermen, properly chosen data treated appro-

priately can often yield valuable information. For several years we have been collecting information on the length-frequency distribution of the landings of cod caught by otter trawl in New England. These have recently been published in sufficient detail to show differences in the catches in broad areas. The length-frequencies for 1957, 1958, and 1959 (Wise and Murray, 1959, 1960, 1961) show definite differences between the western Gulf of Maine and the Georges Bank-southern New England area. While the means and modes of the length distributions are somewhat variable, there is a definite tendency for a greater percentage of the landings from the Gulf of Maine to

be composed of larger fish (above 80 cm.) than those from the more southerly area. If there is any difference in the nets used, it is that those in the Gulf have on the average somewhat smaller meshes. This could not produce the observed effect, as it has been shown experimentally that larger trawl meshes tend to catch a greater number of larger fish (Clark, McCracken, and Templeman, 1958). This length-frequency distribution alone is strong evidence against a free interchange of fish of all sizes between the two areas.

Indeed, there is evidence of a one-way movement of some of the larger fish from southern New England into the Gulf, and this doubtless contributes to the difference in size composition observed.

PARASITE STUDIES

Sherman and Wise (1961) studied the distribution of the long-lived copepod parasite of cod, *Lernaeocera branchialis*, in the New England area. We found heavy infestations, on the order of 20 percent, in the northern coastal region of the Gulf of Maine and moderate infestation, about 10 percent, in the central Gulf. We interpreted this as meaning that mixing between groups of fish in these areas occurs regularly. On Georges Bank and in the South Channel the infestation was much lower, less than 2 percent. This was taken to mean that there was little mixing between these and the Gulf fish. A sample of migrating cod taken off Rhode Island when they were on their way to the New Jersey coast in autumn had no *Lernaeocera* parasites.

MERISTIC STUDIES

Schmidt (1930) published counts of the number of vertebrae and number of rays in the second dorsal fin of cod from various Atlantic areas. He found large, statistically significant, differences between the cod of Nantucket Shoals, Mount Desert Island, and Grand Manan Banks. While these characters are somewhat variable with time, there were greater differences between the vertebral counts of cod from Nantucket Shoals and Mount Desert Island than there were between those of Mount Desert Island in different years. Grand Manan Banks fish were shown as different from either in one year, but only different from Nantucket Shoals in another.

CONCLUSIONS

The cod of the offshore coastal banks and of southwestern Nova Scotia coastal waters are relatively independent of any other groups in the New England area. There is, however, considerable movement within the group. Fish tagged on Georges Bank are most often caught on Georges Bank, but frequently turn up on Browns Bank and to the eastward in following summers. Fish tagged on Browns Bank are caught mainly on Browns Bank, but also to the eastward in following summers (consideration must be given to the small vessel fisheries of the Nova Scotia coast where fishing is prosecuted more heavily in summer than at any other time of year). Some Browns Bank fish cross over to Georges, but not nearly as large a percentage as cross the Fundian Channel in the other direction. Although a few fish from Georges and Browns are caught occasionally in the Bay of Fundy, only a single individual tagged offshore turned up near the shore of the New England States.

The cod of the waters north of a line between Provincetown, Mass., and the Northern Edge of Georges, and west of Nova Scotia, that is the Gulf of Maine proper, did not yield as high a percentage of returns as did the other groups in these experiments, and even when time of tagging and gear differences are taken into consideration, this is in itself a hint of their relative isolation. There is a considerable movement of some of the larger fish from southern New England into the area, probably in summer, but most of the fish tagged in the region and later recaptured were caught within it, the majority of these not far from where they had been marked. A few leave the area, probably via a northern route around the southwestern part of Nova Scotia, and join the fish on the offshore banks. But the returns from current experiments, taken together with results of previous experiments and the high but variable infestation rates with the parasite *Lernaeocera branchialis*, indicate that there are several more or less discrete groups within the Gulf, intermingling with each other to some extent, but far less with fish outside the Gulf, particularly those of the offshore banks.

The cod of southern New England seem the most mobile of all. A great many tagged in the area are recaptured in the area, even after considerable periods of time. Some individuals have

been repeatedly recaptured near where they were tagged. There is, however, a definite tendency for some to wander to the south and westward during the winter when hydrographic conditions are favorable. They do not go as far, though, as those fish which return to the New Jersey coast to spawn and which are the mainstay of the winter fishery there.

During the summer, the fish of southern New England are augmented by the New Jersey cod, while at the same time some of the larger ones work their way north along the Massachusetts and Maine shores, and a few even go as far as Nova Scotia. It seems doubtful, based on extensive summer tagging experiments in the Gulf, in the 1920's, that many of these fish return to southern New England, particularly those which penetrate as far as the coasts of Maine and Nova Scotia.

Thus, in the light of all evidence to date, there are four major groups of cod in the New England area, all perhaps, and one certainly, divided into subgroups:

1. The cod of the offshore banks, (Georges and Browns) closely related to the fish of the southwestern Nova Scotia coast.
2. The cod of the Gulf of Maine, probably divided into many subgroups, and receiving considerable recruitment from the south.
3. The cod of southern New England and the South Channel.
4. The New Jersey coastal cod, which spend part of the year mingled to a greater or lesser degree with the southern New England fish.

DISCUSSION

Consideration of the topography and hydrography of the region shows that the distribution of the fish outlined above is consistent with the physical features of their environment. A line drawn along the 68th meridian separates the offshore and southern Nova Scotia fish from the more inshore groups; this is a line which runs through or close to the important physical barriers of the deep mud bottoms of the central basin of the Gulf of Maine, the extreme shoals of central Georges Bank, and the relatively barren southern edge of the bank. Only around the narrow northern shelf of the Gulf does this line cross suitable bottom for cod, and all evidence points to this being the most likely path for what little interchange does take place.

Within the Gulf the suitable areas are cut up and patchy, the isobaths meander, the bottom is varied, and these factors doubtlessly foster the subdivision of the Gulf fish into several groups. As Cape Cod is approached from the north, the shelf becomes constricted near Provincetown, forming a bottleneck and limiting effective intercommunication of the Gulf fish with the southern New England group.

South and west of Nantucket Shoals, hydrography plays the most important part in the distribution of the fish. In summer the area is uninhabitable by cod, and the New Jersey fish move north to spend the summer with the southern New England fish. As fall approaches and water temperatures drop, the New Jersey fish migrate back to their spawning grounds, while some of the southern New England fish spread out over suitable bottom along the Rhode Island and Long Island shores.

There is evident in the tag returns from nearly all areas, however, a general movement of fish which cannot be accounted for by anything ordinarily thought of as migration; a tendency for fish which move any considerable distance from where they were tagged to move to the north and/or east. This has been noted previously, first by Schroeder (1930), and later in the Proceedings of the North American Council (1935, p. 15), referring to tagging experiments conducted on the Maine coast, ". . . a noticeable scattering of fish takes place north-eastward to the Bay of Fundy-Nova Scotia region. . . ." (See also quote from the same publication above.) However, when the data on tagging experiments in the northeastern part of the New England area and those from the Canadian coast outside of the area are considered, there appears to be no movement of "Canadian" cod of comparable magnitude in the opposite direction. McKenzie (1956) reports many hundreds of returns from about 20,000 cod tagged along the Canadian Atlantic coast, but only a dozen of these came from New England waters. McCracken's (1956) report of tagging near Lockport mentions the recapture of more than 700 fish, but only 7 of these came from Georges Bank and vicinity. Contrast these results with those reported above from New England waters where from several experiments a good number of cod were recaptured along the Nova Scotia coast. An attempt has been made

to treat this movement quantitatively (Wise, 1959).

Of course, this effect could be produced by a fishing intensity increasing from the southwestern part of the New England and Nova Scotia area to the northeastern. This is not the case, however, for when the number of days fished per year by all gears except scallop dredges and harpoons (International Commission for the Northwest Atlantic Fisheries 1959) is considered, it is seen to decrease proceeding north and east, roughly:

	Days
Subdivision 5Z.....	24, 000
Subdivision 5Y.....	14, 000
Subdivision 4X.....	2, 000
Subdivision 4W.....	5, 000
Subdivision 4Vs.....	200

Whether any or all of the groups defined above are genetically self-sustaining subpopulations, or stocks which display nonheritable differences induced by environment is open to question. The movement of the pelagic eggs and larvae of cod, inferred from the nontidal drift of the surface waters, would generally be to the south and west through the area, promoting mixing in this direction, while the movement of larger fish to the north and east would tend to counteract this to some degree. Of course the size of the fish which appear to emigrate (Wise, 1959) is such that it appears likely that they would have spawned one or more times before they move. Thus, as an hypothesis, it is suggested that the first three groups, those of New England proper, are stocks, not genetically separate, while the New Jersey fish are a genetic subpopulation because of the geographic and hydrographic isolation of their spawning grounds. More detailed studies of morphometric and meristic characters of these four groups should shed considerable light on the question.

ACKNOWLEDGMENTS

Grateful acknowledgment must be made to A. C. Jensen, J. R. Clark, and other biologists and aids who assisted in tagging or who occasionally tagged fish when, for one reason or another, I was unable to do so, and to the skippers and crews of the *Albatross III*, *T-79*, and *Alice and Nancy*, without whom this work could not have been done. Special mention should go to David Ryder, owner-

skipper of the *Alice and Nancy*, who cooperated in tagging, and later released tagged fish he had caught after recording their numbers. Careful record-keeping ashore by S. L. Cogswell and detailed checking of records by Mrs. H. E. Murray assisted immeasurably.

LITERATURE CITED

- CLARK, JOHN R., FRANK D. McCracken, and WILFRED TEMPLEMAN.
1958. Summary of gear selection information for the Commission Area. International Commission for the Northwest Atlantic Fisheries, Annual Proceedings, vol. 8, part 4, pp. 83-99.
- HIGGINS, ELMER.
1929. Progress in biological inquiries, 1927. Report of the U.S. Commissioner of Fisheries for the fiscal year 1928, appendix 6, pp. 199-247. (Document 1044, issued January 26, 1929.)
1930. Progress in biological inquiries, 1928, including extracts from the proceedings of the divisional conference, January 2 to 5, 1929. Report of the U.S. Commissioner of Fisheries for the fiscal year 1929, appendix 10, pp. 627-739. (Document 1068, issued January 30, 1930.)
1931a. Progress in biological inquiries, 1929. Report of the U.S. Commissioner of Fisheries for the fiscal year 1930, appendix 15, pp. 1069-1121. (Document 1096, issued February 11, 1931.)
1931b. Progress in biological inquiries, 1930. Report of the U.S. Commissioner of Fisheries for the fiscal year 1931, appendix 3, pp. 553-626. (Issued December 4, 1931.)
1932. Progress in biological inquiries, 1931. Report of the U.S. Commissioner of Fisheries for the fiscal year 1932, appendix 3, pp. 441-529. Issued October 25, 1932.)
1933. Progress in biological inquiries, 1932. Report of the U.S. Commissioner of Fisheries for the fiscal year 1933, appendix 2, pp. 79-147. (Issued August 10, 1933.)
1934. Progress in biological inquiries, 1933. Report of the U.S. Commissioner of Fisheries for the fiscal year 1934, appendix 3, pp. 313-383. (Issued September 26, 1934.)
1936. Progress in biological inquiries, 1934. Report of the U.S. Commissioner of Fisheries for the fiscal year 1935, appendix 3, pp. 331-399. (Administrative Report No. 21, issued January 29, 1936.)
- INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES.
1959. Statistical Bulletin, vol. 7, for the year 1957, 67 pp.
- MARR, JOHN C.
1957. Contributions to the study of subpopulations of fishes. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 208, 129 pp.

- MARTIN, W. R.
1953. Identification of major groundfish stocks in Subarea 4 of the Northwest Atlantic Convention Area. International Commission for the Northwest Atlantic Fisheries, Annual Proceedings, vol. 3, part 4, pp. 57-61.
- MCCRACKEN, F [RANK] D.
1956. Cod and haddock tagging off Lockeport, Nova Scotia. Fisheries Research Board of Canada, Progress Reports of the Atlantic Coast Stations, no. 64, pp. 10-15.
- McKENZIE, R. A.
1934. Cod movements on the Canadian Atlantic coast. Contributions to Canadian Biology and Fisheries, new series, vol. 8, no. 31 (Series A, General, No. 46), pp. 434-458.
1956. Atlantic cod tagging off the southern Canadian mainland. Fisheries Research Board of Canada, Bulletin No. 105, 93 pp.
- NORTH AMERICAN COUNCIL ON FISHERY INVESTIGATIONS.
1932. Proceedings 1921-1930, No. 1, 56 pp.
1935. Proceedings 1931-1933, No. 2, 40 pp.
- RICH, WILLIS H.
1925. Progress in biological inquiries, July 1 to December 31, 1924. Report of the U.S. Commissioner of Fisheries for the fiscal year 1925, appendix 3, pp. 37-64. (Document 990, issued October 24, 1925.)
1926. Progress in biological inquiries, 1925. Report of the U.S. Commissioner of Fisheries for the fiscal year 1926, appendix 1, pp. 1-36. (Document 1003, issued July 28, 1926.)
- ROUNSEFELL, GEORGE A., and W. HARRY EVERHART.
1953. Fishery science, its methods and applications. John Wiley & Sons, Inc., New York, 444 pp.
- SCHMIDT, JOHS.
1930. Racial investigations. X. The Atlantic cod (*Gadus callarias* L.) and local races of the same. Comptes-Rendus des Travaux du Laboratoire Carlsberg, vol. 18, no. 6, 72 pp.
- SCHROEDER, W [ILLIAM] C.
1928. Cod studies, In: Higgins, E. 1928, Progress in biological inquiries, 1926, including the proceedings of the divisional conference, January 4 to 7, 1927. Report of the U.S. Commissioner of Fisheries for the fiscal year 1927, appendix 7, pp. 601-605. (Document 1029, issued January 25, 1928.)
1930. Migrations and other phases in the life history of the cod off southern New England. Bulletin of the U.S. Bureau of Fisheries, vol. 46 for 1930, pp. 1-136. (Document 1081, issued September 9, 1930.)
- SHERMAN, KENNETH, and JOHN P. WISE.
1961. Incidence of the cod parasite *Lernaecera branchialis* L. in the New England area, and its possible use as an indicator of cod populations. Limnology and Oceanography, vol. 6, no. 1, pp. 61-67.
- SMITH, HUGH M.
1902. Notes on the tagging of 4,000 adult cod at Woods Hole, Mass. U.S. Commission of Fish and Fisheries, Part 27, Report of the Commissioner for the year ending June 30, 1901, pp. 193-208.
- TEMPLEMAN, WILFRED.
1953. Knowledge of divisions of stocks of cod, haddock, redfish and American plaice in Subareas 3 and 2 of the Northwest Atlantic Convention Area. International Commission for the Northwest Atlantic Fisheries, Annual Proceedings, vol. 3, part 4, pp. 62-66. Halifax, Nova Scotia, Canada.
- WISE, JOHN P.
1958. The world's southernmost indigenous cod. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 23, no. 2, pp. 208-212. Copenhagen.
1959. Emigration of cod, *Gadus morhua* L. Preprints of papers of the International Oceanographic Congress 31 August-12 September 1959, pp. 358-359. American Association for the Advancement of Science, Washington, D.C. [English summary with Russian abstract.]
- WISE, J[OHN] P., and H[ARRIETT] E. MURRAY.
1959. United States—1957. Length frequencies—cod. International Commission for the Northwest Atlantic Fisheries, Sampling Yearbook, vol. 2, for the year 1957, p. 126. Halifax, Nova Scotia, Canada.
1960. United States—1958. Length frequencies—cod. International Commission for the Northwest Atlantic Fisheries, Sampling Yearbook, vol. 3, for the year 1958, pp. 70-71. Halifax, Nova Scotia, Canada.
1961. United States—1959. Length frequencies—cod. International Commission for the Northwest Atlantic Fisheries, Sampling Yearbook, vol. 4, for the year 1959, pp. 35-36. Halifax, Nova Scotia, Canada.

DISTINGUISHING TUNA SPECIES BY IMMUNOCHEMICAL METHODS

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ABSTRACT

Interspecies differences in the sera of adult tuna (albacore, *Thunnus alalunga*; yellowfin, *Thunnus albacares*; bigeye tuna, *Thunnus obesus*; skipjack, *Katsuwonus pelamis*; little tunny (wavyback skipjack), *Euthynnus yaito*; and dogtooth tuna, *Gymnosarda nuda*) were demonstrated by double diffusion precipita-

tion with antisera produced in rabbits. Studies of the soluble antigens extractable from the flesh of tuna were complicated by spontaneous precipitation. It was possible, however, to distinguish skipjack tuna from albacore and yellowfin by means of immunodiffusion of extractable tissue antigens.

The tunas, an economically and biologically major group of marine fishes, have been the subject of considerable study by fishery scientists. One of the most perplexing problems in these studies has been the identification of larval forms of these fishes. Work on various aspects of this problem using morphological and paper chromatographic methods has been presented by Walter M. Matsumoto (1958, 1959, and 1960), who has discussed at considerable length the ultimate objectives and the difficulties of such research.

Because of difficulties in application of morphological methods, due partly to the lack of known juvenile materials from some of the species, an independent approach to this problem was needed to supplement and check the results of the morphological research. At the suggestion of Albert Tester we made a preliminary study of the applicability of some immunochemical methods we have used extensively in our salmon investigations. Since our time and facilities were largely committed to salmon research, our tuna studies were undertaken on a restricted scale and with limited objectives. These objectives were to determine whether differences could be detected in the

serum antigens of adult tuna which were characteristic of the species. If these objectives could be accomplished, it was considered that it would be reasonable to use appropriate immunological methods for attacking the much more difficult problems involved in identification of the larval forms.

Our preliminary studies, which were carried out over a considerable period as material and time became available, indicated that there were detectable interspecific differences in the serum antigens of adult tuna. Financial support in 1960 from the Bureau's Biological Laboratory, Honolulu, enabled us to make a more complete study of many of the antisera we had prepared and also to make a preliminary study of the soluble antigens of adult tuna flesh.

This paper describes our studies on interspecific differences in the serum antigens of adult tuna. Similar studies on albacore, bigeye, and yellowfin tunas, reaching essentially the same conclusions, have been reported by Suzuki and Morio (1959). Charles Matsumoto had the primary responsibility for our soluble flesh antigen studies and is preparing a manuscript describing them; consequently, only a summary of the most important aspects of our research on these anti-

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gens is presented. Finally, I have made recommendations concerning the direction that future immunochemical or serological research on this problem should take, in light of the results we and others have obtained, and taking into account certain other important factors.

BACKGROUND

The use of immunological methods for the identification of species is based on the specificity of antigen-antibody reaction. Knowledge of this specificity is general, since we know that immunity for one disease will not protect us when we are exposed to another.

Nuttall (1904) established that animal species can be distinguished by the specificity of characteristic antigens present in their serum. He also established that the degree of overlapping or cross reactivity in the specificity of the serum antigens of animals closely paralleled their taxonomic relationships. Many immunologists have subsequently used and extended these findings. Probably the most important studies are those of Irwin (1947) and his associates. They studied the antigenic constitution of the sera of species, species hybrids, and backcross hybrids of pigeons and doves, and demonstrated that the specificities of individual serum antigens were under direct genetic control. Thus, antigenic differences that we find between species can be considered direct consequences of the genetic differences between species.

METHODS AND MATERIALS

THE DOUBLE DIFFUSION PRECIPITIN ANALYSIS METHOD

Throughout this research we have used a modification of the Ouchterlony method of double diffusion precipitin analysis, exactly as described in another paper from this laboratory (Ridgway, Klontz, and Matsumoto, 1961). Since we described this method completely in that paper and it has been fully treated elsewhere in the literature (Ouchterlony, 1958) only a brief description will be given here. The method consists of allowing an antigen solution and an antiserum to diffuse toward each other through a semisolid medium containing a suitable concentration of saline or buffer and a preservative.¹ Where the

molecules of a given antigen meet their specific antibodies in an optimal ratio of concentrations, a line of precipitation will form. Since the position of this line is dependent on the diffusion rates and initial concentrations of the antigen and its specific antibody and since these will vary between separate components, a separate line can form for each antigen-antibody system present. When two antigen solutions diffuse side by side toward a single antiserum the lines for identical antigens will fuse while those for unrelated antigens will cross.

Thus we have a system which allows us to separate out and study the reactions of individual antigens in a complex mixture and to compare the antigenic composition of one preparation with that of other preparations.

Photographic records of all of our tests were made as described in a previous publication (Klontz, Ridgway, and Wilson, 1960).

PRODUCTION OF ANTISERA

Antisera were prepared in rabbits in two different ways. One method consisted of emulsifying 2.5 ml. of pooled sera from several individuals of a given tuna species with 2.5 ml. Difco complete Freund's adjuvant and injecting the emulsion in several regional lymph node sites. After 15 days the rabbits were bled on 3 successive days. After a rest of 1 month, the animals were restimulated by two intraperitoneal injections of 0.25 ml. of serum and bled 4, 5, and 6 days later.

The second method used to produce antisera consisted of giving five to nine intraperitoneal injections of 0.25 to 0.5 ml. of pooled serum and bleeding on the fifth, sixth, and seventh days after the last injection. After 2 to 3 weeks rest, the rabbits were restimulated by two intraperitoneal injections of 0.25 ml. pooled serum and bled 4, 5, and 6 days later. The best antisera were obtained with the latter method. We also prepared several antisera in chickens by giving three intraperitoneal injections of 0.25 ml. pooled albacore serum at 4-day intervals and bleeding 5 days after the last injection. Although potent antibodies were detectable by the usual precipitin method we were unable to obtain useful results with these antisera in double diffusion tests.

¹ The medium we use has the following composition: Difco agar 1.5 g., sodium chloride 0.72 g., sodium citrate 0.6 g., "Merthiolate" Lilly 0.01 g., trypan blue 0.01 g., distilled water to make 100 ml. Adjust pH to 6.7 with hydrochloric acid.

TUNA SERUM SAMPLES

The samples of tuna serum were obtained for this study by the biologists of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

Table 1 gives a list of these samples. Since we have found little evidence for individual differ-

TABLE 1.—*Samples of sera from adult tuna*

Species		Number of individual samples	Vessel	Year collected
Common name	Scientific name			
Albacore.....	<i>Thunnus alalunga</i>	11	<i>John R. Manning</i>	1957
Yellowfin.....	<i>Thunnus albacurus</i>	8	<i>Charles H. Gilbert</i>	1957
Bigeye.....	<i>Thunnus obesus</i>	1	<i>Charles H. Gilbert</i>	1959
		8	<i>Charles H. Gilbert</i>	1958
Skipjack.....	<i>Katsuwonus pelamis</i>	2	<i>Hugh M. Smith</i>	1959
		16	<i>Charles H. Gilbert</i>	1957
Little tunny.....	<i>Euthynnus yaito</i>	19	<i>John R. Manning</i>	1957
		2	<i>Charles H. Gilbert</i>	1957
Dogtooth tuna.....	<i>Gymnosarda nuda</i>	2	<i>John R. Manning</i>	1957
		2	<i>Charles H. Gilbert</i>	1957

TABLE 2.—*The distinction of species of adult tuna by means of double diffusion precipitation analysis of their sera with antisera prepared in rabbits*

Antiserum	Serum (tuna species)	Number of precipitation lines	Number of distinctive lines
Antialbacore.....	Albacore.....	7	3
	Yellowfin.....	4	3
	Bigeye.....	5	3
	Skipjack.....	4	3
	Euthynnus.....	3	4
	Dogtooth.....	2	5
Antibigeye.....	Bigeye.....	11	3
	Albacore.....	8	3
	Yellowfin.....	8	3
	Skipjack.....	5	6
	Dogtooth.....	3	8
Antiyellowfin.....	Yellowfin.....	9	1
	Albacore.....	8	1
	Bigeye.....	8	1
	Skipjack.....	5	4
	Euthynnus.....	5	4
	Dogtooth.....	3	6
Antiskipjack.....	Skipjack.....	3	1
	Albacore.....	2	1
	Yellowfin.....	2	1
	Bigeye.....	2	1
	Euthynnus.....	2	1
	Dogtooth.....	1	2
Anti- <i>Euthynnus</i>	Euthynnus.....	6	1
	Albacore.....	5	1
	Yellowfin.....	5	1
	Bigeye.....	5	1
	Skipjack.....	5	1
	Dogtooth.....	5	1
Antidogtooth.....	Dogtooth.....	11	7
	Albacore.....	4	7
	Yellowfin.....	4	7
	Bigeye.....	6	5
	Skipjack.....	4	7
	Euthynnus.....	4	7

ences, information about the individual samples is not included. Information on place and date of capture, sex, and size are on file in the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

Samples were taken by cutting the isthmus of tuna, collecting the spurting blood in bottles or bowls, allowing it to clot for 1 to 2 hours at air temperature and up to 24 hours under refrigeration. The serum was decanted from the clotted blood and clarified by centrifugation. Serum samples were then frozen and stored at -15°C . to -30°C . At our laboratory, samples being used were separated into small aliquots to avoid repeated thawing and freezing. Most samples were in excellent condition when received and have remained stable under frozen storage.

RESULTS

The results obtained with the most discriminating sera among those we have prepared are summarized in table 2. For example, when testing our most discriminating antialbacore serum, we find that there are seven distinguishable precipitation lines with albacore serum, four of which cross-react with yellowfin serum, five with bigeye serum, four with skipjack serum, three with *Euthynnus* serum and two with dogtooth serum. Thus, with this serum, the number of lines (antigens) which distinguish albacore from the other species are as follows: Three with yellowfin, two with bigeye, three with skipjack, four with *Euthynnus* and five with dogtooth. Illustrations of tests with antidogtooth and antibigeye sera are presented in figures 1 and 2.

Considerable variability exists among the discriminatory abilities of the various antisera, even when we use the best bleedings. (There is, of course, considerably more variability among the antisera in discriminatory ability when one considers the results obtained with some of the poorer ones.) We have antialbacore, antibigeye, and antidogtooth antisera which possess considerable discriminatory power. On the other hand, the discriminatory qualities of our best antiyellowfin, and antiskipjack and anti-*Euthynnus* antisera are not great. This points up the fact that there is considerable variability between individual rabbit sera, so that one may need to immunize 6 to 20 rabbits in order to produce an antiserum of

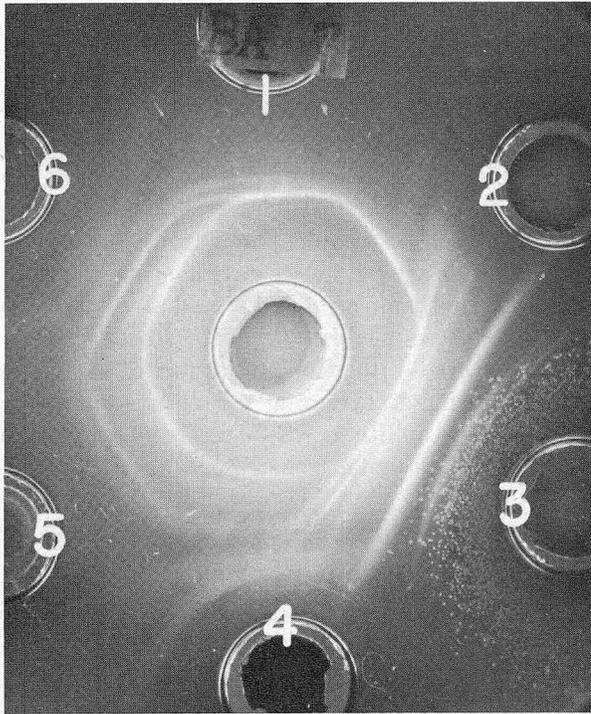


FIGURE 1.—The distinction of dogtooth tuna serum from that of other species. The peripheral wells contain sera of the following species: 1. *Eruthynnus*. 2. Skipjack. 3. Dogtooth. 4. Yellowfin. 5. Albacore. 6. Bigeye. Antidogtooth-tuna-serum rabbit serum in center well. The random dots around dogtooth well are due to crystallization of material, which becomes insoluble on dilution, and have no effect on the immunological reaction.

the specificity necessary to make a particular distinction. We have noted this in some of our other work (Ridgway, Klontz, and Matsumoto, 1961), and this variability among the responses of several rabbits to the same antigenic stimulus has been pointed out by other immunologists.

That tuna species can be distinguished by the antigenic constitution of their sera, as summarized in table 2, has been confirmed by several replications. In the case of the albacore, yellowfin, and bigeye, distinctions were also made by absorption experiments. These absorptions were carried out both by the specific inhibition or intragel absorption method of Bjorklund (1952), which involves incorporating the absorbing tuna serum in the agar medium at a concentration of 20 percent; and by placing the absorbing serum in the center well for an interval of 10 to 20 minutes before adding the antiserum. All absorption ex-

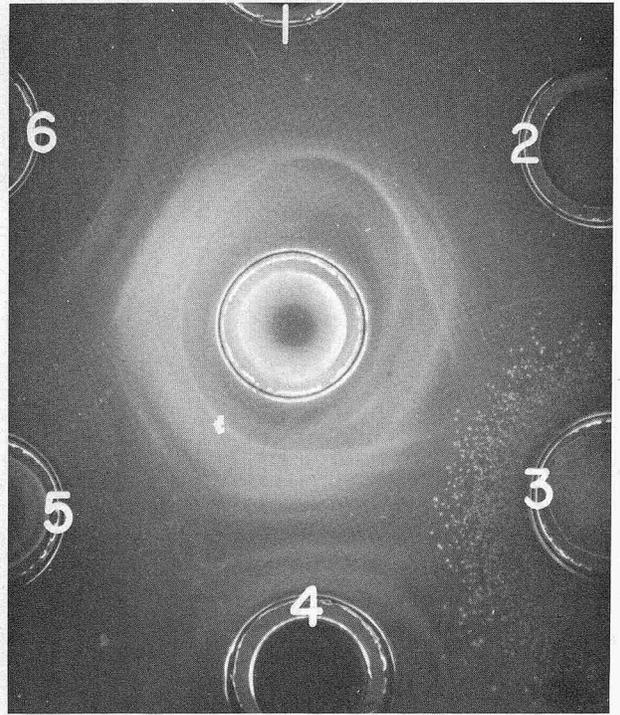


FIGURE 2.—Distinction of bigeye tuna serum from that of other species. The peripheral wells contain sera of the following species: 1. *Eruthynnus*. 2. Skipjack. 3. Dogtooth. 4. Yellowfin. 5. Albacore. 6. Bigeye. Antibigeye-tuna-serum rabbit serum in center well.

periments were carried out using the micromethod of agar diffusion (Ridgway, Klontz, and Matsumoto, 1961). In this method, 2 ml. of hot agar medium is pipetted on the unfrosted portion of a 25×75 mm. microscope slide which has been cleaned with alcohol. The antigen and antiserum wells are cut out of the agar using stainless steel punches of appropriate diameter. In these experiments summarized in table 3, 10 to 20 microliters of tuna sera were placed in the respective wells, the absorbing serum was placed in the central antiserum well also. After a short interval, 20 microliters of antiserum were placed in the center well and diffusion allowed to proceed for 4 hours at 37° C. and overnight in the refrigerator. It is evident from the results presented in table 3 that the closely related species bigeye, yellowfin, and albacore do possess species-specific antigenic factors as part of the constitution of their serum proteins, and that these factors can be detected with immune rabbit sera.

TABLE 3.—*Distinctive reactions of sera of species of adult tuna after removal of cross-reactive antibodies by absorption*

Antiserum	Absorbing serum	Test serum	Reaction (number of precipitation lines)
AntiAlbacore	Bigeeye	Albacore	1
Do	do	Yellowfin	1
Do	do	Bigeeye	0
Do	Yellowfin	Albacore	1
Do	do	Yellowfin	0
Do	do	Bigeeye	0
AntiYellowfin	Albacore	Yellowfin	1
Do	do	Albacore	0
Do	do	Bigeeye	1
Do	Bigeeye	Yellowfin	2
Do	do	Albacore	1
Do	do	Bigeeye	0
AntiBigeeye	Albacore	Bigeeye	2
Do	do	Albacore	0
Do	do	Yellowfin	1
Do	Yellowfin	Bigeeye	2
Do	do	Albacore	1
Do	do	Yellowfin	0

SOLUBLE TISSUE ANTIGEN STUDIES

Encouraged by the results obtained from our studies of serum antigens we undertook some preliminary studies on the soluble antigens of muscle tissue. We felt that such antigens would be more useful for the identification of larval forms since muscle obviously makes up a larger portion of the animal than does blood serum.

In order to adapt the double diffusion precipitin analysis method to the detection and study of soluble tissue antigens of tuna flesh, and characteristic differences in them between species, several problems had to be investigated first. These problems included the development of methods for extraction of soluble antigens from tuna muscle tissue, stabilization of these extracts, and the production of potent and specific antisera.

The results of these studies can be summarized as follows: Extraction of muscle tissue with neutral physiological saline resulted in quite dilute and unstable solutions from which most of the dissolved protein precipitated spontaneously, even on overnight storage at 0° C. to 4° C. The use of alkaline saline solutions (pH 10) increased the efficiency of extraction and the stability of the solutions. From the standpoint of efficiency of extraction and stability of the resulting solution, however, the best extracting medium was found to be 50 ml. glycerol, 1 g. NaCl, and water to make 100 ml. The spontaneous precipitation which occurred in muscle tissue extracts was increased by increasing temperatures or by freezing and thawing. It was not significantly inhibited by heavy metal ions indicating that it may

be due to causes other than the actions of proteolytic enzymes.

Three methods for the production of antisera were tried; intraperitoneal injection of several doses of untreated extract, intramuscular injection of alum precipitated extract, and the incorporation of the extract in Freund's adjuvant for an initial subcutaneous stimulation, followed by several intraperitoneal injections of the untreated extract after 2 to 3 weeks. The last method gave the most potent antisera.

Spontaneous precipitation of the extracts occurred during the diffusion tests which complicated their interpretation. Nevertheless we did find that skipjack differed from yellowfin, albacore, and bigeye by at least one tissue antigen detectable when the tests were run at 4° C. The soluble tissue antigens of yellowfin, albacore, and bigeye were not distinguishable using the antisera and methods we developed, but they did possess a character missing from the skipjack extracts.

The results of our preliminary studies also indicated that the soluble proteins of fish muscle tissue are antigenically quite distinct from the serum proteins of the same species. The few weak reactions obtained on testing tissue extracts with antiserum sera may be attributable to the presence of small amounts of blood and lymph in the tissues. In addition, the degree of cross-reactivity among taxonomic groupings of fish is apparently greater in the case of soluble muscle proteins than in the case of serum proteins. These findings may be of interest from the standpoints of ontogeny and evolution, but they increase the difficulties involved in the utilization of soluble tissue antigens for the distinction of species.

DISCUSSION

The demonstration of interspecific differences in serum protein antigens of tuna with only a small-scale study indicates that there are definite possibilities in the application of immunochemical methods to the problem of identifying the species of larval forms of tuna. This is, of course, dependent on the development of species specificity in antigenic constitution early in embryological development. There are ultramicro precipitin methods available for the study of soluble antigens, for example the double diffusion method can be carried out on cellulose acetate films as reported by Consden and Kohn (1959), with as little as

0.001 ml. of serum. With potent and specific antisera the usual ring test can detect even smaller amounts of antigen. A larger scale program utilizing a great many more rabbits could probably develop such potent and specific antisera.

Nevertheless, it seemed more reasonable to study the soluble antigens of muscle tissue since muscle makes up a much larger portion of the animal than does serum. However, our finding that the soluble antigens of tissue appear to be less distinct than those of serum, coupled with the technical problems involved in preventing spontaneous precipitation of tissue antigens, indicates that soluble tissue antigens may not be the best material for use in the distinction of tuna species. More study of these antigens is warranted, especially the investigation of other methods of immunization in order to produce more discriminating antisera, and the examination of methods for extracting only the more stable antigens.

An even more promising approach is the use of insoluble cellular antigens. There is evidence from the studies of Cushing (1956) and Suzuki, Shimizu, and Morio (1958) that interspecific differences in the red cell antigens of tuna exist. The production of species-specific hemagglutinating antisera is also readily accomplished because of the relative ease of absorption with red cells. On the other hand, removal of cross-reacting precipitins by absorption is difficult to accomplish satisfactorily. The presence of species-specific red cell antigens in other tissues of the larval tuna would, of course, be required for the application of this method. In human beings and certain other mammals red cell antigens have been demonstrated to be present in other tissues. The techniques available for testing for these antigens in tissues include the mixed agglutination method which has been used to demonstrate the presence of A and B antigens in human epithelial cells by Coombs, Bedford, and Rouillard (1956) and the fluorescent antibody techniques of Coons (1954) which are so sensitive that the presence of antigens on individual cells is demonstrable.

Of course, suitable preservation methods will have to be developed for the maintenance of the antigens of larvae from the time the larvae are collected until they can be sorted from the plankton and tested.

Undoubtedly, the way is open for greater application of the ultrasensitive methods of immuno-

chemistry and blood-group serology to problems of fishery biology. The important thing to be recognized is that these methods are not in the nature of "magic wands", but are developed and applied through knowledge and painstaking experimentation.

SUMMARY

Through the application of the Ouchterlony method of diffusion precipitin analysis, with rabbit immune sera, the presence of species-specific differences in serum antigens of adult tuna was demonstrated. The existence of these differences was confirmed by absorption methods.

In studies on soluble antigens of the muscle tissue of tuna, evidence was obtained for distinguishing skipjack from albacore, yellowfin, and bigeye tuna.

No characteristic differences in their soluble tissue antigens were found which allowed the mutual distinction of the latter three species. In the study of soluble tissue antigens, technical problems involving extraction media, stability of extracts, and production of potent antisera were encountered and preliminary methods for their solution developed.

The course which further developments in these and allied fields might take resulting in possible distinction of larval forms was discussed.

ACKNOWLEDGMENTS

Charles Matsumoto, Mary LaRocque Ullman, and George W. Klontz assisted in conducting the experiments described. Biologists of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, collected the tuna blood samples under difficult conditions.

LITERATURE CITED

- BJORKLUND, BERTIL.
1952. Specific inhibition of precipitation as an aid in antigen analysis with gel diffusion method. *Proceedings of the Society for Experimental Biology and Medicine*, vol. 79, no. 2, pp. 319-324.
- CONSDON, R., AND J. KOHN.
1959. Cellulose acetate as a medium for immunodiffusion. *Nature*, vol. 183, no. 4674, May 30, pp. 1512-1513.
- COOMBS, R. R. A., DONALD BEDFORD, AND L. M. ROUILLARD.
1956. A and B blood-group antigens on human epidermal cells demonstrated by mixed agglutination. *The Lancet*, vol. 270, no. 6291, April 21, pp. 461-463.

- COONS, ALBERT H.
1954. Labelled antigens and antibodies. Annual Review of Microbiology, vol. 8, pp. 333-352. Annual Reviews Inc., Stanford, Calif.
- CUSHING, JOHN E., JR.
1956. Observations on serology of tuna. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report-Fisheries No. 183, 14 pp.
- IRWIN, M. R.
1947. Immunogenetics. In: Advances in Genetics, M. Demerec (editor), vol. 1, pp. 133-160, Academic Press, Inc., New York.
- KLONTZ, GEORGE W., GEORGE J. RIDGWAY, AND GEORGE P. WILSON.
1960. An illuminator for observing and photographing precipitin reactions in agar. Journal of the Biological Photographic Association, vol. 28, no. 1, pp. 11-14.
- MATSUMOTO, WALTER M.
1958. Description and distribution of larvae of four species of tuna in central Pacific waters. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin 128, vol. 58, pp. 31-72.
1959. Descriptions of *Euthynnus* and *Auxis* larvae from the Pacific and Atlantic oceans and adjacent seas. The Carlsberg Foundation's Oceanographical Expedition Round the World 1928-30 and Previous Dana—Expeditions, Dana-Report no. 50, 34 pp.
1960. The application of paper chromatography in identifying tuna larvae. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report-Fisheries No. 337, 9 pp.
- NUTTALL, GEORGE H. F.
1904. Blood immunity and blood relationship; a demonstration of certain blood relationships amongst animals by means of the precipitin test for blood. Cambridge, University Press, 444 pp.
- OUCHTERLONY, ORJAN.
1958. Diffusion-in-gel methods for immunological analysis. In: Paul Kallos (editor), Progress in Allergy, vol. 5, pp. 1-78, S. Karger, Basel, Switzerland, and New York.
- RIDGWAY, GEORGE J., GEORGE W. KLONTZ, AND CHARLES MATSUMOTO.
1961. Intraspecific differences in serum antigens of red salmon demonstrated by immunochemical methods. International North Pacific Fisheries Commission, Bulletin 8, pp. 1-13.
- SUZUKI, AKIMI, YASUYUKI SHIMIZU, AND TADA0 MORIO.
1958. Serological studies of the races of tuna. 1. The fundamental investigations and the blood groups of albacore. Report of Nankai Regional Fisheries Research Laboratory, (Sanbashi-dori, Kochi, Japan) no. 8, March, pp. 104-116. (In Japanese, with English summary.)
SUZUKI, AKIMI, AND TADA0 MORIO.
1959. Serological studies of the races of tuna. III. Preliminary investigation on the antigens in tunas sera by the agar-plate-diffusion method. Report of the Nankai Regional Fisheries Research Laboratory (Sanbashi-dori, Kochi, Japan), No. 11, December, pp. 165-173. (In Japanese, with English summary.)

THEORY ON DEVELOPMENT OF MOUNDS NEAR RED BLUFF, CALIF.

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ABSTRACT

Photographs are presented showing mounds in various stages of development in the flood zone of the Sacramento River near Red Bluff, Calif., and the ter-

rain on which the mounds are located. A theory is presented to explain how the mounds were formed.

Rounded mounds of earth, such as in figure 1, are found in many parts of North, Central, and South America and possibly in other parts of the world. The striking appearance and puzzling features exhibited by the mounds have long made them objects of scientific curiosity. Of the many theories proposed during the last 100 years to account for their formation, none is universally accepted. Literature on the subject is too extensive to be cited here, but Scheffer (1947, 1958) and McGinnies (1960) list sufficient references to give a good review.

Incidental to an ecological investigation of streams as nursery areas for the production of chinook salmon (*Oncorhynchus tshawytscha*), a section of the Sacramento River near Red Bluff, Calif. (fig. 2) was studied, where mounds are in many stages of growth. When one looks at these mounds, he finds that in a restricted area, they constitute a family. They tend toward an ellipsoidal form, and their long axes are parallel to one another. If one cuts through a mound, he finds that it is composed largely of silt with some sand, stones, and decayed matter (fig. 3). The substratum of the mound is made up of gravel and coarse sand.

Our curiosity having been aroused by these observations, we developed a theory to explain how the mounds were formed. Although the sub-

ject of mounds is not directly a part of fishery studies, the agents that we think lead to the formation of mounds—namely, flooding of the stream and erosion of soil materials—also kill salmon by scouring the stream gravel or by depositing silt in the streambed. This action destroys incubating spawn by removing gravel and washing out the eggs and by depositing silt and subsequently smothering the eggs. Similarly, larvae and other aquatic forms that the salmon fry eat are either washed out or the habitat of these forms is destroyed by deposition of silt, and the food supply for the young salmon is greatly diminished.

Mounds thus serve as tangible evidence of stream phenomena that are of vital concern to the fishery biologist. We believe that an understanding of the agents involved in the formation of mounds will contribute to a better understanding of the factors that determine whether the streambed will be a productive habitat for salmon when spawning.

How dynamic conditions during flood seasons lead to the formation of mounds can best be seen by photographs. The purpose of this report therefore is to present pictures of mounds in various stages of formation and then to give a theory summarizing the photographic observations.

Note.—Approved for publication June 21, 1961.

PHOTOGRAPHIC OBSERVATIONS



FIGURE 1.—Mounds near Red Bluff, Calif.



FIGURE 2.—The mounds shown in figure 1 were near the middle of the extreme right area.

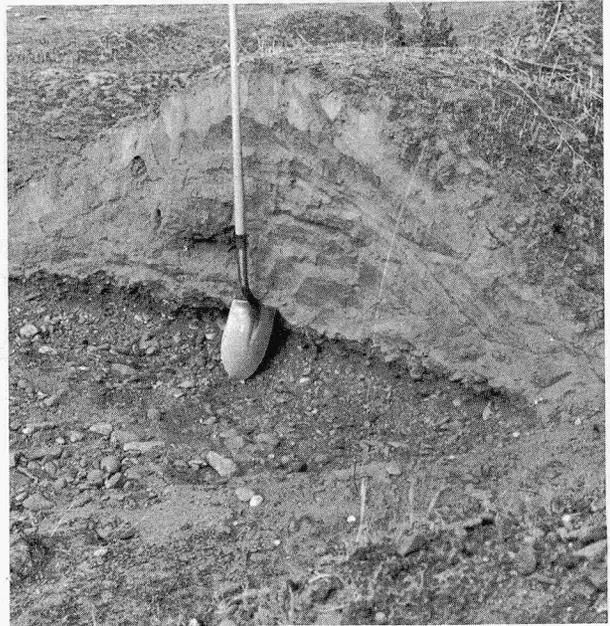


FIGURE 3.—A cross section cut through a typical mound shows a deposition of silt, some decayed organic matter, sand, and an occasional stone on a substratum of gravel and coarse sand. This particular ellipsoidically shaped mound was 3 feet high, 13 feet wide, and 20 feet long.



FIGURE 4.—During flood season, water moved down the river channel with tremendous force, carrying gravel, boulders, and debris and depositing these materials wherever the current slowed. The brush piled against this tree indicates how the streambed is changing continuously during a flood.

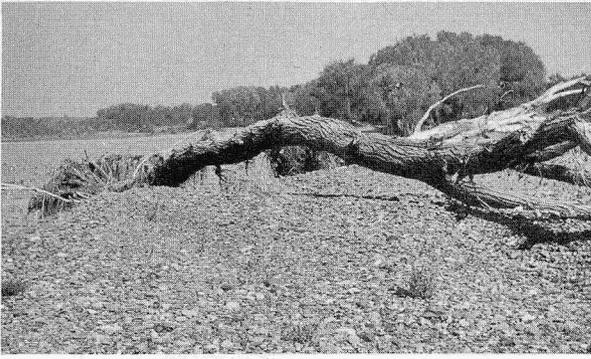


FIGURE 5.—Gravel accumulated by the force of flooding waters elevated the streambed. Note how the roots of this large tree are partially hidden by the gravel bar in the foreground. Bars such as this one are several feet above the normal height of the river seen at the base of the trees in the far distance. The large tree left here when the river receded indicates how the river valley changes during a flood. It shows how both the streambed and the direction of flow of water must be continuously varying.

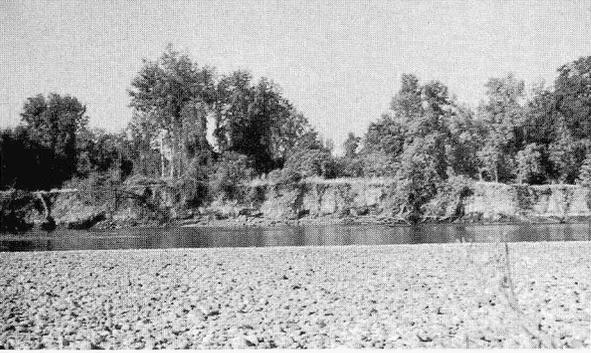


FIGURE 6.—With the increase in height of the bed, the river changed its course because a new channel was readily eroded through the comparatively light soil of the adjacent area.



FIGURE 7.—In time, the river became completely diverted from its old channel, demonstrating the dynamic and continuously changing conditions during the flood season.



FIGURE 8.—The elevated streambed was inundated during floods but was dry during a sufficiently long period of the year to allow plants such as mountain monardella (*Monardella odoratissima* Benth) and brickellbush (*Brickellia californica*) to become established and grow.

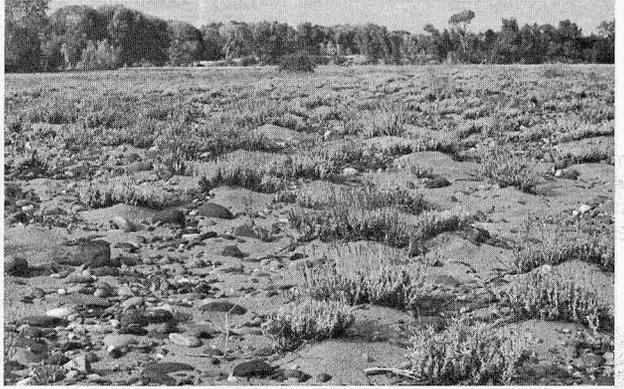


FIGURE 9.—Almost any plant in the area, such as wild buckwheat (*Eriogonum wrightii*), shown here, was capable of forming incipient mounds.



FIGURE 10.—During flood seasons, the plant was an obstacle to the flow of the soil-bearing stream, causing the rate of flow to be reduced sufficiently so that soil was deposited immediately downstream from the plant. Some of the deposits measured as long as 65 feet.



FIGURE 11.—As the incipient mound grew, the stream contoured it into teardrop shape.

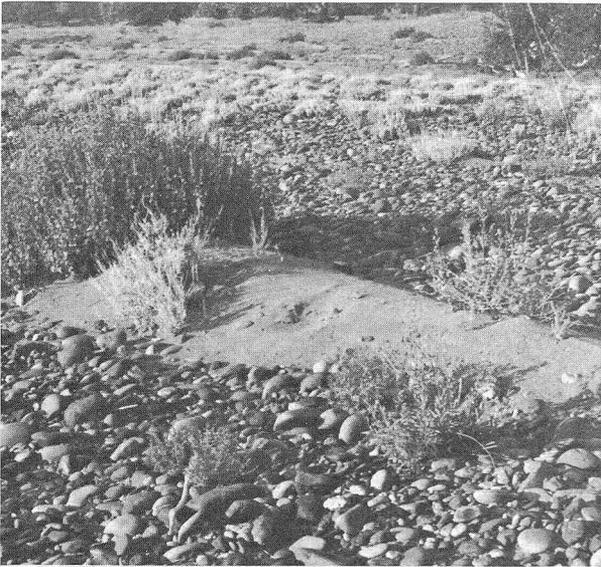


FIGURE 12.—Continued deposition resulted in a shallow, elongated accumulation of silt, sand, and pebbles.

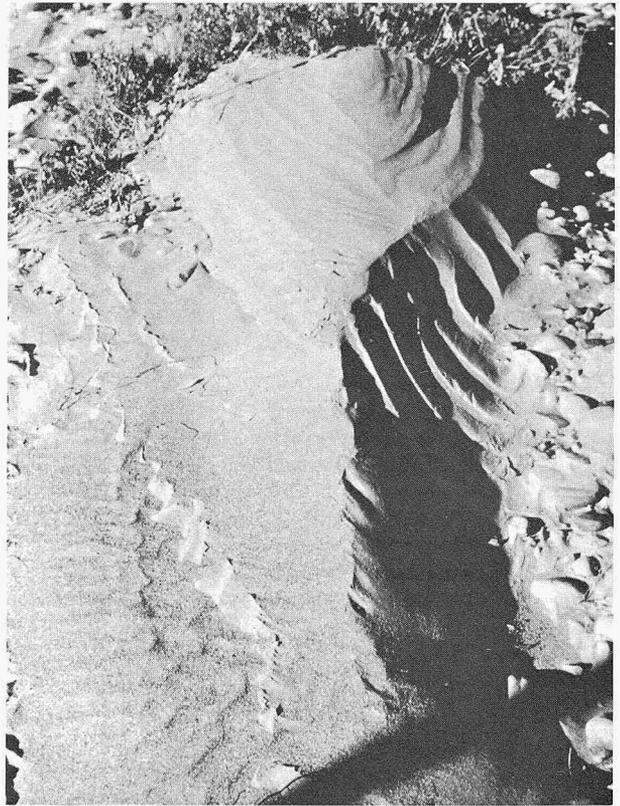


FIGURE 13.—Growth of the mound changed the local direction of the stream. Note how the head of the deposit was contoured into an ellipsoidal form. The head of the mound was composed of finer material than the tail, indicating that the flow was less swift close to the plant.



FIGURE 14.—The precise shape of the deposit was determined by the relative rates of deposition and erosion as the stream continuously changed direction of flow.



FIGURE 15.—If the velocity of the stream became too great, the mound was eroded badly, especially if large changes took place in the direction of the stream as might occur when the stream was rising or falling in a somewhat sloping area.

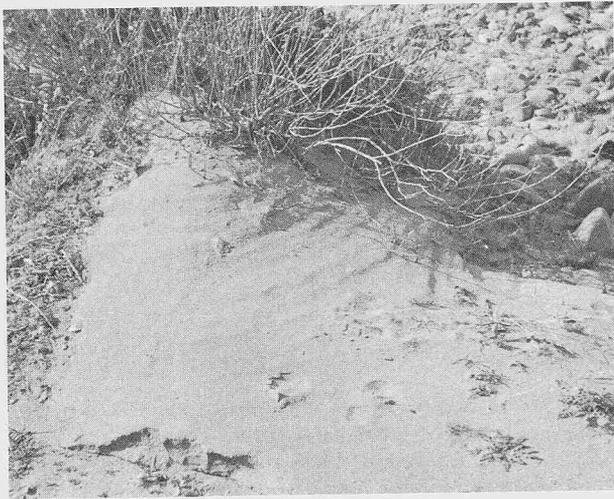


FIGURE 16.—The changes in the direction of flow of the stream tended mostly to favor the deposition and erosion of the mound into ellipsoidal or hemispherical shape. Note the circular contours on this developing mound. Note also how the growth of plants is helping to stabilize the mound.

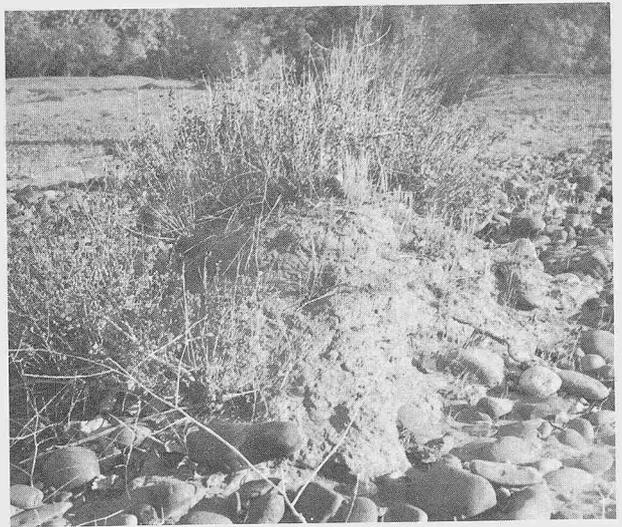


FIGURE 17.—Large changes in the direction of the stream, accompanied by high rate of flow, produced drastic changes in the shape of the mound, the change tending, however, to favor the ellipsoidal or hemispherical form.

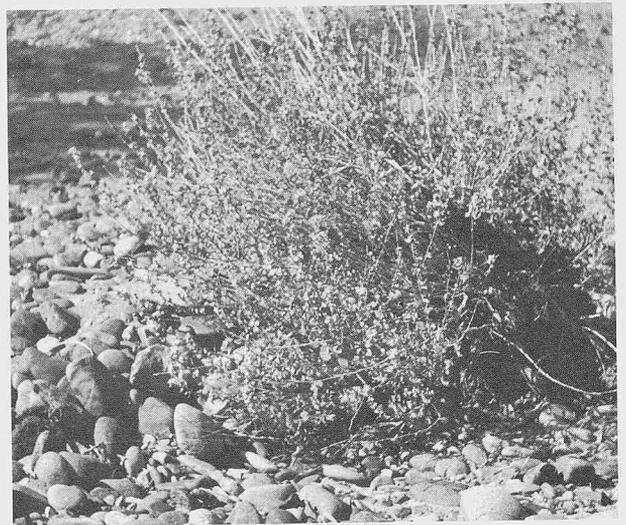


FIGURE 18.—If the stream became too rapid, the entire mound was eroded leaving the roots of the original mound-forming plant exposed.



FIGURE 19.—Only plants with exceptionally strong roots could withstand the force of the river under high velocities and changing directions of flow, and only plants such as brickellbush, which grows even when soil accumulates around it, could form mounds of appreciable size.



FIGURE 22.—Under conditions of equilibrium, mounds attained a stable form and continued to increase in size.



FIGURE 20.—A surviving plant (see figs. 18 and 19) started the formation of a new mound. This photograph was taken 1 year later.



FIGURE 23.—Because of the shift in the course of the river, the environment changed, creating conditions adverse to the mound-forming plants and resulting in the death and disappearance of these plants on the mounds farthest from the stream.



FIGURE 21.—Mounds were haphazardly distributed, depending upon where the plants happened to grow.

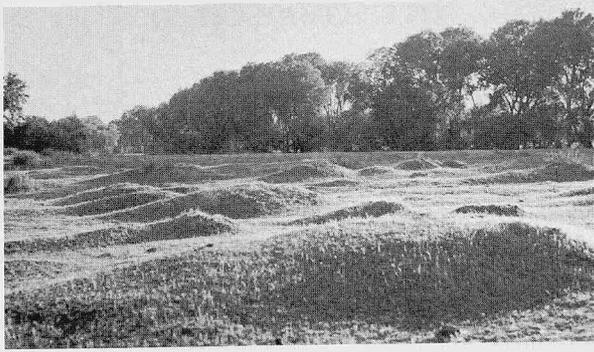


FIGURE 24.—The mounds were all oriented with the elongated axes in the direction of flow of the river. This photograph was taken at right angles to the flow and points in the direction that the river channel has shifted. Moving away from the camera toward the river, we find three zones of transition: first, no brickellbush (in the foreground); second, brickellbush struggling for existence (in the middle background); and finally closest to the river, healthy brickellbush (left background).



FIGURE 25.—On the older mounds, all signs of the original mound-forming plants disappeared except possibly for the partially decayed roots (brickellbush in this case). Roots such as these extended down into the substratum at the upstream extremity of all mounds examined.

THEORY

1. During flood seasons such plants as mountain monardella and brickellbush, which grow on the flood plain between flood seasons, are obstacles to the flow of water. Because the rate of flow has been slowed, silt is deposited in an elongated pattern immediately downstream from the plants. During the period of early growth of the mound,

the elongated deposit tends to be molded into a teardrop shape by the stream.

2. The head of the mound, being protected by the mound-forming plants, tends to be more permanent than is the tail. Any major changes in the direction of flow of the floodwater will tend to erode the tail faster than the head.

3. As the head of the mound grows in size, it produces local changes in the direction of flow of the floodwater in such a manner as to contour the mound into ellipsoidal form, with the hemispherical form being the limit toward which the contouring tends.

4. Owing to the mounds having been formed by deposition of silt, sand, and stones from moving floodwater, the long axes of the mounds are all parallel to one another and to the direction of flow of the floodwater.

5. Any plant growing on the flood plain can form an incipient mound, but only plants that have strong roots, that can withstand having their lower portion covered gradually by silt, and that have a long life span, such as brickellbush, will form large mounds.

6. Shifting of the streambed produces a change in environment that is unfavorable to the mound-forming plant, so it eventually dies and disappears. The mound now exhibits no surface evidence of this essential agent in its formation.

SUMMARY

Photographs taken on the flood plain of the Sacramento River near Red Bluff, Calif., are presented showing present-day development of mounds in all stages from incipient to mature. A theory is given summarizing the photographic observations.

The essential feature of the theory is that the mounds are formed immediately downstream from certain plants such as mountain monardella (*Monardella odoratissima* Benth) and brickellbush (*Brickellia californica*) during flood seasons, owing to the resistance offered by the plant to the flow of water and consequent slowing of the stream and deposition of suspended soil. The ellipsoidal shape of the mounds is explained as the product of two opposing tendencies: Deposition and erosion. The deposition is elongated downstream from the plant, whereas the erosion tends to shape the deposit into hemispherical form—that being the most stable to changing direction of flow.

The parallel orientation of the long axes of the mounds is explained by all of the mounds being formed by deposition from the same stream.

ACKNOWLEDGMENTS

T. C. Fuller and S. T. Ancell of the California Department of Agriculture identified the plants mentioned in the report. John Riggs of the California Department of Fish and Game took the photograph in figure 2. Albert Redamonti gave permission to make the observations on his property.

LITERATURE CITED

MCGINNIES, WILLIAM J.

1960. Effect of Mima-type microrelief on herbage production of five seeded grasses in western Colorado. *Journal of Range Management*, vol. 13, no. 5, pp. 231-234.

SCHEFFER, VICTOR B.

1947. The mystery of the Mima mounds. *Scientific Monthly*, vol. 65, no. 4, pp. 283-294.
1958. Do fossorial rodents originate Mima-type microrelief? *The American Midland Naturalist*, vol. 59, no. 2, pp. 505-510.

EFFECT OF FISHWAY SLOPE ON PERFORMANCE AND BIOCHEMISTRY OF SALMONIDS¹

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ABSTRACT

The effect of fishway slope on the performance and biochemical state of salmonids was studied in two experimental "endless" fishways with slopes of 1 on 8 and 1 on 16. A locking device in each fishway permitted recycling of fish so that pool-and-overfall fishways of any height could be simulated. Ascents were generally confined to a rise of 104 feet, but a number of fish were permitted to ascend over several hundred feet and one fish was allowed to ascend over 6,000 feet. Principal species tested were chinook salmon (*Oncorhynchus tshawytscha*), sockeye (Columbia River blueback) salmon (*O. nerka*), and steelhead trout (*Salmo gairdneri*).

Comparisons of individual passage times, patterns of movement, and biochemical phenomena associated with muscular activity showed no evidence of fatigue

The slope of a pool-type fishway is a major factor in determining the cost of its construction. A fishway that rises 1 foot for every 8 feet of length (1-on-8 slope) needs to be only one-half as long as a fishway that rises 1 foot for every 16 feet of length (1-on-16 slope) to gain the same elevation. On the Columbia River the present standard slope for major fishways is 1 on 16, (e.g., Bonneville Dam, The Dalles Dam and Rocky Reach Dam). An earlier dam, Rock Island Dam, was built with fishways with a 1-on-10 slope, and one dam, McNary Dam, has fishways with a slope

of the fish in either fishway when proper hydraulic conditions existed. Data indicated that ascent of a properly designed pool-and-overfall fishway is only a moderate exercise for salmonids and that the rate of ascent will not decline in the upper end of a long fishway. Hydraulic conditions were shown to control rate of ascent and pattern of movement through fishways. Differences in rate of movement and in blood lactate levels were measured between species.

The effects of size, sex, maturity, and disease on performance and biochemical state of fish were also examined. Significant relationships were found only for length of male chinook and performance (larger fish were slower), and sex and blood lactate level for chinook (female chinook had higher blood lactate levels).

of 1 on 20. There are many dams yet to be built on the Columbia River and its tributaries, and significant reduction in fishway costs would be possible if satisfactory fishways could be designed with slopes steeper than the present 1 on 16.

To determine the feasibility of steeper fishway slopes the effect of fishway slope on the rate of passage of chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*), and steelhead trout (*Salmo gairdneri*) was studied at the research project at Bonneville Dam during 1956 and 1957. This was done by comparing the passage times of the salmonids through short experimental fishways with slopes of 1 on 8 and 1 on 16. Both fishways were of the pool-and-overfall type without submerged orifices, and both achieved a total gain in elevation of 6 feet. The results of these experi-

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ments (Gauley, 1960, p. 11) were quite favorable. For all three species of fish the rate of passage through a 1-on-8-slope fishway having 1-foot overfalls between pools was as fast or faster than the rate of passage through the conventional 1-on-16-slope fishway. This was true whether the tests were made with individual fish or with groups of fish. However, because the tests in 1956 and 1957 were made with only short segments of fishways, the question still remained whether the steeper slopes were suitable for longer fishways. The possibility that the steeper slope might dangerously fatigue fish in a long fishway had to be investigated.

A study of the effect of fishway slope on fish performance in long fishways was begun at the Fisheries-Engineering Research Laboratory during the 1958 season. Two specially designed "endless" fishways with slopes of 1 on 8 and 1 on 16 were utilized. These endless fishways were experimental pool-and-overfall fishways constructed so that each made a complete circuit, with the highest pool connected to the lowest pool by means of a lock. When a fish had ascended to the top of one of these fishways it was then rapidly locked to the lowest pool to ascend again. Fishways of any desired length could thus be simulated. Knowledge of the effect of fishway slope on fish passage was sought through a comparison of the performance and behavior of the fish in the two endless fishways and through a study of the related biochemical phenomena associated with fatigue.

DESCRIPTION AND OPERATION OF ENDLESS FISHWAYS

INITIAL DESIGN

Features of the 1-on-16 and 1-on-8-slope endless fishways and essential auxiliary channels and pools (entrance channel, collection pool, release compartment, introductory pool and exit by-pass) are shown in plan view in figure 1. An enlarged view of the 1-on-8-slope unit showing pool elevations in feet above mean sea level appears in figure 2. All subsequent reference to the various pools will be made by numbers indicating their surface elevation in feet above mean sea level. The same pool elevations apply to the 1-on-16-slope unit. Perspective views of the two fishways are presented in figures 3, 4, 5, and 6.

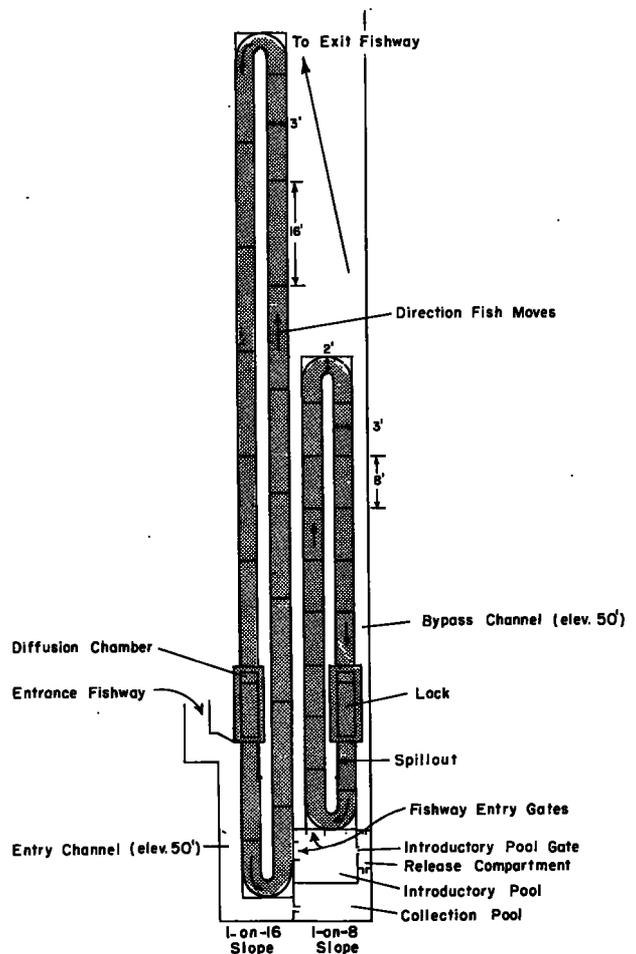


FIGURE 1.—Plan view of the 1-on-16-slope and 1-on-8-slope endless fishways with auxiliary approach channels and pools.

Each fishway was comprised of 16 pools including 2 turn pools and a locking pool. There was a 1-foot rise between pools and a total rise of 16 feet in the complete circuit. With the exception of the lock and turn pools, the average water depth in each pool was approximately 6.8 feet. Pools were 3 feet wide and either 8 or 16 feet long, depending on the slope of the respective fishway. A 3-foot freeboard prevailed throughout each fishway. Weir crests were 3 feet long and 2 inches wide and were painted white on the square crest to aid in the observation of fish. All other interior surfaces were painted camouflage brown. There were no orifices in the weirs, but a single, 2-inch drain hole was provided in the base of each weir to permit draining during unwatering. A steel

flap plate covered each hole when the fishway was operative.

All principal structures were of wood with the exception of the exterior steel supports on the lock

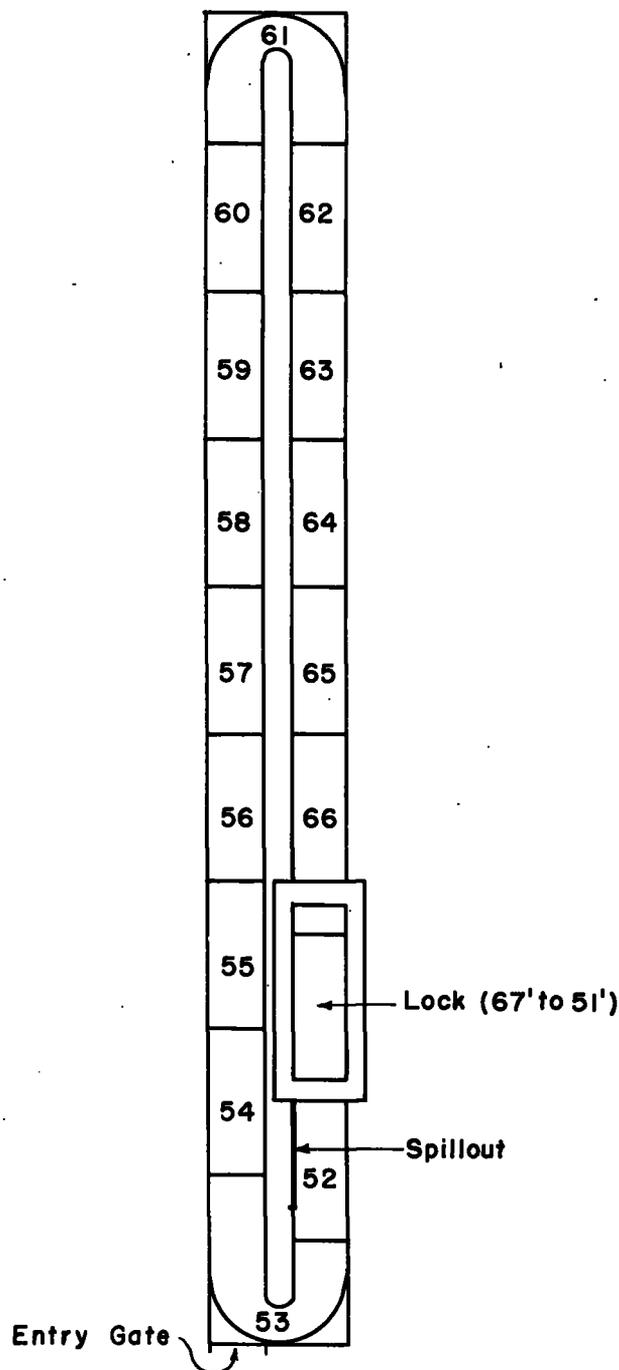


FIGURE 2.—Plan view of 1-on-8-slope fishway showing pool elevations in height above mean sea level.

and certain gates in the two fishways. A cross-sectional view of a typical series of pools in the 1-on-8-slope unit, showing the box-type construction with level floor, is presented in figure 7.

Dimensions of the turn pools (53 and 61) were in keeping with the established slope in each fishway, i.e., the inside longitudinal footage totaled 8 feet in the 1-on-8-slope fishway and 16 feet in the 1-on-16-slope fishway. While pool depth was approximately 6.8 feet, passage area available to the fish was limited to the upper 2 feet of the pool by a horizontal grill. The corners of the pool were coved, and the pool width at the 90° point of the turn was reduced from 3 to 2 feet (figs. 1 and 8).

The lock pool (elevation 67' to 51') in each fishway was 8 feet long, 3 feet wide, and 23 feet deep when filled and 7 feet deep when drained. At the lower discharge level (elevation 51'), the lock functioned as a typical pool. A picketed barrier was installed on the crest of the downstream weir of the lock (elevation 50') to prevent fish from drifting back into the drain area. Ideally, to be consistent with the slope design, the lock in the 1-on-16-slope fishway would have been 16 feet long. Since space limitations and structural considerations posed barriers to the construction of a 16-foot unit, the lock in the 1-on-16 fishway was built identical to that in the 1-on-8-slope unit.

To encourage the fish to pass from the lock pool after the water had been discharged from elevation 67' to 51', a horizontal grill was placed in the pool, limiting the depth available to fish to 2 feet. This alteration served to expedite the movement of fish from the lock into the next upstream pool (52).

Operational features of the endless fishway units may be conveniently described by visualizing the passage of a fish into and through the various sections of the laboratory and through an endless fishway. Steps involved in this passage are as follows:

(1) Fish were diverted from the Washington-shore fishway into the entrance fishway (fig. 1) without handling, a unique feature of the research. The fish then ascended the entrance fishway to the entry channel and moved on into the collection pool. This pool was 5 feet by 12 feet by 6 feet with the surface elevation at 50'.

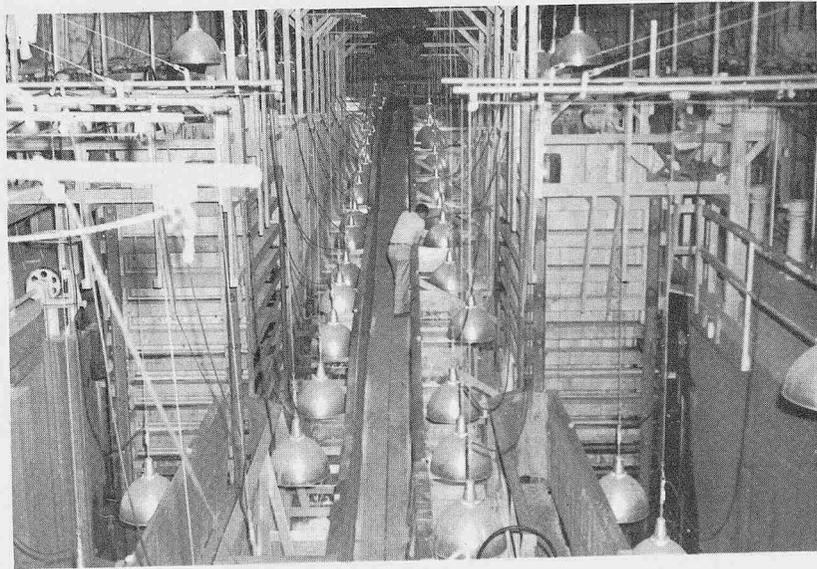


FIGURE 3.—Looking upstream at the 1-on-16 (left) and 1-on-8-slope (right) endless fishways. The locking units in each fishway appear in the left and right foreground.

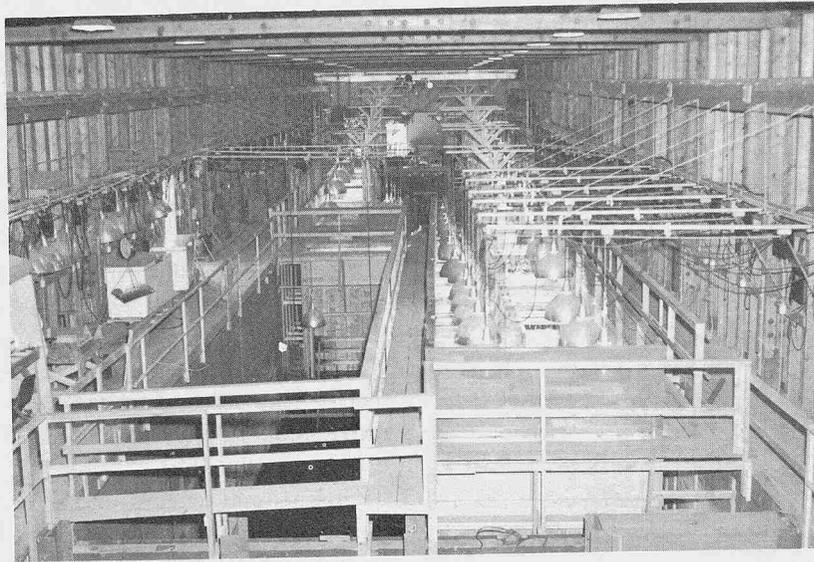


FIGURE 4.—View from the upper turn pool showing respective lengths of the 1-on-16 (right) and 1-on-8-slope (left) fishways. Each fishway rises 16 feet.

(2) From the collection pool a single fish was permitted to pass through an 8-inch-wide gate and enter the release compartment where it was diverted into the introductory pool through an adjoining gate. Water flow from the bypass channel provided the necessary attraction for the movement into the release compartment.

(3) As the fish entered the introductory pool, a wooden drop gate was lowered at the juncture of the release compartment and the introductory pool. This isolated the fish in a quiet pool, which was 6 feet wide, 9 feet long, and 2 feet deep. The water level at this point remained at elevation 50'.



FIGURE 5.—Looking upstream from pool 53 in the 1-on-8-slope endless fishway.

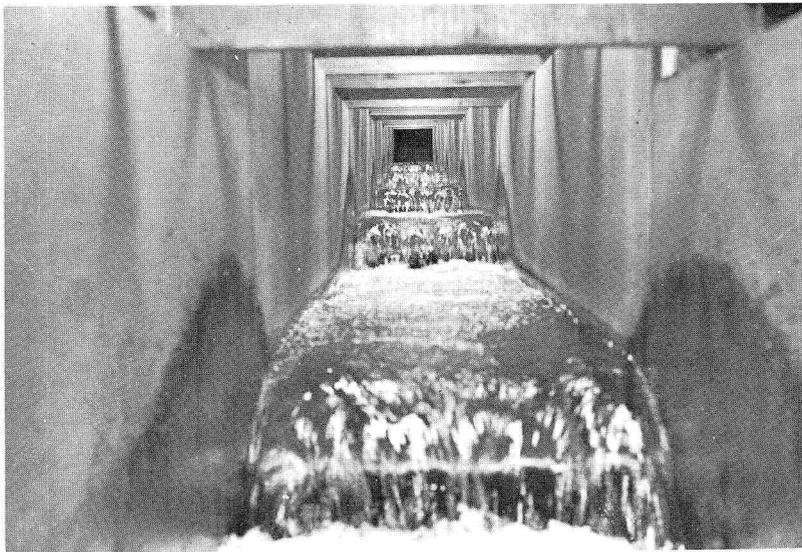


FIGURE 6.—The 1-on-16-slope endless fishway viewed from pool 53.

(4) Passage of the fish from the introductory pool to one of the endless fishway units was facilitated by raising a fishway entry gate joining pool 53 with the introductory pool. This permitted the water in the fishway to spill into the introductory pool, filling it to approximately

elevation 52.5'. At this level, excess water passed through a grill on the downstream rim of the introductory pool and spilled into the collection pool. The fish was now in a position to swim from the introductory pool (fig. 9) into the fishway.

(5) Immediately after the fish passed into pool

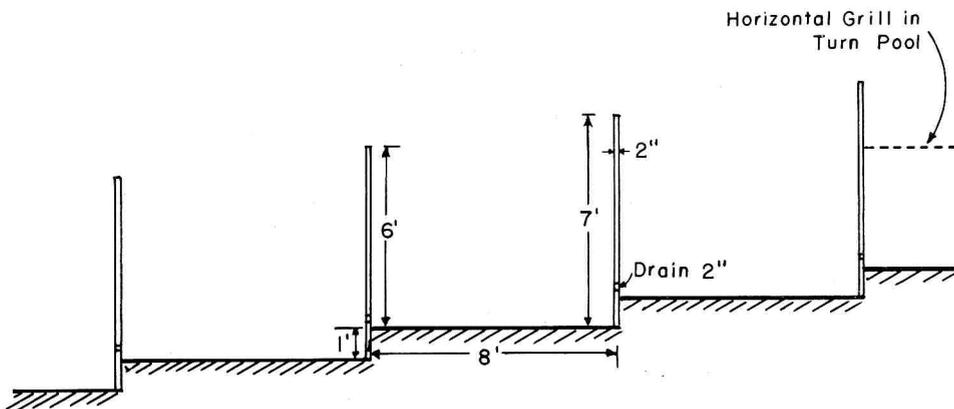


FIGURE 7.—Sectional view of 1-on-8-slope fishway. Note level floors.

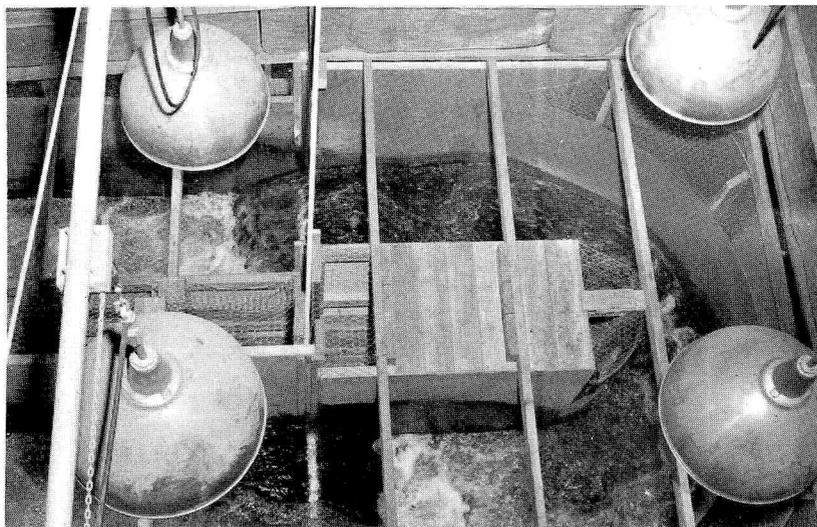


FIGURE 8.—Upper turn pool in the 1-on-8-slope fishway.

53, the fishway entry gate was dropped, isolating the fish in the now closed circuit of the endless fishway.

(6) From pool 53 (see fig. 2 for pool elevations) the fish ascended the straightaway section through pools 54-60 and then around the upper turn pool (61) and again up a straightaway section to pool 66. At this point the fish was ready to enter the lock (fig. 10). Dimensions of the diffusion chamber were 3 feet by 3 feet by 7 feet. A 16-inch pipe with grill openings on the under side entered the base of the chamber and provided a constant water supply for the fishway. Diffusion baffles

were placed above the pipe and a finger grill submerged approximately 6 inches beneath the water surface, prevented the fish from sounding into the chamber as it passed from pool 66 into the lock.

(7) After the fish passed over the diffusion chamber grill, the drop gate (A, fig. 10) was lowered to separate the lock pool from the diffusion area. A motor-driven winch, connected to a steel cable (B, fig. 10), raised a steel flap gate at the base of the drain area directly beneath the diffusion chamber. This permitted drainage of the lock to elevation 51'. Discharge of lock water was



FIGURE 9.—Introductory pool with water level at elevation 52.5'. Entry gate to the 1-on-16 slope fishway is open (upper center) to permit entry of fish into pool 53.

normally accomplished in about 30 to 40 seconds. Figure 11 shows drop gate (A) in down position, isolating the diffusion chamber and the remainder of the fishway from the lock which has been drawn down.

(8) Figure 12 presents a view of the lock after discharge of water from elevation 67' to 51'. The vertical gate (C) has been raised, and water from pool 52 may be seen spilling into the lock. (Previous to the opening of the pre-vertical gate (C), all water in the fishway spilled out a screened overflow in pool 52.) The fish was now in position to move from the lock into pool 52.

(9) When the fish had passed through pool 52 and the lower turn pool (53) the vertical gate (C) was lowered and the lock drainage gate closed. This readied the lock for filling as the fish began another circuit of the fishway. Filling the lock (fig. 13) required about 1 minute. As the water level in the lock approached elevation 67', the 16-inch supply valve was gradually closed. At this level the drop gate (A) (figs. 10 and 11) was raised, and the lock was now ready to receive the fish when it once again ascended to this level.

LIGHTING AND HYDRAULICS

A constant light supply approximating an average intensity of 800 foot-candles at the water surface prevailed during all experiments. This was

provided by a battery of 1,000-watt fluorescent mercury-vapor lamps placed at 6-foot intervals throughout the course of each fishway. The distance from the lamp reflectors to the water surface was 6 feet.

Water supply for operation of the fishway units came from the forebay of Bonneville Dam, which fluctuated from elevation 82.5' to 72.5' during these experiments. This provided a minimum operating head of 5.5 feet (water level of lock and diffusion chamber when filled was approximately at elevation 67'). Water for the bypass channel (fig. 1) came from the Washington-shore fishway which was joined with the laboratory by an exit fishway.

Head on the weirs (measured 4 feet upstream of the weir crest) was controlled by adjusting the valve supplying water to the diffusion chamber. This head was set at 0.8 foot, the approximate upper limit at which a plunging flow (strong directional flow reaches bottom of pool) could be maintained under the prevailing nonorifice condition. Total discharge in each fishway was approximately 7.2 cubic feet per second (c.f.s.).

Flows into the lock pool were changed from the established plunging condition to a streaming motion (strong directional flow along surface of pool) by raising the lip of the lock spillout slightly above elevation 50'. This was done to increase the sur-

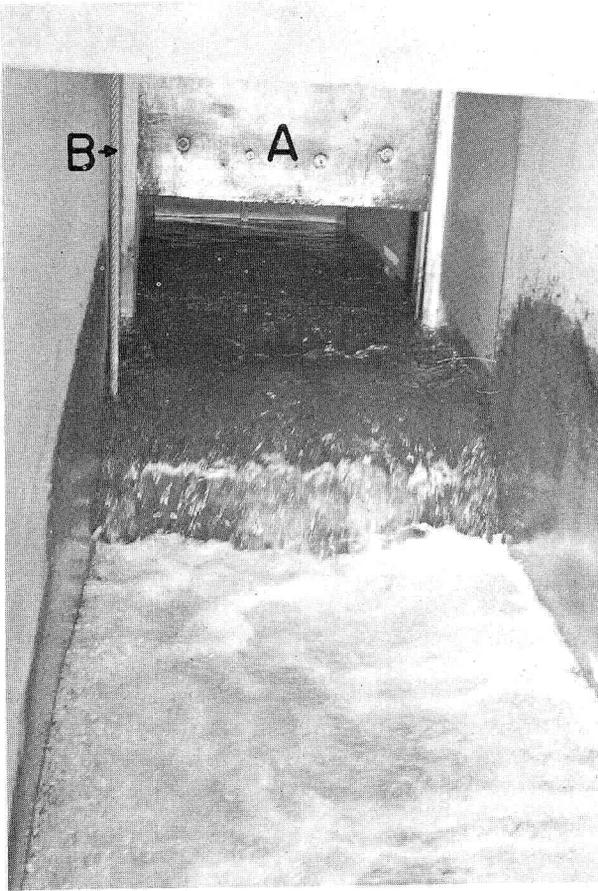


FIGURE 10.—Looking upstream from pool 66 over diffusion chamber and into lock. As fish enters lock, the drop gate (A) is lowered to isolate fish in lock. A motor-driven winch connected to the cable (B) raises a gate at base of lock, discharging water to elevation 51'.

face velocity and encourage the exit of fish from this pool.

SUBSEQUENT DESIGN MODIFICATIONS

During the 1958 experiments, several physical changes were incorporated in the fishways for the purpose of creating special hydraulic conditions designed to facilitate the passage of fish. The turn pools (53 and 61) in both fishways that had previously been grilled to limit fish passage to the 2-foot surface layer were further modified by installing a floor over the grill and placing 6-inch-high baffles on the floor at approximately 4-foot intervals across the width of the pool. These changes created a turbulent, rapidly flowing water

pattern which served to prevent the fish from using the turn pools as resting areas.

Following the above modifications, the 1-on-8-slope fishway was altered further by installing baffles on the weir crests (fig. 14). The three types of baffle placements were employed during tests conducted in September 1958.

A comparison of the various fishway conditions applicable to the 1958 tests is given in table 1. Subsequent reference in the text will refer to these conditions by number and slope.

PROCEDURE

The comparison of the two fishway slopes was to be based on an analysis of (a) the performance of individual salmonids in the respective fishways and (b) certain biochemical characteristics of the fish after exercise in the ascent of a fishway. Per-

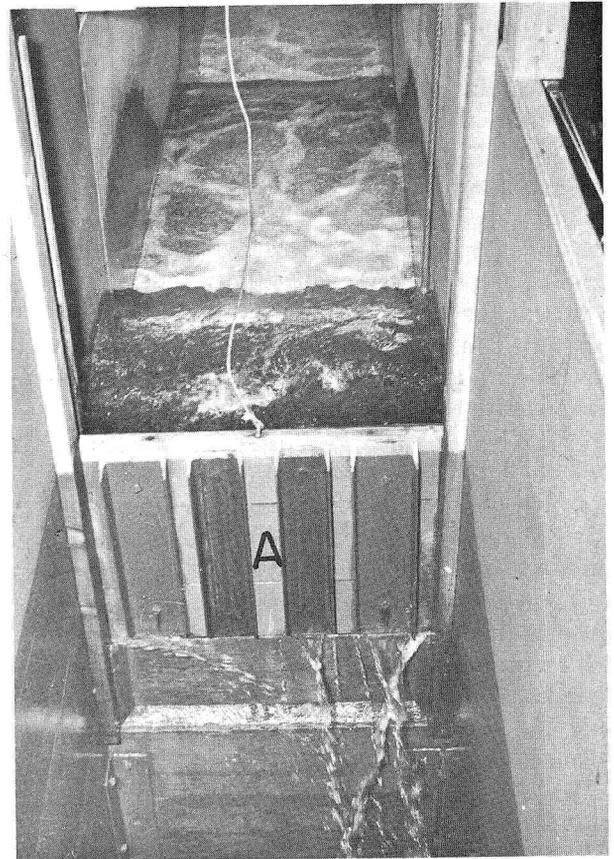


FIGURE 11.—Drop gate (A) in down position separating diffusion chamber from lock (foreground). Water in lock (foreground) has been discharged to elevation 51'.

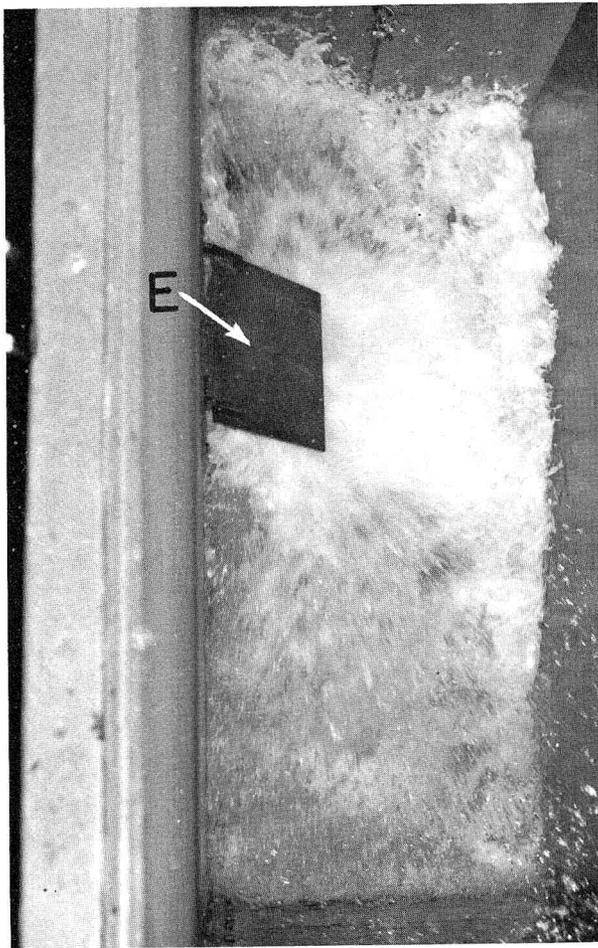


FIGURE 12.—Looking down into lock. Vertical gate (C) has been raised to permit exit of fish from lock into pool 52. Water passes from lock through grill (D) and out drain gate opening behind grill.

TABLE 1.—Physical features of 1-on-8 and 1-on-16 slope endless fishways¹

Fishway		Weirs		Calculated flow	Turn pool conditions
Condition	Slope	Length	Modifications		
1.....	1-on-8	<i>Inches</i> 36.0	<i>c.f.s.</i> 7.2	With rest areas.
1.....	1-on-16	36.0	7.2	Do.
2.....	1-on-8	36.0	7.2	Turbulent.
2.....	1-on-16	36.0	7.2	Do.
2A.....	1-on-8	17.0	Center notch— type A.	3.9	Do.
2B.....	1-on-8	26.5	In-line baffles— type B.	5.3	Do.
2C.....	1-on-8	26.5	Alternating baffles—type C.	5.3	Do.

¹ Fishway pools were 8 and 16 feet long respectively, 3 feet wide and 6.8 feet deep. Head on weirs was 0.8 foot and height of overfall 1 foot.

formance was measured in terms of time and ability to ascend the two fishway and the biochemical characteristics measured were the levels of lactate of whole blood, inorganic phosphate of blood plasma, lactate of the muscle tissue, and inorganic phosphate of the muscle tissue.

FISH COLLECTION

Fish utilized for experimental purposes in the endless fishways were diverted from the Washington-shore fishway each day and allowed to ascend to the collection pool (fig. 1). The time required to collect a sufficient number of fish generally was not more than several hours. In the early part of the season, the collection period commenced at about 2:00 p.m. and by 4:00 p.m., 6 to 20 fish

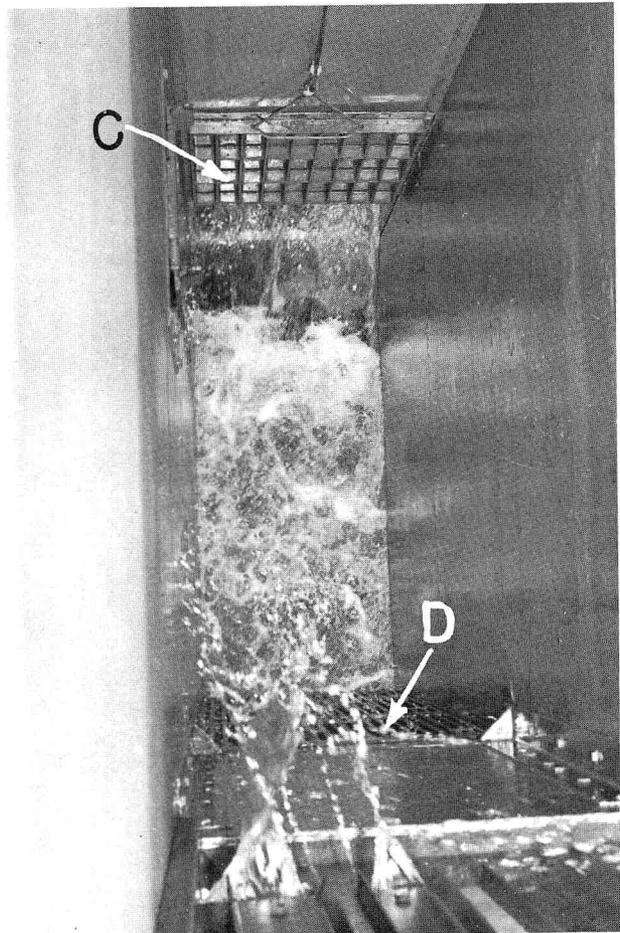


FIGURE 13.—Filling lock. Flap plate (E) returns to "down" position when level reaches elevation 67' and supply valve is closed.

would be present in the collection pool. The pool entrance was then closed, and covers were placed over the pool to keep the fish quiet during the hold over period which extended to the following morning. Thus, each fish present in the pool was held from 14 to 20 hours depending on the time it entered the pool and the time it subsequently left the pool to enter the experimental area on the following day. The assumption was then made that this procedure placed each fish in a relatively equal state of rest prior to its release into one of the endless fishways. Figures 15 and 16 present views of the collection pool when fish were entering and when the pool was covered during the hold over period.

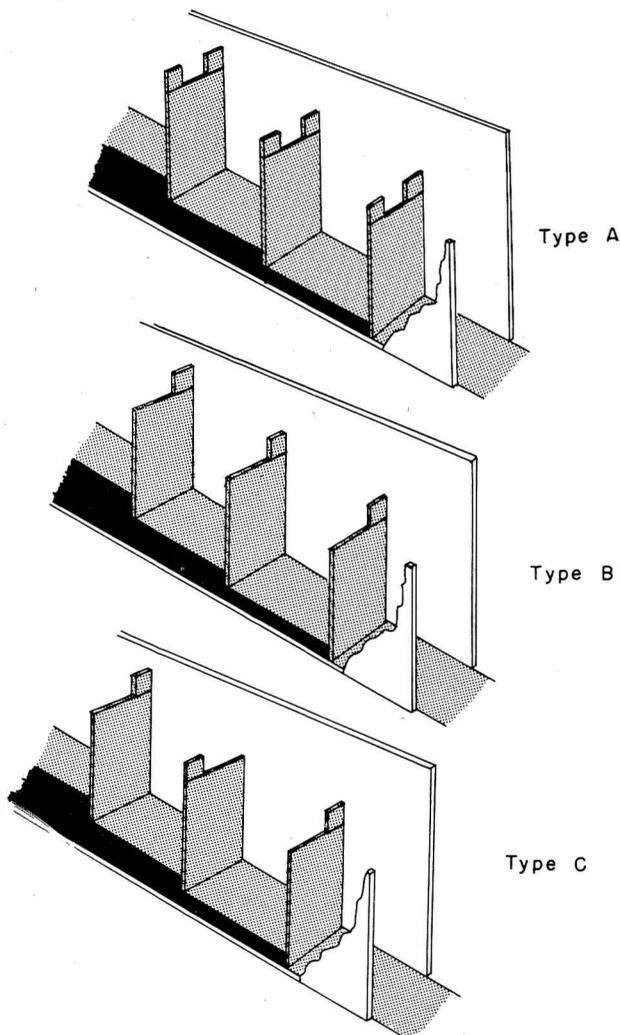


FIGURE 14.—Baffle placements showing notched, in-line, and alternate arrangements on weirs of 1-on-8-slope fishway.

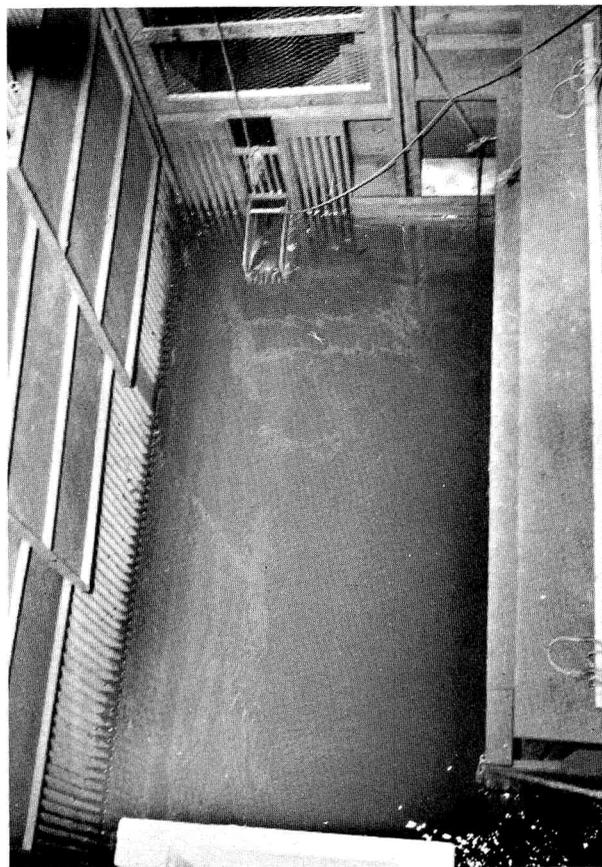


FIGURE 15.—Collection pool open for fish. Note finger fyke at entry gate (upper center).

All fish remaining in the collection pool at 2:00 p.m. each day were released into the bypass channel (fig. 1) where they passed through the laboratory and out into the Washington-shore fishway. A brail on the floor of the collection pool was raised to ensure the exit of all remaining fish previous to the entry of a new group for use in the succeeding day's experiments.

During the latter part of the season this procedure was modified by reducing the time the fish were held in the collection pool to periods not exceeding 6 hours and not less than 1 hour. The change in technique was made to save time. This was done after a comparison of blood lactate levels of fish held overnight with those of fish held for only a few hours indicated no difference in the physical states of the fish.

RELEASE AND TIMING

For each test, an individual fish from the collection pool was permitted to enter the release

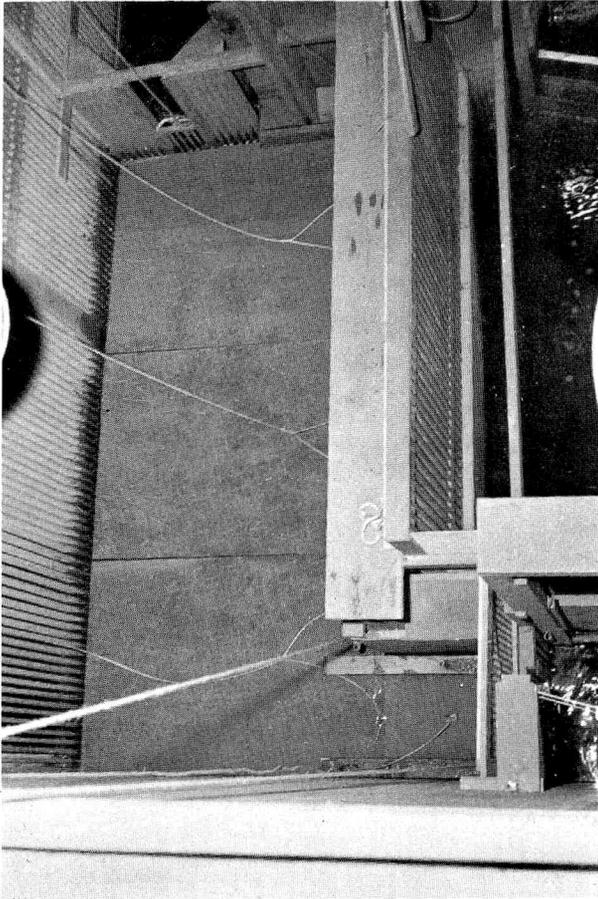


FIGURE 16.—The fish collection pool with covers in place during hold over period.

compartment where it was observed briefly to determine species and physical condition. Fish bearing visible evidence of serious injuries, such as deep cuts or large abrasions, were rejected. There was no selection on the basis of size. The fish was then allowed to enter the introductory pool.

A fish swimming from the introductory pool into the fishway was the signal to start a test. The ascent was timed by a pair of observers who moved along with the fish as it proceeded up the fishway. A button switch was located on a hand-rail above each weir in the fishway, and as the fish passed from pool to pool, an observer pressed the button for the respective weir. This signal was in turn transmitted to an operations recorder that noted on a continuously revolving time tape the exact time of fish passage over each weir.

Another attendant stood by to operate the lock and transfer the chronological record of ascent from the tape to an operations sheet.

When the fish entered the lock, the two observers promptly descended a walkway to the base of the lock and recorded the fish's movement as it entered pool 52 following discharge of lock water from elevation 67' to 51'.

PERFORMANCE

Two types of performance tests were conducted during the June and July chinook and sockeye salmon migrations. One test consisted of permitting a fish to ascend through 104 pools ($6\frac{1}{2}$ circuits of the endless fishway) at which point the fish was immediately removed from the fishway and samples of blood and muscle tissue taken for biochemical analysis. The 104-pool ascent was an arbitrary choice but nevertheless in keeping with a simulated passage over a typical Columbia River dam. The foregoing tests were conducted on Sunday, Wednesday, Thursday, and Saturday of each week, and performance was measured in terms of minutes required to pass through 104 pools. On the remaining days—Monday, Tuesday, and Friday—a "prolonged ascent" test was carried on. These trials were designed to examine performance trends and biochemistry of fish subjected to a long ascent of generally more than 200 feet. As the latter tests often required lengthy periods of observation, they were normally discontinued after (a) approximately 13 hours or (b) after a fish had spent 60 minutes in a single pool.

Individuals removed from the fishway immediately following a specified ascent were called "terminated" fish as contrasted to "volitional" fish, which were those that stopped of their own volition for 60 minutes in a single pool and were then removed. Thus, the former can be considered as having been in an actively ascending state and the latter in a resting state at the time of their removal. All fish removed immediately after ascending 104 pools are, therefore, classified as terminated, while those removed after ascending in excess of 104 pools may be classed as terminated or volitional, depending on the circumstances of their removal. Occasionally, due to the time limitations or operational difficulties, a test was terminated before a 104-pool ascent was completed. There were also a number of instances

in which fish came to a volitional stop before reaching 104 pools.

A special category—volitional-terminated—was later assigned to a limited group of summer chinook exhibiting what appeared to be obvious signs of stress or fatigue. These fish generally displayed a pattern of extremely rapid ascent followed by a drift or fallback movement which usually carried them completely down the fishway to the lowermost pool. At this point, the fish became impinged against the spillout grill in the lock, or if the lock was closed, it would appear against the spillout screen in pool 52. When this occurred the fish was removed from the fishway for immediate sampling of blood and tissue for biochemical analysis.

Performance trials conducted during August and September were confined solely to comparisons of the time required to make 104-pool ascents in the 1-on-8 and 1-on-16-slope fishways.

BIOCHEMISTRY

Immediately following the completion of a performance test, the fishway water supply was shut off and the fish was netted from the fishway and immobilized by a sharp blow on the head. In successive steps, and as rapidly as possible, 5 cc. of blood and several muscle-tissue cores were extracted (figs. 17 and 18) from the fish. Muscle cores were always taken from the area directly between the dorsal fin and the lateral line at a right angle to the left side of the fish. A heart puncture, made with a hypodermic syringe inserted through the body wall, served to extract the blood. Similar samples were taken each day from a control fish netted from the collection pool. Records were kept of the time required from the moment the fish was netted from the fishway until (1) the blood was extracted and (2) the tissue was weighed and placed in cold, 5-percent trichloroacetic acid.

After the blood and tissue samples were extracted, they were processed and placed in individual polyethylene containers and stored in a deep freeze for subsequent biochemical determinations. The length and sex of each fish were recorded, and the gonads were weighed for the purpose of determining sexual maturity. Lactate levels of the blood and muscle were determined by the method of Barker and Summerson as described in Hawk, Oser, and Summerson (1954,

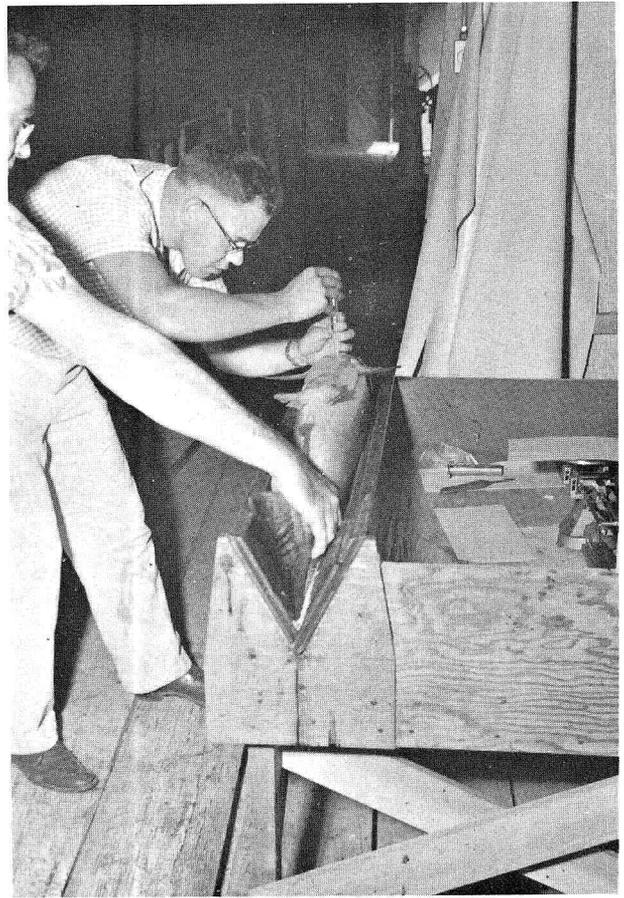


FIGURE 17.—Extracting blood from heart of a chinook salmon.

p. 622-624). King's modification of the Fiske and Subbarow method (King, 1932) was used to determine level of inorganic phosphate in the blood plasma and muscle tissue.

In addition to the foregoing, extracts of liver tissue and muscle tissue were also obtained for glycogen analysis, and a limited number of muscle tissue samples were taken for fat analysis. Glycogens were determined by the method of Montgomery (1957). Scales were also taken from many of the fish for subsequent age analysis. Special examinations for disease were made during August and September.

PERFORMANCE

Comparisons of the performance of chinook salmon, sockeye salmon, and steelhead trout with respect to slope consider (1) the passage

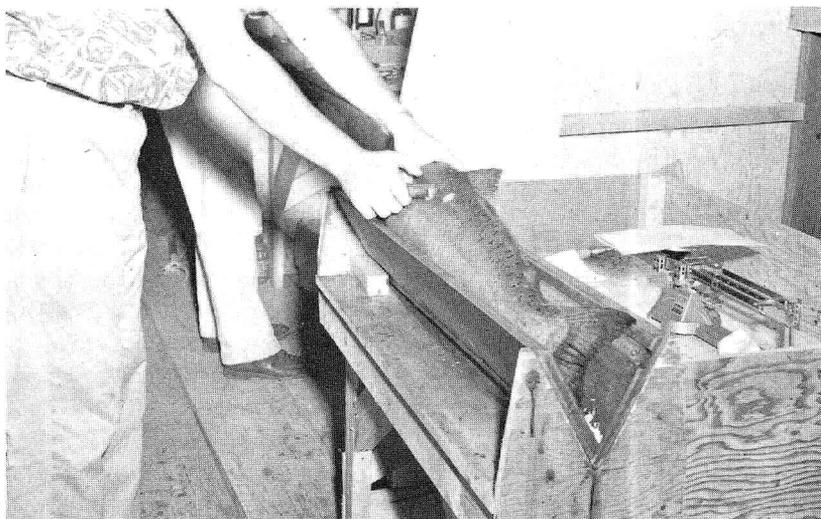


FIGURE 18.—Removing muscle core from side of chinook salmon.

time in minutes required to ascend a specified number of pools, (2) the pattern of movement or the "work-rest" relation, and (3) the willingness to ascend the respective fishways, the latter arbitrarily established as the percentage of fish negotiating 100 pools without stopping for 1 hour in a single pool. In addition, the work level at which fatigue might become apparent was examined by comparing mean rates of ascent at various levels of ascent in the fishway.

Examination of each of the foregoing aspects of performance will be treated in accordance with the prevailing fishway conditions as given in table 1; namely, (1) turn pools with rest areas, (2) turn pools turbulent, and (3) restricted weirs (1-on-8-slope).

Turn pools with rest areas (condition 1)

On June 9, 1958, tests in the endless fishways with rest conditions provided in the turns began with the passage of a limited number of chinook salmon. These were followed by sockeye salmon which continued in sufficient abundance for test purposes until July 20. A comparison of individual passage times of chinook and sockeye salmon through the 104-pool ascent level is given in table 2.

Chinook salmon ascending the 1-on-8-slope fishway required approximately 2.7 minutes per pool, while the mean rate in the 1-on-16-slope fishway was 2.0 minutes per pool. With the

limited sample size, the difference in mean passage time for the 104-pool ascent is not statistically significant (table A-1). Because of the small sample size, however, there is a high risk of error in concluding that no true difference exists in the mean rates. A subsequent analysis comparing mean time per circuit (16 pools) showed a consistent (significant) difference between the time taken by chinooks ascending each of 6 circuits in

TABLE 2.—Time in minutes to ascend 104 pools in endless fishways having slopes of 1 on 8 and 1 on 16 with turn pools providing rest areas (condition 1): Chinook salmon—June 9-20, sockeye salmon—June 21 to July 20, 1958

Fish number	Chinook salmon		Sockeye salmon	
	1-on-8 slope	1-on-16 slope	1-on-8 slope	1-on-16 slope
1	321	148	167	162
2	430	198	155	155
3	152	237	149	180
4	251	171	177	184
5	207	334	192	217
6	302	308	198	129
7	273	329	204	123
8		135	167	126
9			130	173
10			144	303
11			144	254
12			167	94
13			197	127
14			198	213
15			169	173
16			179	187
17			176	158
18			179	180
19			151	182
20			150	138
21			175	132
22			134	214
23			151	139
Mean	285	232	168	175

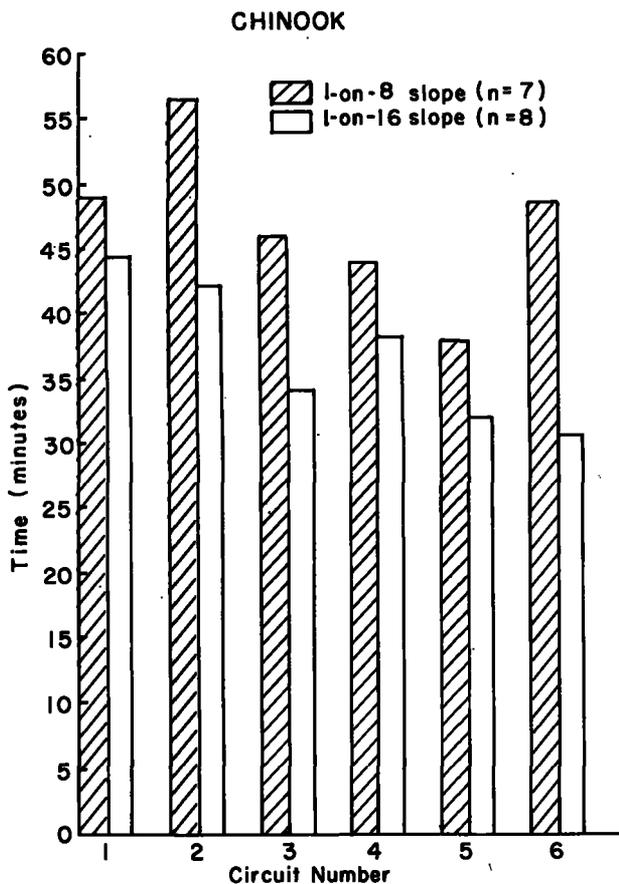


FIGURE 19.—Mean passage time per circuit (16 pools) taken by chinook salmon negotiating endless fishways having slopes of 1 on 8 and 1 on 16. June 9–21, 1958.

the two fishways. The average time per circuit in the 1-on-8-slope fishway was 44.1 minutes as compared to 36.4 minutes in the 1-on-16-slope fishway, or an average of 21 percent longer time in the 1-on-8 unit. (Comparative times per circuit are given in figure 19.)

Mean rates of ascent for sockeye over the 104-pool ascent level were virtually equal, being 1.6 minutes and 1.7 minutes per pool, respectively, in the 1-on-8- and 1-on-16-slope fishways.

The foregoing trials revealed a rather pronounced work-rest pattern of ascent, particularly in the fishway having a slope of 1 on 8. A somewhat similar but less exaggerated pattern of ascent was evidenced in the 1-on-16-slope fishway.

Because of the manner in which the endless fishways were constructed, every eighth pool was a turn pool. These turn pools created hydraulic conditions which were considerably different from

those occurring in pools in the straightaway sections of the fishway. When the rates of ascent in both fishways were examined on the basis of time spent in each individual pool, the data indicate that the turn pools apparently were preferred resting areas. Chinook salmon ascending the 1-on-8-slope fishway passed through most of the straightaway pools in a matter of seconds and then usually remained in the turn pools for more than 15 minutes before starting to ascend again. In the 1-on-16-slope fishway, chinook spent an average of approximately 1 minute per pool in the straightaway sections and about 3 to 5 minutes in the turn pools (fig. 20).

Locking the fish appeared to cause relatively little delay in both fishways. The average time from the moment the fish crossed the upper weir until it actually left the lock was less than two minutes. The time spent in the pool following the lock was, however, greater than in straightaway pools. This may have been due to the change in hydraulic conditions encountered after leaving the lock.

A work-rest pattern of ascent similar to that of the chinook was evidenced by sockeye salmon ascending the endless fishways (fig. 21). In the 1-on-8-slope fishway, the average time per pool in the straightaway sections was about 23 seconds as compared to approximately 11 minutes per pool in each of the two turns. Sockeye ascending the fishway with a slope of 1 on 16 spent an average of 54 seconds in each of the straightaway pools and approximately 5 minutes in each turn pool.

The willingness to ascend the two fishway slopes appeared to be about equal when respective performances by chinook and sockeye were considered. Figure 22 gives the percentage of fish ascending 100 pools without stopping for 1 hour in an individual pool. Seven of 13 chinook in the 1-on-8 fishway and 8 of 12 in the 1-on-16 fishway completed the 100-pool ascent without prolonged stops in individual pools. Successful completions of the 100-pool ascent by sockeye were 25 out of 29, and 24 out of 31, respectively, in the 1-on-8 and 1-on-16-slope fishways. With the small number of fish in the samples, differences in the respective percentages completing the 100-pool ascent by species are not statistically significant.

To examine the possibility that ascending the experimental fishways might be fatiguing to fish, and that fatigue might be reflected in lowered per-

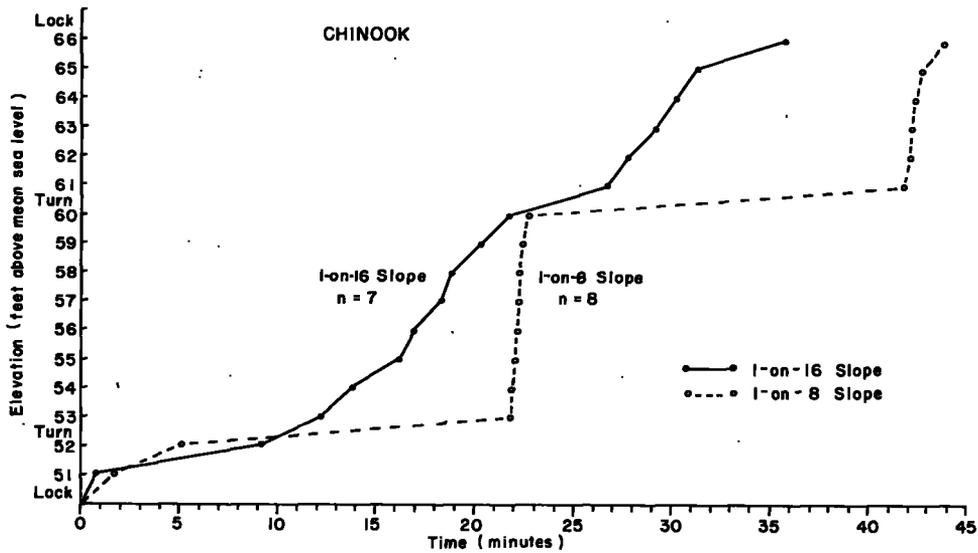


FIGURE 20.—Ascent pattern of chinook salmon in endless fishways having slopes of 1 on 8 and 1 on 16. Based on mean pool times of fish completing 6 or more circuits. June 9-21, 1958.

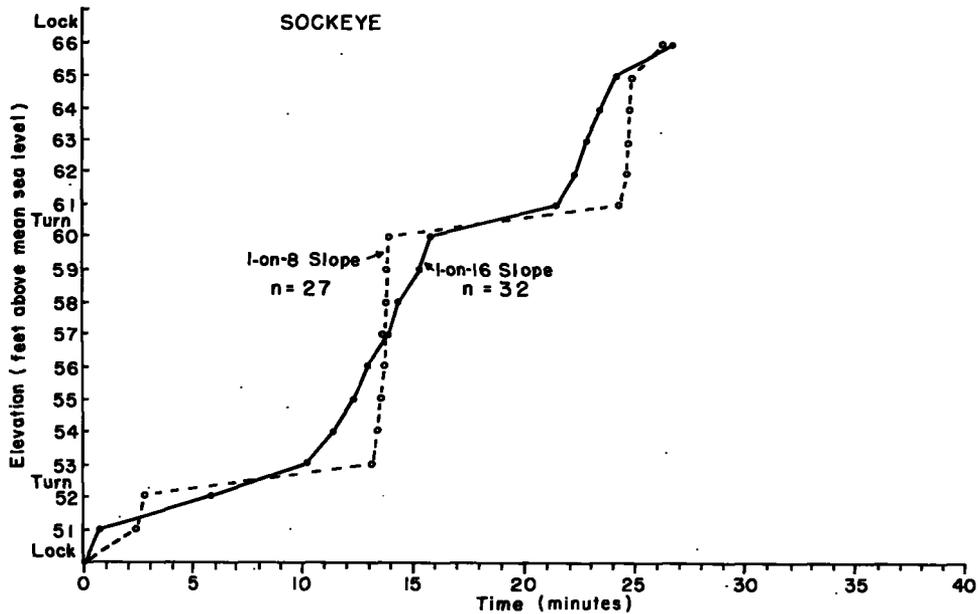


FIGURE 21.—Ascent pattern of sockeye salmon in endless fishways having slopes of 1 on 8 and 1 on 16. Based on mean pool times of fish completing six or more circuits. June 21 to July 20, 1958.

formance as the total work accomplished increased, the mean times per circuit for the first six circuits were plotted. These are given in figure 19 for chinook and in figure 23 for sockeye. Inspection of these graphs shows no evidence of a declining

rate of movement in either fishway following successive ascent of each 16-pool circuit.

In the search for a work level at which fatigue might become apparent in the performance of the fish, a number of fish were permitted to ascend

REST AREAS IN TURN POOLS
(Condition 1)

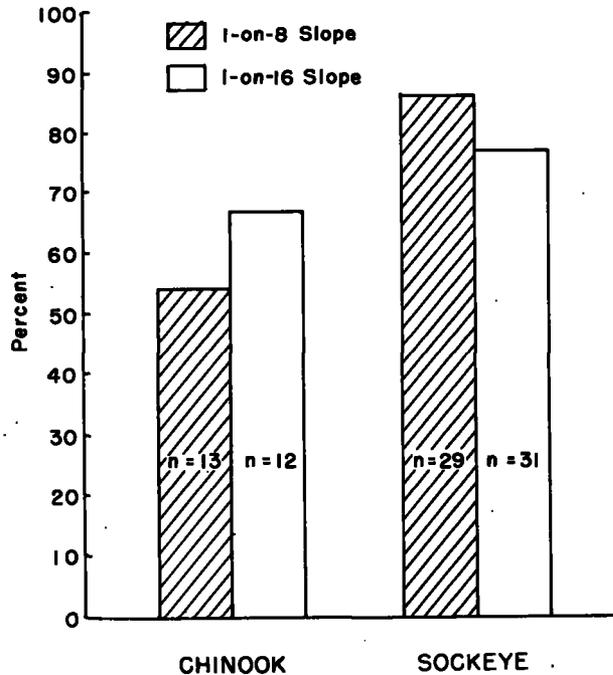


FIGURE 22.—Percentage of chinook and sockeye salmon ascending 100 pools in 1-on-8 slope and 1-on-16 slope endless fishways without stopping for 1 hour. Fishway condition 1 (rest areas in turns).

beyond the 104-pool ascent level in both fishways. Portions of the performance record of the fish that was permitted to ascend the greatest number of pools are shown in figure 24. This sockeye ascended the 1-on-8-slope fishway for 5½ days without stopping, and in that time it passed through 6,648 pools. There was no evidence of fatigue indicated by impaired performance until the fish had ascended more than 5,000 feet. The performance of this fish is discussed in greater detail by Collins, Gauley, and Elling (1962).

Perhaps the most significant finding to come from these extended ascent tests was the fact that salmonids are capable of ascending fishways of considerable height and do so without apparent physical stress.

Turn pools turbulent (condition 2)

While the preceding trials indicated that both chinook and sockeye salmon appeared to make satisfactory ascents in both the 1-on-8-slope fishway and the 1-on-16-slope fishway, the exaggerated

work-rest pattern of ascent in the 1-on-8 slope posed a serious question.

Ideally, a pool-type fishway should function so that each pool provides a suitable resting area. This is important as it permits fish to distribute themselves throughout the fishway and does not overtax the physical capacities of even the less vigorous swimmers. If, however, only a small percentage of all pools in a fishway provide resting areas, we may then expect the fish to concentrate in these pools, eventually leading to the possibility of serious overcrowding. Also, if the rest pools are spaced at lengthy intervals, some fish may never complete their ascent because of their inability to pass from one rest area to another.

The foregoing considerations led us to examine the built-in pacing pattern which in effect was the result of the particular design of the endless fishways. The question to be answered was: Will fish ascending the endless fishways be able to pace themselves if the rest areas are eliminated from the turns? To accomplish this end, the turn pools

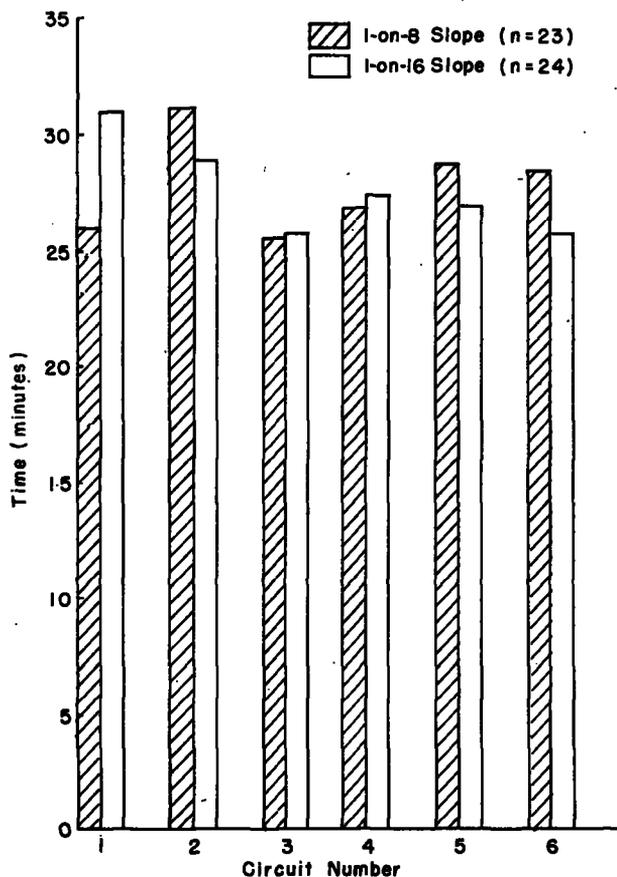


FIGURE 23.—Mean passage time per circuit (16 pools) taken by sockeye salmon negotiating endless fishways having slopes of 1 on 8 and 1 on 16. June 21 to July 20, 1958.

were made so turbulent that they no longer provided satisfactory resting areas.

Passage of fish through the endless fishways having turbulent turn pools began on July 24 and continued until September 7. During this period, river temperatures ranged from 68° to 74° Fahrenheit. Chinook salmon and steelhead trout were the principal species tested in this period. A few sockeye and silver salmon (*O. kisutch*) were also passed during this time.

Table 3 presents the passage times of chinook and steelhead ascending the endless fishways with turbulent turn pools (condition 2). Both chinook and steelhead made significantly slower ascents in the 1-on-8-slope fishway than did their counterparts in the 1-on-16-slope unit (table A-1).

Most apparent in the foregoing tests was the obvious difficulty chinook salmon displayed in their ascent of the 1-on-8-slope fishway. Only 43 percent of all chinook entering the 1-on-8-slope fishway completed the 100-pool ascent without stopping in some pool for an hour (fig. 25).

Steelhead trout fared much better than chinook in the 1-on-8 fishway and were able to negotiate the 100-pool ascent without stopping in approximately the same proportion as those ascending the 1-on-16 fishway (fig. 25).

The difficulty encountered by chinook in the 1-on-8-slope could be traced to their inability to pace themselves when the rest areas were eliminated from the turns. Their pattern of ascent

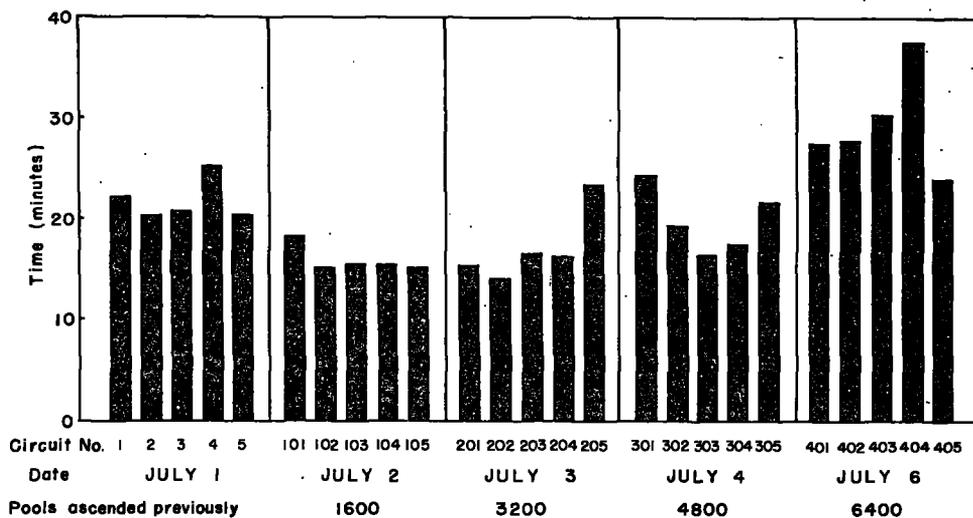


FIGURE 24.—Performance of an individual sockeye salmon in endless fishway with 1-on-8 slope. July 1-6, 1958.

TURBULENT TURN POOLS
(Condition 2)

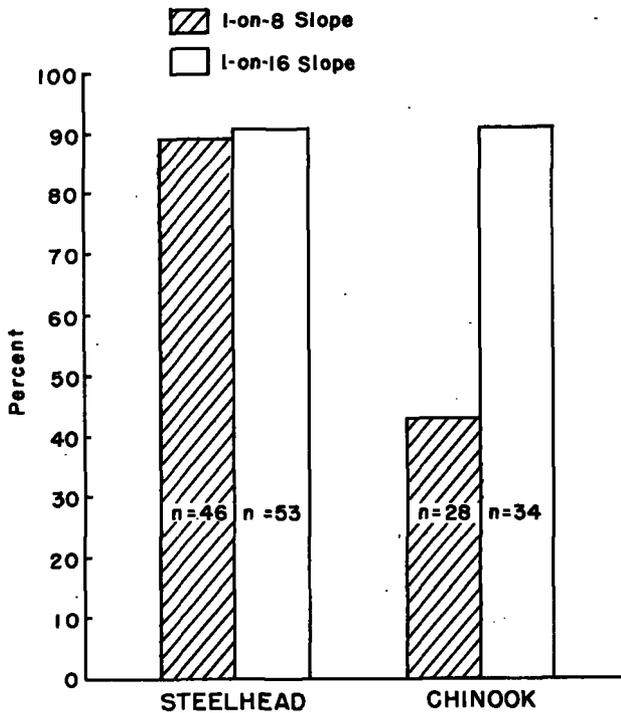


FIGURE 25.—Percentage of chinook salmon and steelhead trout ascending 100 pools in 1-on-8-slope and 1-on-16-slope endless fishways without stopping for 1 hour. Fishway condition 2 (turbulent turns).

was again similar to that evidenced in the earlier trials (fig. 19) with the exception that the rest was usually taken in a straightaway pool after a very rapid ascent through a number of preceding pools. However, in several instances chinook salmon were observed to prolong a swift ascent for approximately 16 to 20 pools. At this point they appeared to be in a state of exhaustion and on occasion were actually swept back down the fishway, seemingly lacking the strength to maintain equilibrium within a pool. Subsequent examination of the biochemical state of these fish confirmed the observation that they were experiencing physical stress.

In contrast to chinook, steelhead did not experience the same difficulty in pacing their movements through the 1-on-8 fishway. A comparison of mean ascent times by individual pools in the two fishways is given in figure 26. While steelhead

required more time to ascend the 1-on-8 slope, the work-rest pattern was not greatly divergent from that evidenced in the 1-on-16 slope.

Restricted Weirs (1-on-8 Slope) vs. Condition 2 (1-on-16 Slope)

Because of the apparent inability of a large percentage of the chinook to pace themselves successfully in the 1-on-8-slope fishway when resting areas had been removed from the turn pools, an attempt was made to pace the fish by altering the hydraulics in all pools of the fishway. This was done by restricting the water flows over the weirs by means of baffles. The reduction in the total volume of water entering each pool resulted in considerably reduced turbulence and also created a definite lateral component in the pool flow pattern. The three methods used to

TABLE 3.—Time in minutes to ascend 104 pools in endless fishways having slopes of 1 on 8 and 1 on 16 with turbulent turn pools (condition 2)

[Chinook salmon—July 24 to September 7; steelhead trout—July 24 to September 2, 1958]

Fish number	Chinook		Steelhead	
	1-on-8 slope	1-on-16 slope	1-on-8 slope	1-on-16 slope
1	275	197	182	169
2	227	261	213	139
3	178	107	243	212
4	208	111	306	161
5	230	122	250	245
6	303	285	178	193
7	300	307	247	247
8	232	157	236	286
9	190	159	154	133
10	374	129	251	100
11	244	249	221	97
12	314	115	174	171
13		109	271	109
14		121	170	151
15		111	152	145
16		183	165	186
17		198	244	206
18		165	252	119
19		241	148	105
20		166	144	105
21		202	202	118
22		171	181	186
23		205	378	149
24		200	139	145
25		153	205	180
26		264	196	180
27		187	331	123
28		207	137	139
29			236	111
30			303	106
31			103	127
32			233	135
33			140	258
34			280	105
35			219	177
36			266	190
37			208	174
38				119
39				143
40				131
41				149
42				175
43				123
44				146
45				131
46				212
Mean	255	194	222	155

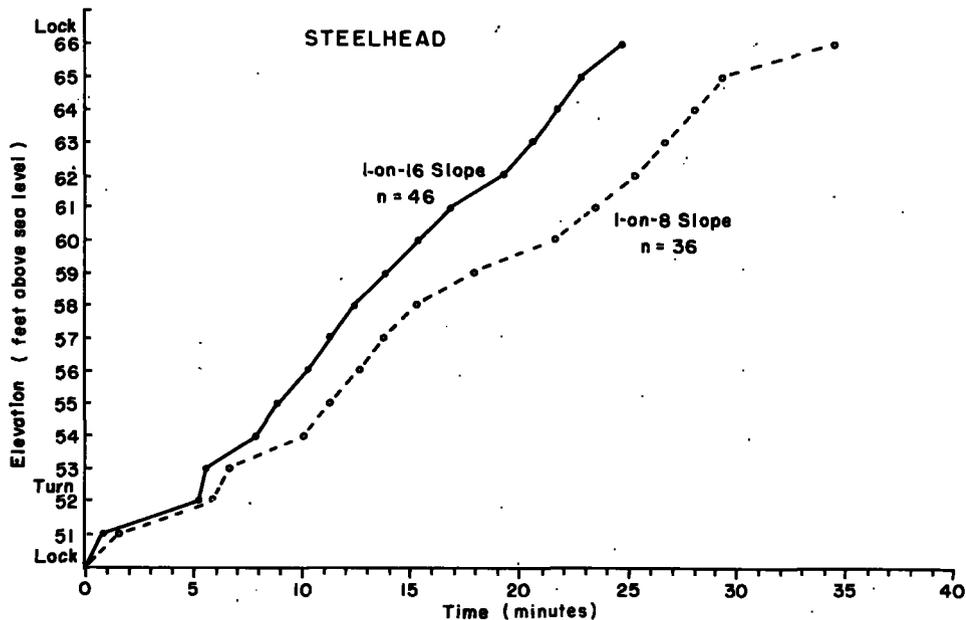


FIGURE 26.—Ascent pattern of steelhead trout in endless fishways having slopes of 1 on 8 and 1 on 16. Based on mean pool times of fish completing 6 or more circuits. Condition 2 (turbulent turn pools).

restrict flows are shown in figure 14. These baffle arrangements were applied only to the 1-on-8 fishway. Condition 2 (table 1) continued to prevail in the 1-on-16 fishway during these tests.

On September 10 and 11, several exploratory trials utilizing condition 2A (center-notched weir fig. 14) revealed an improved work-rest pattern in the 1-on-8 fishway. The rate of ascent and willingness to ascend, however, did not compare favorably with that shown in the 1-on-16 fishway. Rather than continue further experiments with this design, we made a series of tests during the remainder of September employing the other baffle arrangements, in-line baffles B and alternating baffles C (fig. 14).

A comparison of chinook salmon passage times in the two fishways for the period September 12-29 is given in table 3. While the mean ascent time of chinook in the 1-on-8-slope fishway with in-line baffles (condition 2B) was significantly slower (table A-1) than that in the 1-on-16-slope fishway, the final trials employing alternating baffles (condition 2C) in the 1-on-8-slope fishway show no difference in the time of ascent in the two fishways.

The patterns of movement resulting in the foregoing tests are shown in figures 27 and 28.

Notably, chinook salmon paced their movements in the 1-on-8-slope fishway as well as they did in

TABLE 4.—Chinook salmon passage time in minutes to ascend 104 pools in endless fishways with slopes of 1 on 8 and 1 on 16

[Weir baffles in-line (condition 2B) and alternating (condition 2C) in the 1-on-8 fishway. Turbulent turn pools (condition 2) in the 1-on-16 fishway.]

Fish number	September 12-23		September 24-29	
	1-on-8 slope condition 2B	1-on-16 slope condition 2	1-on-8 slope condition 2C	1-on-16 slope condition 2
1.....	382	193	183	182
2.....	339	190	108	258
3.....	233	223	112	91
4.....	184	134	133	153
5.....	211	210	138	178
6.....	178	132	165	132
7.....	272	147	165	123
8.....	314	182	175	140
9.....	157	146	178	135
10.....	317	138		
11.....	209	236		
12.....	125	206		
13.....	251	111		
14.....	188	106		
15.....	159	264		
16.....	179	166		
17.....	139	201		
18.....	153	103		
19.....	191	172		
20.....	113	127		
21.....	243	188		
22.....	173	131		
23.....	167	169		
24.....	224	153		
25.....	179	136		
26.....	203	154		
27.....		122		
28.....		177		
29.....		136		
30.....		128		
31.....		176		
Mean.....	209	164	151	160

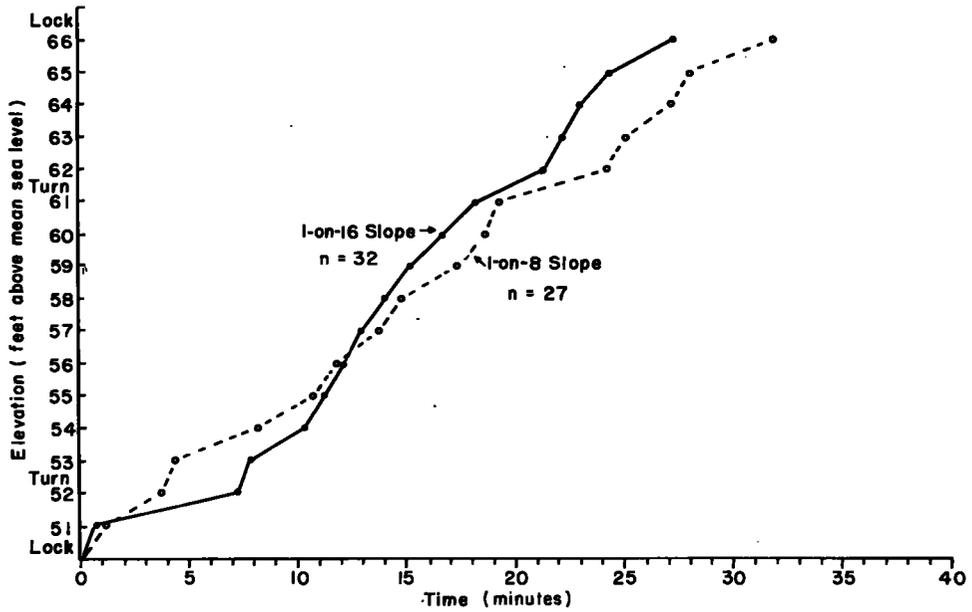


FIGURE 27.—Ascent pattern of chinook salmon in endless fishways having slopes of 1 on 8 (condition 2B, in-line baffles) and 1 on 16 (condition 2). Pool times derived from mean of 6 trips. September 12-23, 1958.

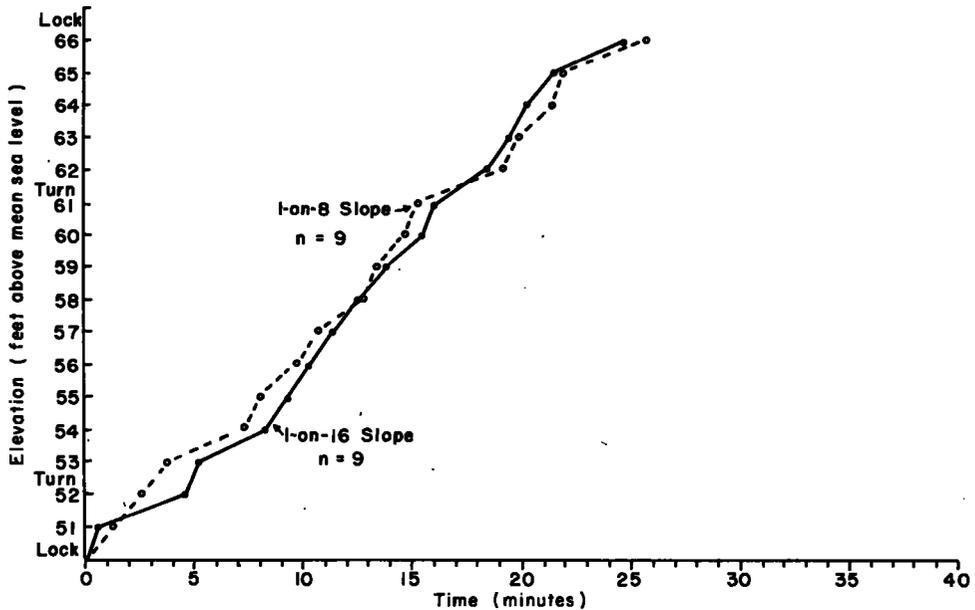


FIGURE 28.—Ascent pattern of chinook salmon in endless fishways having slopes of 1 on 8 (condition 2C, alternate baffles) and 1 on 16 (condition 2). Pool times derived from mean of 6 trips. September 24 to 29, 1958.

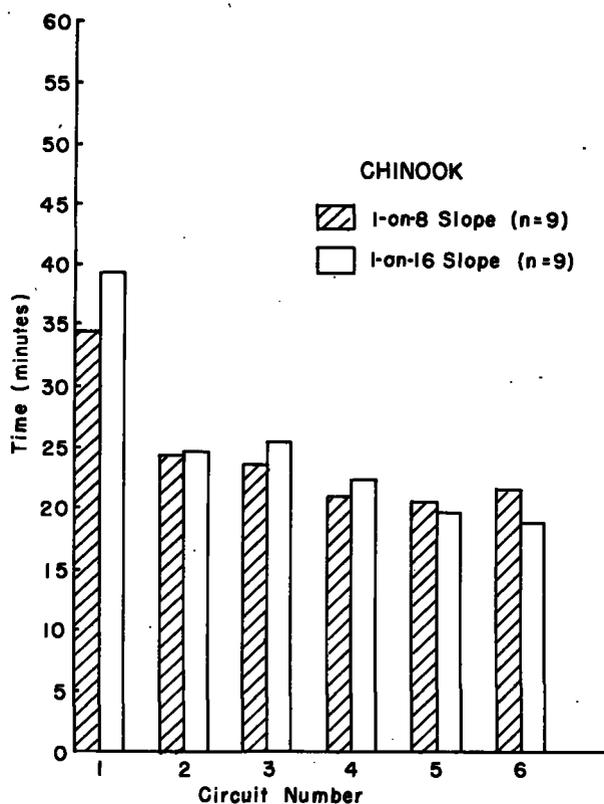


FIGURE 29.—Mean passage time per circuit taken by chinook salmon negotiating endless fishways having slopes of 1 on 8 (condition 2C, alternate baffles) and 1 on 16 (condition 2). September 24-29, 1958.

the 1-on-16-slope fishway. Evidence of the exaggerated work-rest pattern was completely lacking in both fishways.

Another encouraging aspect of the performance in the 1-on-8 fishway was that all chinook tested when conditions 2B and 2C prevailed completed the 100-pool ascent without stopping in an individual pool for 1 hour. In the same period, 93 percent of all chinook entering the 1-on-16 fishway passed the 100-pool ascent level without stopping.

Comparisons of the mean passage time per circuit for first 6 circuits show no evidence that chinook salmon were tiring after successive trips in either fishway (fig. 29). By inspection the first circuit appears to have required the longest time, and thereafter the time per circuit was about the same.

BIOCHEMISTRY

In further search for evidence that one fishway might be more fatiguing than another, lactate and inorganic phosphate levels were measured in

the blood and muscle of the experimental fish. The basis for study of these chemical compounds is well documented in biochemical literature. Black (1958a) has prepared an excellent summary on the subject of chemical correlates associated with muscular activity and recovery from fatigue in fishes. The four correlates selected for study in this experiment have all been shown to increase in level following muscular activity. The degree of muscular activity, i.e., minimal, moderate, and maximal, has been somewhat more difficult to assess because of the lack of recognizable standards. In this study, we reasoned that if the ascent of one fishway were to require more effort than that in another, the difference would be reflected in the chemistry of the fish. In addition, a comparison between the chemistry of exercised and unexercised fish (controls) was expected to provide some insight on the degree of muscular activity that may be necessary in the ascent of fishways.

In this study, the unexercised controls may be considered to represent a minimal state of activity. It should be pointed out, however, that these fish were by no means quiescent since they were free to swim about in the collection pool prior to their removal. To prepare a control fish for chemical extractions, it was necessary to net and then lift the fish approximately 14 feet to floor level in the laboratory. While this was accomplished as rapidly and efficiently as possible, some struggling did occur before the fish could be immobilized. The combination of these circumstances conceivably may have produced somewhat higher chemical values than would normally be expected in unexercised fish.

The majority of fish removed from the fishway while actively ascending (terminated treatments) were expected to be representative of an intermediate stage of muscular activity in the broad range between minimal and maximal activity. Again, the circumstances of fish removal from the fishway may have had some effect on the chemical values. Since most of the terminated treatments were taken from the shallow, upper turn pool, netting and immobilization of these fish were accomplished quite rapidly and generally with a minimum of struggling.

Fish stopping for 1 hour in an individual pool (volitional treatments) were of particular interest in this study inasmuch as the chemistry of these

fish would be expected to yield certain information on the degree to which fish might recover from their exertions in the ascent of a fishway. Removal of these fish was not always accomplished as easily as was the case with the terminated treatments. If a fish stopped at a point other than in the turns or the lock, it was necessary to net the fish from a pool which was 6 feet deep. This was readily accomplished if the fish surfaced when the fishway water supply was shut off, but if the fish remained in the depths of the pool, it was occasionally necessary to chase the fish some time before capture.

Capture and removal of the volitional-terminated treatments were achieved with little or no struggling as these fish were incapable of vigorous evasive action, probably due to exhaustion resulting from a rapid and improperly paced ascent. As will be pointed out later in the text, the chemistry of these fish suggests they may have been subjected to a period of maximal activity.

The following analysis of the biochemical determinations is made in accordance with the prevailing fishway conditions as was done under the section on performance. As may be seen in the subsequent tables, lactate of whole blood appears to have been the most sensitive of the four chemical measurements obtained.

Turn pools with rest areas (condition 1)

Summaries of the biochemical measurements on chinook and sockeye salmon ascending the 1-on-8

and 1-on-16-slope fishways when condition 1 prevailed appear in tables 5 and 6. Inspection of tables 5 and 6 indicates that levels of blood lactate in exercised fish terminated while still actively moving and regardless of the height ascended were approximately equal in both fishways. Blood lactates of terminated treatments were significantly higher than the unexercised controls (table 7). With the exception of a few fish having special case histories, none of the blood lactates from exercised fish exceeded 100 mg. percent. Levels of whole blood lactate in terminated treatments of exercised sockeye were significantly higher than similarly treated chinook salmon (1-on-8 slope, $t=3.757$, d.f. 26, $P<.01$; 1-on-16 slope, $t=2.516$, d.f. 25, $.02>P>.01$).

The blood lactate level of fish that stopped for an hour on their own volition (at a variety of ascent levels) did not differ significantly from that of the unexercised control fish (table 7). This suggests that the fish were able to rest in either fishway slope, and that they had recovered from exercise within an hour.

Levels of muscle lactate and inorganic phosphate of the blood plasma and muscle tissue indicate the possibility that similar patterns may exist for these measurements. However, the sample sizes are so small and the variation between individuals so great that only gross differences are detectable with any degree of confidence.

TABLE 5.—*Biochemistry of chinook salmon ascending 1-on-8- and 1-on-16-slope endless fishways with 36-inch weirs and turn pools providing rest areas (condition 1)*

[Mean values in mg. percent, June 9-21, 1958 ¹]

Substance	1-on-8 slope				1-on-16 slope				Controls	
	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Unexercised
Lactate of whole blood.....	7	39.1	6	29.3	8	38.4	4	23.1	11	24.3
Lactate of muscle tissue.....	7	318	6	293	8	334	4	347	11	306
Inorganic PO ₄ of blood plasma.....	7	11.6	6	10.3	8	10.7	4	11.4	11	12.2
Inorganic PO ₄ of muscle tissue.....	7	183	6	163	8	179	4	173	11	172

¹ Mean daily water temperature during test period: 63° F. (17.2° C.).

TABLE 6.—*Biochemistry of sockeye salmon ascending 1-on-8- and 1-on-16-slope endless fishways with 36-inch weirs and turn pools providing rest areas (condition 1)*

[Mean values in mg. percent, June 21-July 20, 1958 ¹]

Substance	1-on-8 slope				1-on-16 slope				Controls	
	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Unexercised
Lactate of whole blood.....	21	68.5	9	25.0	19	57.9	11	28.5	19	21.8
Lactate of muscle tissue.....	20	370	10	261	18	337	12	332	18	298
Inorganic PO ₄ of blood plasma.....	21	14.0	10	10.4	17	13.3	11	12.9	18	11.8
Inorganic PO ₄ of muscle tissue.....	21	151	10	152	19	139	12	147	18	137

¹ Mean daily water temperature during test period: 67° F. (19.4° C.).

TABLE 7.—Tests of significance between mean blood lactate levels (mg. percent) in exercised and unexercised chinook and sockeye salmon in endless fishways with slopes of 1-on-8 and 1-on-16 (condition 1)

Fishway slope	Species	Exercised				Unexercised		Degrees of freedom	Value of <i>t</i>
		Number of fish	Terminated	Number of fish	Volitional	Number of fish	Control		
1-on-8	Chinook	7	39.1			11	24.3	16	2.60*
	Chinook			6	29.3	11	24.3	15	.94 N.S.
	Sockeye	21	63.5			19	21.8	38	10.43**
	Sockeye			9	25.0	19	21.8	26	.36 N.S.
1-on-16	Chinook	8	33.4			11	24.3	17	2.33*
	Chinook			4	23.1	11	24.3	13	.18 N.S.
	Sockeye	19	57.9			19	21.8	30	7.06**
	Sockeye			11	28.5	19	21.8	28	1.33 N.S.

*Significant at 0.05 level.
 **Significant at 0.01 level.
 N.S. Not significant.

Turn Pools Turbulent (Condition 2)

Chinook salmon and steelhead trout were the principal species tested during the period of July 24 to September 7 when the turbulent turn pools (condition 2) were employed in the endless fishways.

Note is made of the abnormally high river temperatures prevailing during this time. At Bonneville, records³ show these ranged from 68°–74° Fahrenheit (20°–23.3° C.). The mean August temperature (71.7° F.) was the highest on record since construction of the dam. During the 20-year period 1938 to 1957, mean August water temperatures ranged from 63° to 69.7° F., with a 20-year mean of 67.5° F.

Summary data covering the biochemistry of chinook and steelhead ascending the endless fishways when condition 2 prevailed are presented, respectively, in tables 8 and 9. A few sockeye were also tested in the fishways during the above period, but the limited data from these tests were not considered in this analysis.

Examination of tables 8 and 9 reveals several points of interest with respect to the levels of lactate of whole blood. Mean blood lactate levels of both chinook and steelhead, terminated while actively ascending the fishways, appear to be somewhat higher in the 1-on-8 slope than in the 1-on-16 slope. These differences, however, were not significant: chinook— $t=1.735$, d.f. 41, $.09 < P < .10$; steelhead— $t=1.213$, d.f. 56, $.2 < P < .3$. Blood lactates of the terminated fish were significantly higher than those of the control fish (table 10) as they were in the earlier trials under condition 1. Again, a similar but not always consistent trend was evidenced by the

lactate of muscle and inorganic phosphate of blood plasma and muscle tissue.

By inspection, mean blood lactates of volitional treatments (fish that had exercised and stopped for 1 hour in a fishway pool) of both chinook and steelhead are considerably higher than those of the control treatments; however, because of the small sample sizes involved and the unequal variance between samples, the differences in lactate level generally were not significant (table 10). In the case of chinook salmon ascending the 1-on-8-slope fishway, the blood lactate of volitional treatments was significantly higher than that of the controls. This represents a clear departure from the trend evidenced in the earlier trials under condition 1 when volitional treatments yielded blood lactate levels quite comparable to those of the controls. It may also be noted that the blood lactate levels for exercised chinook salmon (terminated and volitional) in both fishways were higher under condition 2 than in condition 1 (tables 5 and 8), but the differences were statistically significant only for volitional treatments in the 1-on-8-slope fishway.

Whether or not the comparatively high blood lactate levels under condition 2 are linked in some way with the prevailing high water temperatures during this period is a matter of speculation. Examination of the work pattern of the volitional fish in both fishways shows the pattern was generally that of rapid ascent followed by the 1-hour stop. Presumably the fish had not fully recovered from the vigorous exercise which preceded the volitional stop. Additional studies will be necessary to determine the relationship between water temperature and blood lactate levels in exercising fish.

³ Daily operation reports, U.S. Army Corps of Engineers, Bonneville Dam.

TABLE 8.—*Biochemistry of chinook salmon ascending 1-on-8 and 1-on-16-slope endless fishways with 36-inch weirs and turbulent turn pools (condition 2)*

[Mean values in mg. percent, July 24–September 7, 1958¹]

Substance	1-on-8 slope				1-on-16 slope				Controls	
	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Unexercised
Lactate of whole blood.....	13	51.6	12	89.1	31	42.0	3	81.5	13	26.0
Lactate of muscle tissue.....	12	329	12	324	31	315	3	376	13	295
Inorganic PO ₄ of blood plasma.....	6	9.0	9	12.8	19	8.8	3	14.2	8	9.9
Inorganic PO ₄ of muscle tissue.....	11	163	12	170	31	164	3	164	13	159

¹ Mean daily water temperature during test period: 71° F. (21.7° C.).

TABLE 9.—*Biochemistry of steelhead trout ascending 1-on-8 and 1-on-16-slope endless fishways with 36-inch weirs and turbulent turn pools (condition 2)*

[Mean values in mg. percent, July 24–September 2, 1958¹]

Substance	1-on-8 slope				1-on-16 slope				Controls	
	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Unexercised
Lactate of whole blood.....	42	42.4	5	57.1	47	34.5	5	46.5	29	21.6
Lactate of muscle tissue.....	45	350	5	401	49	371	6	391	30	326
Inorganic PO ₄ of blood plasma.....	42	10.4	5	11.0	44	10.2	5	11.9	29	9.1
Inorganic PO ₄ of muscle tissue.....	45	167	5	162	47	165	6	171	30	164

¹ Mean daily water temperature during test period: 72° F. (22.2° C.).

TABLE 10.—*Tests of significance between mean levels of blood lactate (mg. percent) in exercised and unexercised chinook and steelhead ascending 1-on-8 and 1-on-16-slopes endless fishway (condition 2)*

Fishway slope	Species	Exercised				Unexercised		Degrees of freedom	Value of <i>t</i>
		Number of fish	Terminated	Number of fish	Volitional	Number of fish	Control		
1-on-8.....	Chinook.....	12	51.6			13	26.0	18	3.96**
	Chinook.....			12	89.1	13	26.0	13	5.34**
	Steelhead.....	42	42.4			29	21.6	55	5.36**
	Steelhead.....			5	57.1	29	21.6	4	1.39 N.S.
1-on-16.....	Chinook.....	31	42.0			13	26.0	42	3.43**
	Chinook.....			3	81.5	13	26.0	2	2.33 N.S.
	Steelhead.....	47	34.5			29	21.6	75	4.821**
	Steelhead.....			5	46.5	29	21.6	4	1.52 N.S.

**Significant at the 0.01 level.
N.S. Not significant.

Attention is called to the biochemistry of a special group of chinook salmon that displayed visible evidence of physical stress during their ascent of the 1-on-8-slope fishway. For lack of a more appropriate term, this group was classified "volitional-terminated" and includes only those individuals evidencing an obvious loss of equilibrium, i.e., an inability to maintain position in the fishway following a period of exercise. In all cases, these fish made extremely rapid ascents of a succession of pools (several seconds per pool) at which point they appeared to reach a state of exhaustion and drifted completely down the fishway to the lowermost pool where they became impinged against the spillover screen. Analysis of the biochemistry of these fish appears in table

11. While there are exceptions, notably in the levels of inorganic phosphate of the plasma and muscle tissue, the majority of these measures clearly affirm the observation that the fish were experiencing physical stress. The levels of blood lactate appear to be the most consistent in indicating the state of fatigue. All approached or exceeded 100 mg. percent, which from our experience to date is well above the blood lactate response expected in fish exhibiting a uniform work-rest pattern during ascent of a fishway.

Four of the five fish listed in table 11 were tested during the period of high river temperatures and when condition 2 prevailed in the 1-on-8-slope fishway. The lone entry occurring during the earlier period, when condition 1 applied,

TABLE 11.—*Biochemistry of chinook salmon taken from the 1-on-8-slope endless fishway following evidence of physical stress, 1958*

Fish number	Date	Temperature		Fishway condition	Substance—mg. percent			
		F.	C.		Lactate of blood	Lactate of muscle	Inorganic PO ₄ of plasma	Inorganic PO ₄ of muscle
1.....	June 13	Degrees 62	Degrees 16.7	1	123.1	347	16.5	163
2.....	July 25	72	22.2	2	168.2	474	17.4	210
3.....	July 28	74	23.3	2	120.6	630	22.6	165
4.....	July 31	73	22.8	2	98.0	245	16.3	153
5.....	Aug. 18	71	21.7	2	105.4	401	11.9	128
Mean.....		70	21.3		123.1	419	16.9	161

TABLE 12.—*Biochemistry of chinook salmon ascending 1-on-8 (condition 2B) and 1-on-16-slope (condition 2) endless fishways*
[Mean values in mg. percent, September 12-23, 1958¹]

Substance	1-on-8 slope				1-on-16 slope				Controls	
	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Terminated	Number of fish	Volitional	Number of fish	Unexercised
Lactate of whole blood.....	20	35.5	0		24	36.5	2	33.0	12	19.7
Lactate of muscle tissue.....	20	281	0		24	303	2	403	12	315
Inorganic PO ₄ of blood plasma.....	20	10.1	0		17	9.4	2	9.4	12	10.0
Inorganic PO ₄ of muscle tissue.....	18	156	0		24	153	2	161	12	152

¹ Mean daily water temperature during test period: 66° F. (18.9° C.).

² Includes 1 fish ascending less than 104 pools.

was a 40-pound 6-ounce male, the largest fish encountered in all of the tests.

Restricted Weirs (1-on-8 Slope) vs. Condition 2 (1-on-16 Slope)

Following structural adjustments designed to reduce turbulence in the 1-on-8-slope fishway, a series of biochemical measurements was obtained from chinook salmon tested during the period of September 12 to 23, inclusive. These were compared with similar measurements from fish ascending the 1-on-16-slope fishway which remained unchanged structurally from the previous period (condition 2, July 24 to September 7). Results of these analyses appear in table 12. With a single exception, all terminated treatments include fish that had completed an ascent of 104 pools. Examination of the blood lactate levels of fish terminated immediately after exercise shows there was no difference in the lactate response of fish ascending either the 1-on-8- or 1-on-16-slope fishways. Blood lactate levels of terminated treatments in the 1-on-16-slope fishway ranged from 16.8 to 62.5 mg. percent while those in the 1-on-8-slope fishway ranged from 20.1 to 48.3 mg. percent. Thus, the installation of weir baffles in the 1-on-8-slope fishway appears to have created hydraulic conditions which were no more fatiguing than those in the 1-on-16-slope fishway.

The blood lactate of terminated treatments in both fishways was significantly higher than that of the controls. A slightly less than twofold increase was indicated.

Levels of muscle lactate and inorganic phosphate of the blood plasma appear to be less sensitive than the whole blood lactate measurements, but in general they indicate comparable work levels for fish ascending either fishway.

Recovery following exercise in fishways

A number of investigators have demonstrated delayed effects due to strenuous exercise that have resulted in mortalities of test fish (von Buddenbrock, 1938; Secondat and Diaz, 1942; Bates and Vinsonhaler, 1957; Black, 1957; Parker and Black, 1959; Parker, Black, and Larkin, 1959). Black (1958b) in summarizing available evidence states that death in fish occurs ½ to 3 hours following severe muscular activity and is the result of a combination of adverse factors as yet not completely described. Parker and Black (1959) found that mortalities among troll-caught chinook salmon in salt water occurred from 1 to 7½ hours following capture and that death was significantly correlated with high blood levels of lactic acid.

To explore the possibility of serious latent or delayed effects due to exercise in the fishways, a number of exercised fish were held overnight in a

relatively quiet fishway pool (upper turn pool, elevation 61'). The procedure followed during the holding period was as follows: at the moment the fish entered the 105th pool, screen barriers were placed on the upstream and downstream weirs of the pool. Flows in the fishway were then reduced to approximately .25 c.f.s. and the pool was completely covered with plywood sheets. On the following morning, generally between 12 and 16 hours after the fish had entered the pool, the plywood covers were removed and the fish were carefully netted and immobilized in preparation for the usual biochemical extractions.

Eight chinook salmon in each fishway were held overnight in the foregoing manner, and in each instance no mortality was observed. Analysis of the biochemistry of these fish appears in table 13. In general, it may be seen that the condition of these fish approximated that of the controls for the same period, and on the basis of these limited observations, at least, we consider it very unlikely that delayed mortality would result from the physical exertion needed to ascend a properly designed fishway. This appears to be in keeping with investigations by Parker, et al. (1959), who in working with nonfeeding silver salmon in fresh water, found no mortalities and lower lactate levels than occurred under similar circumstances in sea water.

TABLE 13.—*Biochemistry of chinook salmon held overnight (12–16 hours) after ascending 104 pools in endless fishways with slopes of 1-on-8 and 1-on-16, September 15–23, 1958*

[Mean values in mg. percent]

Substance.	1-on-8 slope		1-on-16 slope		Controls	
	Number of fish ¹	Held after exercise	Number of fish ¹	Held after exercise	Number of fish ¹	Unexercised
Lactate of whole blood	7	24.5	8	18.7	9	19.4
Lactate of muscle tissue	7	254	8	277	9	308
Inorganic PO ₄ of blood plasma	6	8.4	7	9.4	9	10.1
Inorganic PO ₄ of muscle tissue	7	172	8	158	9	154

¹ Eight fish were held overnight in each fishway but certain measurements were not obtained from all fish.

Other factors affecting performance and biochemical state

In the preceding discussions, all comparisons of performance in the two fishways (1-on-16 and 1-on-8 slopes) have been based on the assumption that the individual capacity to perform was randomly distributed among all fish. We have previously noted that individual fish were entered

into each fishway with no distinction as to size, sex, or visible physical condition. Only those fish having obvious severe physical injuries were rejected.

Aside from the slope and prevailing hydraulics of the respective fishways, other factors which may have influenced performance and biochemical state are the size, sex, maturity, racial origin, and physical condition (injured or diseased) of the fish. Water temperature and turbidity possibly may also be related to performance and biochemical state, but as a common water source served both fishways, these variables need not be considered in evaluating respective ascents in the two fishways.

In the recent tests, data are available to permit limited analysis of the effects of size, sex, and maturity of the fish on performance and biochemical state. The effect of disease on performance is also considered briefly. Available data were not considered adequate for study of the relationship between performance and biochemical state and racial origin of the fish.

Size and sex.—Table 14 lists sex composition and length frequency distributions of the various species tested during respective trials in each slope. These data show that sex ratios of fish tested in each of the specific conditions in the 1-on-8 and 1-on-16-slope fishways were not always equal, but differences in the average size of fish passed in the two fishways generally were negligible.

An examination of the effect of size and sex on the performance of fish was made by utilizing appropriate data from tests in the 1-on-16-slope fishway for the period July 24 to September 29 when condition 2 prevailed. Steelhead trout and chinook salmon were the principal species present during this period. As several physical changes were made in the 1-on-8-slope fishway during this same period, data from these trials were not considered in this analysis.

In relating size and sex of fish to their performance, the fork length in centimeters was used to denote size, and performance was expressed in terms of the time (minutes) required to ascend 104 pools. Respective relationships for male and female chinook salmon and steelhead trout are shown in figure 30. With the exception of male steelhead trout, all regression lines exhibit a positive correlation, i.e., the larger the fish the longer

TABLE 14.—Length and sex of salmonids tested in endless fishways, 1958

Species and slope	Condition	Test periods	Number		Fork length—inches				Mean, all fish
			Males	Females	Males		Females		
					Range	Mean	Range	Mean	
Chinook:									
1 on 8.....	1	June 9 to July 20.....	7	7	28.0-42.5	31.7	25.6-34.6	31.2	31.4
1 on 16.....	1		3	9	24.4-26.6	25.5	32.3-40.0	35.6	33.0
1 on 8.....	2	July 24 to Sept. 7.....	16	13	19.1-37.0	28.2	25.2-39.6	34.0	30.8
1 on 16.....	2		23	11	18.3-39.2	29.2	27.9-37.6	32.6	30.4
1 on 8.....	2A	Sept. 10 and 11.....	2	3	29.5-30.7	30.1	32.1-37.2	35.0	33.0
1 on 16.....	2		2	2	30.1-34.3	32.2	33.1-35.6	34.3	33.3
1 on 8.....	2B	Sept. 12 to 23.....	9	18	30.3-34.3	32.4	28.1-36.6	31.7	31.9
1 on 16.....	2		17	17	26.6-41.7	32.2	29.7-38.2	32.7	32.4
1 on 8.....	12C	Sept. 24 to 30.....	6	2	26.0-32.0	28.7	30.0-32.0	31.0	29.3
1 on 16.....			12	2	7	24.0-30.0	27.0	28.0-40.0	32.5
Sockeye:									
1 on 8.....	1	June 21 to July 20.....	14	18	16.7-21.7	20.0	15.7-21.5	20.2	20.1
1 on 16.....	1		18	13	15.4-21.5	18.3	16.7-21.9	20.4	19.1
1 on 8.....	2	July 23 to Aug. 7.....	1	3	16.1	16.1	18.7-21.9	20.2	19.1
1 on 16.....	2		1	1	21.7	21.7	19.9	19.9	20.8
Steelhead:									
1 on 8.....	2	July 24 to Sept. 2.....	19	32	21.1-35.4	25.0	20.5-32.9	25.1	25.1
1 on 16.....			13	41	22.4-30.9	24.5	21.1-33.3	25.7	25.4

¹ Lengths estimated. Sex based on external features (not dissected).

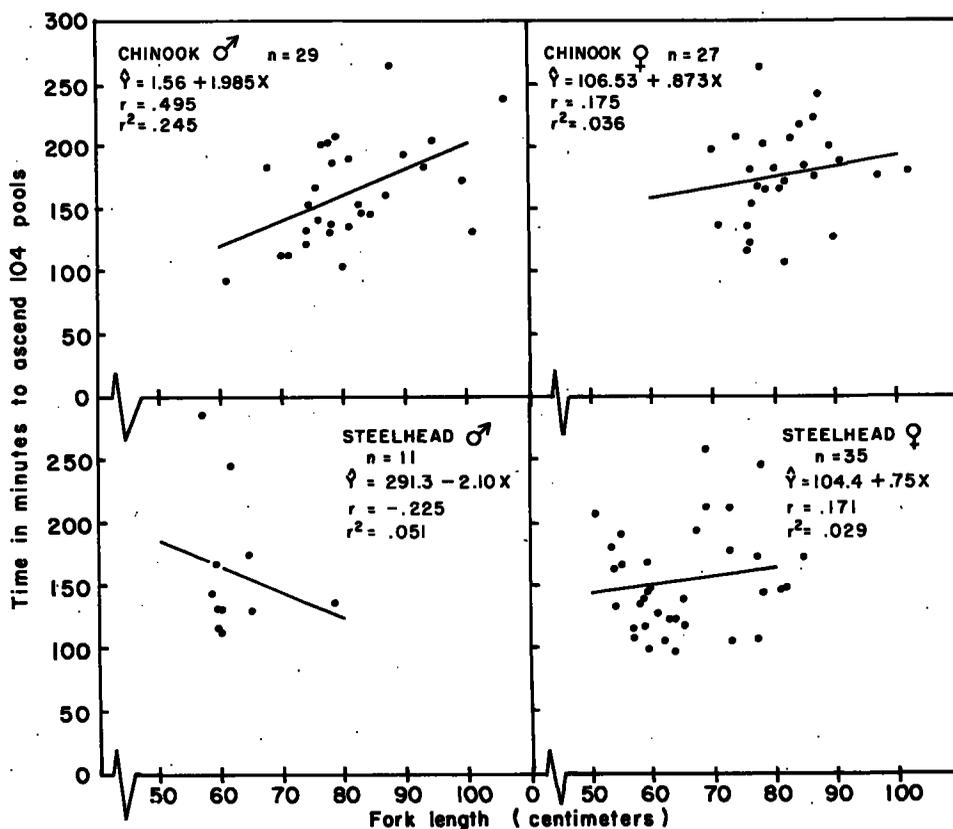


FIGURE 30.—Relationship between performance and fork length of male and female chinook salmon and steelhead trout ascending 104 pools in a 1-on-16-slope endless fishway. Chinook, September 2 to 29; steelhead, July 26 to August 30.

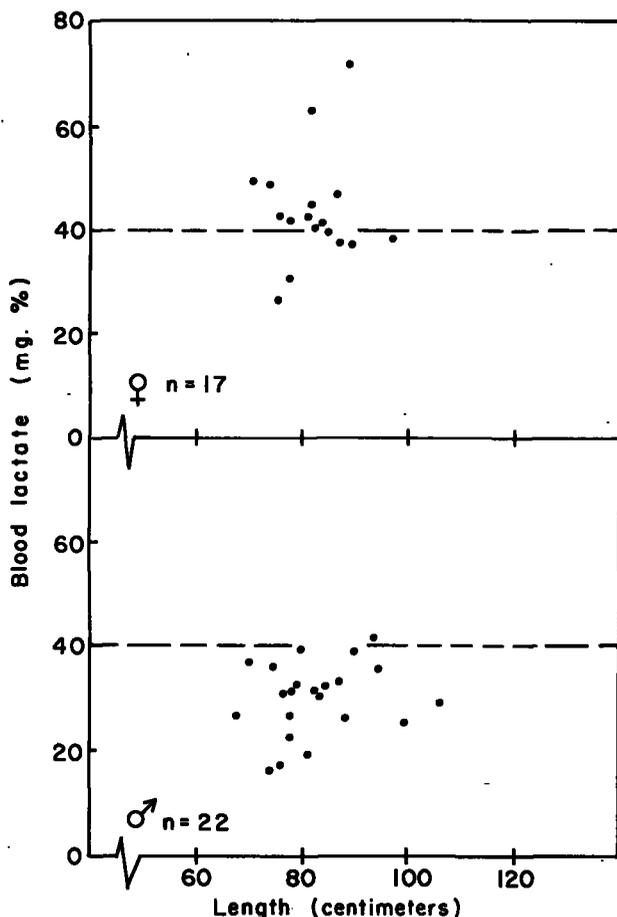


FIGURE 31.—Levels of blood lactate (mg. percent) in exercised chinook salmon according to length and sex.

the ascent time. Only in the case of male chinook salmon, however, was the regression found to be significant. Therefore, on the basis of these data, size of fish influenced performance only in the case of male chinook salmon.

Testing for the difference in the regression lines between sexes for chinook salmon and steelhead, respectively, no significant differences were found. This suggests performance within species occurred independently of sex.

When respective blood lactate levels were plotted against size of the fish tested in the endless fishways, no relation was found. In chinook salmon, however, the lactate level in females was significantly higher than that in the males (fig. 31). Further opportunity for study of this relation (as yet unexplained) will be afforded when results of a subsequent series of tests conducted in 1959 are analyzed. Lactate levels of male and female

chinook salmon ascending the two fishways (1-on-8 and 1-on-16) were re-examined separately. However, no differences between fishways were found.

Sexual maturity.—Comparisons of sexual maturity and performance consider only chinook salmon for the period September 2–23. The state of sexual maturity as used herein was the gonad weight expressed as a percentage of body weight. Performance was again measured in terms of the time required to ascend 104 pools. Steelhead were not utilized in this analysis, because gonad development in virtually every specimen was uniformly immature, generally representing less than 1 percent of the body weight. This may be explained by the fact that spawning in this species usually does not take place until late winter or early spring of the following year. On the other hand, chinook salmon passing Bonneville Dam in September are present in varying stages of sexual maturity. Some may commence spawning within several weeks after passing Bonneville while others bound for the more distant upriver tributaries may not begin spawning for several months.

The relationship between gonad development and the respective performances of male and female chinook salmon is plotted in figure 32. From the figure it is obvious that there was very little agreement between the two variables. The r^2 values indicate that only 1.5 percent of the variation in performance of males and 0.2 percent in the females was associated with variability in gonad development (sexual maturity). The difference between the regressions of males and females was found to be nonsignificant, i.e., there was no difference in performance of males and females with respect to sexual maturity.

Considering the effect of sexual maturity on the biochemical state of the fish tested, blood lactate levels were compared with gonad development and no relationship was found.

Disease.—In the Columbia River a number of highly virulent strains of *Chondrococcus columnaris*, the etiological agent of columnaris disease, have been isolated in adult and young salmon (Rucker, Earp, and Ordal, 1953). These authors further state that strains of this type when tested with young salmon in an experimental hatchery caused mortalities often reaching 100 percent in 12 to 24 hours. Particularly virulent strains appear to be associated with water temperatures in excess

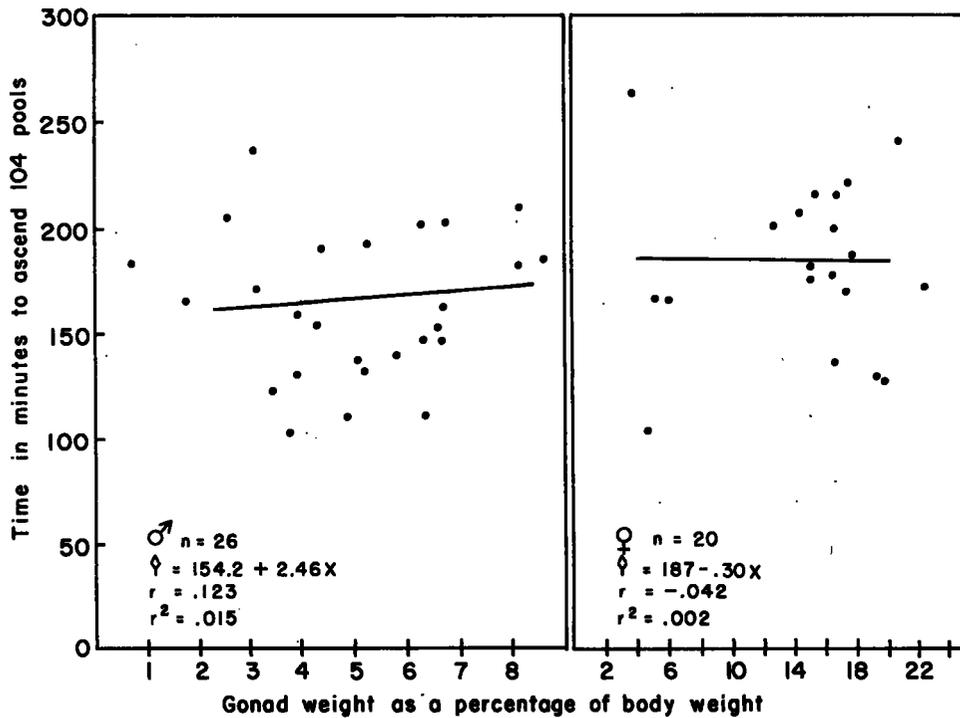


FIGURE 32.—Relationship between performance and sexual maturity. Chinook salmon, September 2-23, 1958.

of 70° F. (Fish and Rucker, 1943; Ordal and Rucker, 1944.)

During our tests from August 6 to September 23, inclusive, 245 salmonids were examined for presence of *C. columnaris*. Minor to severe lesions were found in 30 (12.2 percent) individuals. Water temperatures during this period ranged from 64° to 73° F.

A comparison of the performance of infected and noninfected fish may be made by examining the passage times of fish tested in the 1-on-16-slope fishway, which remained structurally unchanged during the period when examinations for columnaris disease were made. Only steelhead trout and chinook salmon were sufficiently abundant to be considered in this analysis.

A total of 60 chinook, 7 infected and 53 noninfected, ascended 104 pools in the 1-on-16-slope fishway during these examinations. The seven infected fish had minor to severe lesions from which *C. columnaris* was isolated. The mean ascent time for 104 pools among the infected fish was 190 minutes and that of the noninfected group was 170

minutes. This difference in performance was not significant ($t=1.06$, d.f. 58, $P>.2$).

Comparison of steelhead performances reveals that 5 infected fish ascended 104 pools in a mean time of 218 minutes while 28 noninfected individuals negotiated the same rise in a mean time of 141 minutes. Passage times for infected fish ranged from 123 to 397 minutes and from 105 to 206 minutes in the noninfected group. Despite the apparent variation in performance of the two groups of steelhead, the difference was not significant ($t=1.498$, d.f. 4, $P>.2$). This result possibly may have been influenced by the small sample size of infected fish.

Similar analyses were conducted to determine whether or not the blood lactate level was influenced by columnaris infection. No significant difference between the lactate level of infected and noninfected fish was found for either chinook salmon or steelhead trout. Again, the small sample sizes of infected fish and the degree of individual infection may have been instrumental in affecting the end result of these analyses.

DISCUSSION

One of the most significant aspects of the information gained from the foregoing experiments is the complete lack of evidence for any serious fish fatigue in either test fishway when the proper hydraulic conditions existed. The biochemical measurements on spring chinook and sockeye salmon, admittedly from small numbers of fish with large individual variations, were sensitive enough to detect significant species differences and differences between treatments "terminated" and "volitional," yet were unable to detect a difference between "volitional" fish that had stopped for 1 hour and the unexercised control fish. The implication is that the fish stopped either for reasons other than muscular fatigue or that their fatigue was so slight that they recovered very quickly. The performances of the fish in the fishways appear to bear this out. A review of the performance records of all fish ascending 96 pools or more shows that the fish did not slow down in six complete circuits. As to the sockeye salmon that was permitted to ascend for more than 5 days, there was no indication of fatigue or slowing down for at least 5,000 pools. Most of the evidence seems to point to the conclusion that when suitable hydraulic conditions prevail, the ascent in either of the two fishways is only a moderate exercise for the fish, possibly similar to that of swimming at a cruising speed which can be maintained for long periods of time.

The different patterns of ascent and rates of passage in the 1-on-8-slope fishway illustrate the manner in which hydraulic conditions can influence the pacing of fish movements through a pool-and-overfall fishway. Under condition 1, both chinook and sockeye followed an exaggerated work-and-rest pattern that resulted in the fish spending 70 percent of the time in the turn pools. Under conditions 2A, 2B, and 2C, when the weirs had been restricted to reduce turbulence and introduce lateral eddies in the pools, the fish distributed their time evenly throughout all of the pools. Under condition 2A, the rate of passage in the 1-on-8-slope fishway was much slower than in the 1-on-16-slope fishway even though the pattern of ascent was very similar. Condition 2B produced a rate of passage only slightly slower than that in the 1-on-16 slope (fig. 27), and condition 2C resulted in a rate of passage almost

identical (fig. 28) to that in the 1-on-16-slope fishway.

With this clear demonstration of the importance of hydraulic conditions in a fishway, two questions remain to be answered: what is the most desirable rate of ascent, and what are the proper hydraulic conditions to achieve this rate? To either of these questions we have as yet no sure answer. For the purpose of these experiments, we arbitrarily selected as the desired rate the rate of ascent in the 1-on-16-slope fishway now standard on the Columbia River. Further studies will be necessary to determine the range of rates of ascent within which fish will ascend indefinitely without stress or fatigue. How broad this range may be is a matter of great practical interest. There is a strong suggestion in the data (see figs. 21, 27, and 28) that ascending fish may have a tendency to accomplish a definite amount of work per unit time regardless of the pattern of movement or the slope of the fishway. Note how sockeye, with a pronounced run-and-rest pattern of ascent, in the 1-on-8-slope fishway (fig. 21), consistently ascended the 16 pools in the same time as sockeye in the 1-on-16-slope fishway using a very different pattern of ascent.

With a rate of ascent arbitrarily selected, it was possible in these experiments to modify the hydraulic pattern in the 1-on-8-slope fishway by restricting weirs until it produced the desired effect on fish movement. However, the degree to which this solution, satisfactory for an experimental fishway only 3 feet wide and without orifices, will apply to fishways of larger dimensions and different design is a matter of speculation. Clearly, the task of defining "proper hydraulic conditions" is one of the important fishway problems ahead of us.

SUMMARY AND CONCLUSIONS

The effect of fishway slope on fish performance and biochemical state in long fishways was studied with two experimental "endless" fishways constructed so that each made a complete circuit, with the highest pool connected to the lowest pool by means of a lock. Fish that ascended to the top of these fishways were rapidly locked to the bottom pool to begin the ascent again, and in this manner fishways of any desired length were simulated.

The initial experiments were made with turn

pools in each fishway that could be used as resting pools. Performances of sockeye showed no significant difference between fishways in rates of movement or in willingness to ascend. For chinooks a slower rate of passage in the 1-on-8 fishway was observed. There was, for both species, a major difference in patterns of movement in the two fishways. A pronounced work-and-rest pattern was observed in the 1-on-8-slope fishway with the fish spending 70 percent of their time in the turn pools while fish in the 1-on-16-slope fishway showed a tendency to distribute their time more evenly in all pools. Examination of biochemical indices of fatigue showed no significant difference between fishways for blood lactate levels of fish actively ascending or for fish that had stopped for 1 hour. Significant species differences in blood lactate levels and in rates of ascent were noted, but in neither the biochemistry of the fish nor in their performance was there any indication of fatigue in either fishway. Most of the experiments were with 104-pool ascents, a few with extended ascents of a few hundred pools, and one sockeye salmon was permitted to ascend more than 6,600 pools before the test was arbitrarily terminated.

A second group of experiments was made with the turn pools in each fishway modified so as to be very turbulent and not suitable as resting areas. Both the chinook and steelhead tested were significantly slower in the 1-on-8-slope fishway under these conditions, and only 43 percent of the chinook salmon in the 1-on-8-slope fishway completed 100-pool ascents compared to 91 percent in the 1-on-16-slope fishway. Steelhead were equally successful in completing 100 pools in both fishways and their well-paced patterns of movement were similar in each. Chinook salmon appeared unable to pace themselves successfully in the 1-on-8-slope fishway, and the lactate levels of the fish swept back showed definite evidence of distress.

A third set of experiments was done with the turn pools still turbulent but with the weirs of the 1-on-8-slope fishway restricted to reduce pool turbulence and to induce lateral eddies in the pool flow pattern. When the weirs were restricted with baffles arranged either in line or in alternating sequence, the chinook tested showed a pattern of movement similar to that in the 1-on-16-slope fishway. All of the chinook entering the 1-on-8-

slope fishway under these conditions completed 100 pools compared to 93 percent completing in the 1-on-16-slope fishway. With in-line baffles the rate of movement was slower in the 1-on-8-slope fishway; with alternating baffles on the weirs the rate of movement in the 1-on-8-slope fishway was equal to the rate in the 1-on-16-slope fishway. There were no significant differences between blood lactate levels of fish ascending either fishway.

Assessments were made of the effect of size, sex, maturity, and disease on performance and biochemical state of the fish. Significant relationships were found only for length of male chinook and performance (larger fish were slower), and sex and lactate level for chinook (female chinook had higher lactate levels). No delayed mortalities resulting from exercise were observed in fish held overnight in each fishway. Initial increases in rates of movement of fish in both fishways indicate that fish learn to ascend. This suggests that changes in hydraulic patterns from pool to pool may adversely influence rates of movement. A tendency for the ascending fish to accomplish a definite amount of work per-unit of time regardless of the slope of the fishway or the pattern of movement was also observed.

The major conclusions reached were:

1. A 1-on-8 slope is as suitable for a long pool-and-overfall fishway for salmonids as the standard 1-on-16 slope provided that the proper hydraulic conditions are obtained.
2. The ascent of a properly designed pool-and-overfall fishway of either slope is only a moderate exercise for salmonids.
3. Hydraulic conditions in the pools can control the rate of ascent and the pattern of movement through a fishway.
4. For all practical purposes, the rate of movement of ascending salmonids will not decrease in the upper end of a long pool-and-overfall fishway and so result in crowding or delay.
5. A 1-on-8-slope fishway with a full weir length overfall and conventional depth (6.5') in the pools does not have hydraulic conditions desirable for a long fishway and is not recommended for the passage of large chinook salmon.

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LITERATURE CITED

- BATES, DANIEL W., and RUSSEL VINSONHALER.
1957. Use of louvers for guiding fish. Transactions of the American Fisheries Society, vol. 86, pp. 38-57.
- BLACK, EDGAR C.
1957. Alterations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. III. Sockeye salmon, *Oncorhynchus nerka*. Journal of the Fisheries Research Board of Canada, vol. 14, no. 6, pp. 807-814.
- 1958a. Energy stores and metabolism in relation to muscular activity in fishes. In: The Investigation of Fish-Power Problems. H. R. MacMillan Lectures in Fisheries. P. A. Larkin, Editor. University of British Columbia, Vancouver, pp. 51-67.
- 1958b. Hyperactivity as a lethal factor in fish. Journal of the Fisheries Research Board of Canada, vol. 15, no. 4, pp. 573-586.
- COLLINS, GERALD B., JOSEPH R. GAULEY, and CARL H. ELLING.
1962. Ability of salmonids to ascend high fishways. Transactions of the American Fisheries Society, vol. 91, no. 1, January 1962; pp. 1-7.
- FISH, FREDERICK F., and ROBERT R. RUCKER.
1943. Columnaris as a disease of cold-water fishes. Transactions of the American Fisheries Society, vol. 73, pp. 32-36.
- GAULEY, JOSEPH R.
1960. Effect of fishway slope on rate of passage of salmonids. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries 350, 23 pp.
- HAWK, PHILIP B., BERNARD OSER, and WILLIAM H. SUMMERSON.
1954. Practical physiological chemistry. 13th ed. Blakiston, New York, 1,439 pp.
- KING, EARL JUDSON.
1932. The colorimetric determination of phosphorus. Biochemical Journal, vol. 26, no. 2, pp. 292-297.
- MONTGOMERY, R.
1957. The determination of glycogen. Archives of Biochemistry and Biophysics, vol. 67, no. 2, pp. 378-386.
- ORDAL, E. J., and ROBERT R. RUCKER.
1944. Pathogenic mycobacteria. Proceedings of the Society for Experimental Biology and Medicine, vol. 56, pp. 15-18.
- PARKER, ROBERT R., and EDGAR C. BLACK.
1959. Muscular fatigue and mortality in troll-caught chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of Canada, vol. 16, no. 1, pp. 95-106.
- PARKER, R. R., E. C. BLACK, and P. A. LARKIN.
1959. Fatigue and mortality in troll-caught Pacific salmon (*Oncorhynchus*). Journal of the Fisheries Research Board of Canada, vol. 16, no. 4, pp. 429-448.
- RUCKER, ROBERT R., BRIAN J. EARP, and ERLING J. ORDAL.
1954. Infectious diseases of Pacific salmon. Transactions of the American Fisheries Society, 1953 (1954), vol. 83, pp. 297-312.
- SECONDAT, MARCEL, and DIEGO DIAZ.
1942. Recherches sur la lactacidémie chez le Poisson d'eau douce. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris), tom 215, pp. 71-73.
- VON BUDDENBROCK, W.
1938. Beobachtungen über das Sterben gefangener Seefische und über den Milchsäuregehalt des Fischblutes. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 101, 4^{eme} Partie, 2nd part, pp. 3-7.

APPENDIX

Table A-1.—Summary of significance tests between salmonid passage times in fishways with slopes of 1-on-8 and 1-on-16

Species and slope	Con- dition	n	Mean passage time in minutes 104 pools	d.f.	t value	Signifi- cance
Chinook:						
1 on 8.....	1	7	285			
1 on 16.....	1	8	232	13	1.16	N.S.
1 on 8.....	2	12	255			
1 on 16.....	2	28	184	38	3.67	(**)
1 on 8.....	2A	2	282			
1 on 16.....	2	3	193			
1 on 8.....	2B	26	209			
1 on 16.....	2	31	164	38	2.85	(**)
1 on 8.....	2C	9	151			
1 on 16.....	2	9	160	16	.49	N.S.
Blueback:						
1 on 8.....	1	23	168			
1 on 16.....	1	23	171	44	.36	N.S.
Steelhead:						
1 on 8.....	2	37	222			
1 on 16.....	2	46	155	66	5.61	(**)

** Significant at the .01 level.
N.S.—Not significant, $P > .05$.

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Created in 1849, the United States Department of the Interior—a department of conservation—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

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SEXUAL MATURATION AND SPAWNING OF ATLANTIC MENHADEN

BY JOSEPH R. HIGHAM AND WILLIAM R. NICHOLSON, *Fishery Biologists*
BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

This study of the sexual development and incidence of spawning of the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), is based on an examination of ovaries collected along the Atlantic Coast of the United States from 1956 to 1959. Description of the distribution and developmental stages of ovarian ova was based on diameter measurements. Four developmental groups of ova were distinguishable in the ovaries of near-spawning fish: immature, intermediate, maturing and ripe. Two groups, each in a different stage of maturation, simultaneously developed but it could not be determined whether the second group was spawned.

A numerical relation, called the "ovary index," was established between the length of the fish and the weight of both ovaries and used to distinguish sexually

active and inactive fish. Based on changes in the mean ovary index and numbers of sexually active fish in commercial catches, it was concluded that spawning occurred at different times in different areas of the coast. In the North Atlantic Area, spawning apparently took place during summer; in the Middle Atlantic Area, in spring and again in autumn; and in the South Atlantic Area, during winter.

Most females became sexually mature at age 2, and the estimated number of ova spawned by an individual each season ranged from 38,000 to 631,000 ova.

Seasonal variation in spawning was considered in relation to differential size and age distribution of the fish, seasonal migrations, and population structure.

The life history and biology of the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), are studied by the Bureau of Commercial Fisheries as part of a research program to determine causes of variations in the distribution, availability, and abundance of this species. Sexual maturation and spawning are among the more important aspects of the biology which must be understood to interpret such variations. Determination of the time and place of spawning not only may explain seasonal variations in the distribution and availability of adults, but is fundamental to a study of the distribution and survival of embryos and larvae. Knowledge of fecundity and of the size and/or age at first spawning may be used to assess the reproductive potential of the spawning stock.

The work had several aims: (1) to describe the macroscopic changes of ovarian ova as they

develop to maturity, (2) to develop a method of determining rapidly and objectively the relative maturity of ovaries, (3) to investigate the distribution of near-spawning fish in time and space, (4) to determine the age and size at first spawning, and (5) to estimate the fecundity of fish of different sizes.

COLLECTION AND PRELIMINARY TREATMENT OF OVARIES

Most of the ovaries used in this study were obtained from routine length and age samples taken from purse seine catches landed throughout the fishing season at Portland, Maine; Gloucester, Mass.; Amagansett, N.Y.; Port Monmouth, N.J.; Lewes, Del.; Reedville, Va.; Beaufort-Morehead City, N.C., from 1956 to 1959 (fig. 1). Additional specimens were obtained from pound net catches landed at Port Monmouth and Reedville prior to commencement of the purse seine fishing season

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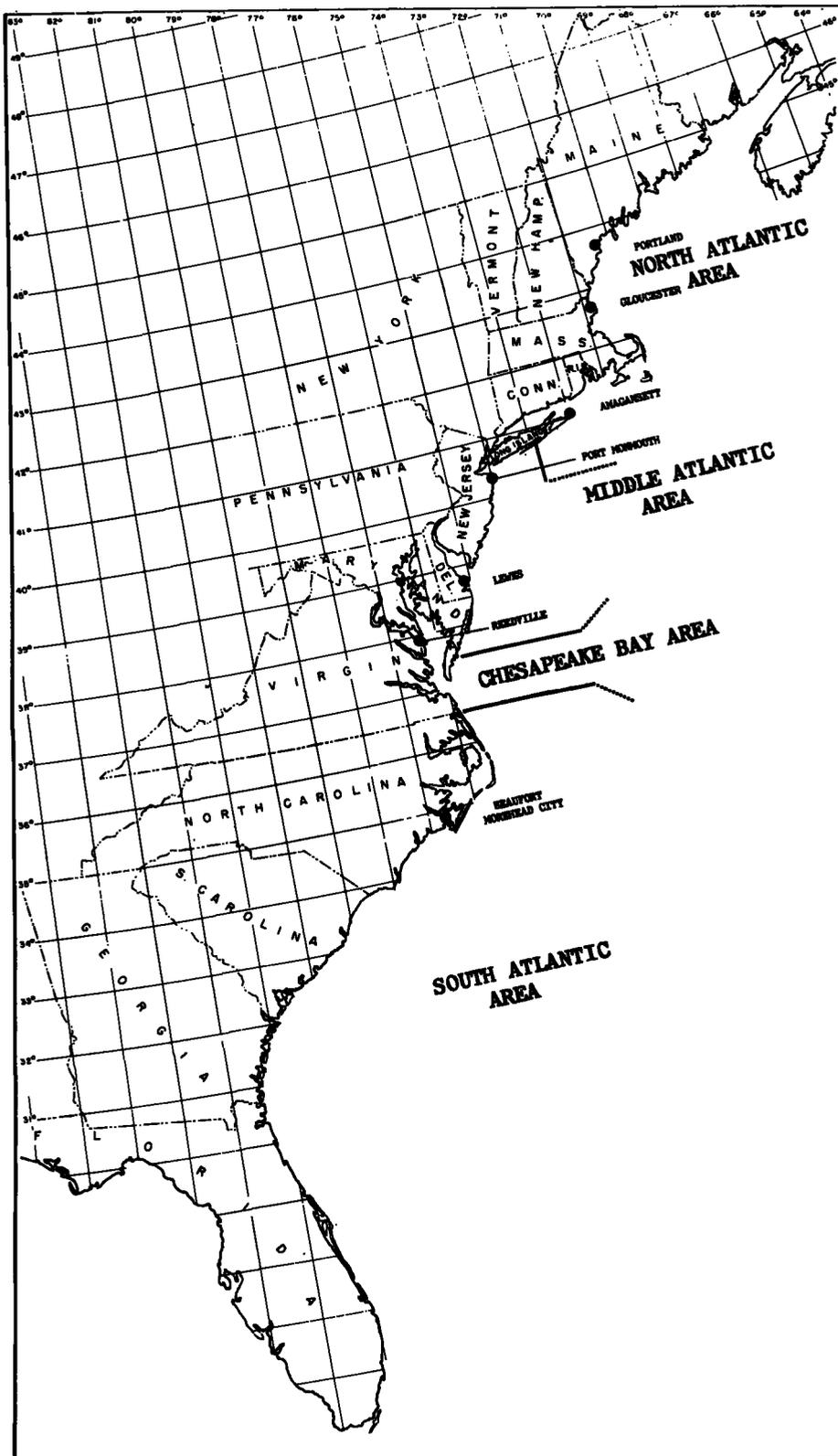


FIGURE 1.—Collection localities and areas used in summarizing maturity and spawning data on Atlantic menhaden.

and from incidental landings in various localities by otter trawlers. Methods of sampling the catch followed those described by June and Reintjes (1959).

At the time of collection, both ovaries were removed from each female, weighed to the nearest 0.1 g., and assigned an arbitrary stage of sexual maturity. In 1956 and 1957, ovaries of the first five females in each catch sample were labeled, wrapped in cheesecloth, and preserved in 10 percent formalin. Only those containing ripe ova were preserved in 1958 and 1959. Arbitrary stages of maturity assigned to ovaries in the field were:

Stage I. Ovaries small, torpedo-shaped, deep red, and occupying a small fraction of the body cavity. Ova invisible to the naked eye.

Stage II. Ovaries red to yellow, occupying about one-third to one-half of the body cavity. Ova invisible to the naked eye.

Stage III. Ovaries swollen, yellow, and occupying about two-thirds of the body cavity. Ova visible through the ovarian membrane.

Stage IV. Ovaries occupying about three-fourths or more of the body cavity. Ova yellow and readily separated from the follicles when the ovarian wall was pressed.

Stage V. Ovaries flabby, bloodshot, and occupying less than one-half of the body cavity. Intact, ripe ova present in the lumen of an ovary.

The primary purposes of examining ovaries and assigning arbitrary stages of maturity in the field were: (1) to insure collection and preservation of all ripe specimens (Stage IV), and (2) to distinguish recently spent specimens (Stage V), since after hardening in formalin, the latter usually were indistinguishable from those in the early maturing stage (Stage II).

Preserved ovary specimens collected in 1956 and 1957 were used for detailed study of maturation. Several specimens containing ripe ova which were collected and preserved in 1958 and 1959 also were used. Specimens length, and at least one specimen, when available, was chosen at random from each half-centimeter length class represented in the weekly catch samples at each port. This method of selection resulted in nearly equal representation of all length and age classes appearing in the catch samples during the 1956 and 1957 fishing seasons. Of 3,945 preserved specimens, 1,030 (26.1 percent) were used for

detailed study. During the 1956-59 fishing seasons, ovaries of 37,548 females were examined in the field for determination of stage of maturity.

MEASUREMENT OF OVA FOR MATURITY DETERMINATIONS

The distribution and stages of relative maturity of ova within the ovaries were determined from diameter measurements. Since all preserved ova were not spherical, it was necessary to choose some arbitrary method of measuring their diameters. Two methods were compared. One hundred of the most mature ova in a single ovary first were measured along the axis which, by chance, was parallel to the graduations of an ocular micrometer. The same ova were then measured along the shortest and longest axes and the two measurements averaged (table 1). The variance of the mean of single measurements was 4.27 and of two measurements, 1.48. Single measurements, however, were made in one-third the time required for two measurements. Thus, for expediency, all ova subsequently were measured once along whatever axis fell parallel to the ocular micrometer

TABLE 1.—Comparison of measurements of random diameters and the mean of maximum and minimum diameters of 100 ova from a single ovary (specimen 3.3583), in micrometer units¹

Random diameter	Mean diameter	Random diameter	Mean diameter	Random diameter	Mean diameter
35	33.0	31	31.5	34	34.0
33	33.0	31	34.0	33	34.5
34	34.0	34	35.0	32	33.0
35	35.0	39	24.5	35	35.5
38	34.5	35	34.0	37	36.0
36	35.5	32	34.0	39	36.0
32	32.5	34	35.5	37	35.5
32	35.0	33	34.5	36	34.5
33	33.5	38	35.0	33	36.5
34	35.0	35	34.5	37	35.5
33	34.5	38	36.5	37	34.5
39	36.0	35	36.0	33	34.0
34	34.0	36	35.0	35	35.0
34	24.5	34	35.0	34	33.5
37	35.5	33	32.5	38	33.0
33	33.0	38	36.0	31	34.0
34	34.0	34	33.5	33	34.5
33	34.0	35	34.5	32	34.0
35	32.5	34	36.0	34	32.0
35	35.0	36	36.5	35	34.0
30	33.0	33	31.5	37	35.0
31	32.5	30	34.5	36	35.5
32	32.5	37	35.5	33	34.5
34	31.5	35	35.5	39	36.5
38	32.0	35	36.0	32	35.0
33	32.5	36	35.0	35	34.0
32	33.5	36	35.0	35	34.0
35	33.0	34	36.5	35	34.0
34	35.5	32	34.5	36	36.0
35	33.5	32	34.0	34	35.0
32	32.5	34	33.5	35	35.0
33	33.5	35	36.5	37	34.5
35	34.0	35	34.0		
35	35.5	38	34.0		
Mean				34.49	34.36
Variance				4.27	1.48

¹ One micrometer unit equals 0.033 mm.

TABLE 2.—Diameter-frequency distributions of maturing ova in samples from various locations within a single ovary (specimen 0.10812)

[P=Periphery; M=Mid-section; I=Interior]

Diameter	Location								
	Anterior			Central			Posterior		
	P	M	I	P	M	I	P	M	I
<i>Millimeters</i>	<i>Number</i>								
0.73	2	2	2	1	2	2	1	1	1
.76	2	1	3	4	3	3	3	7	3
.79	1	5	5	9	8	6	5	13	8
.82	12	16	13	11	12	23	16	16	16
.86	10	12	19	22	15	28	26	13	24
.89	20	28	23	26	21	27	26	24	29
.92	27	34	40	22	21	36	32	34	44
.96	31	24	33	35	12	26	35	31	31
.99	28	21	30	19	36	40	35	34	31
1.02	19	13	13	15	11	17	18	25	18
1.06	14	6	7	4	12	17	12	9	9
1.09	4	7	2	3	5	4	7	5	9
1.12	5	1	2	3	2	1	2	3	2
1.16	1	2	1	4	4	1	5	1	2
1.19		2	2		2		1	1	
1.22			1				1	3	
1.25							1		
Total	176	174	195	177	164	207	187	188	201
Mean diameters (mm.)	0.95	0.94	0.93	0.93	0.95	0.95	0.96	0.96	0.95
Weight of sample (g.)	.084	.088	.94	.088	.082	.092	.094	.084	.092

graduations. This method has been applied by other investigators (Clark, 1934; June, 1953; Schaefer and Orange, 1956; Yuen, 1955) and was judged to be sufficiently precise in the present study.

Different areas within a single ovary of a pair were sampled to determine if the maturing ova were distributed uniformly. A cross section, approximately 1 millimeter (mm.) thick, was cut from the anterior, central, and posterior parts and a wedge removed from each section. Each wedge was divided into three parts, corresponding to the periphery (P), mid-section (M), and interior (I), and a subsample of approximately 0.09 g. taken. Diameters were measured and counts were made of all maturing ova in each of the nine subsamples and the results (table 2) analyzed statistically. Neither the differences in mean diameters, nor the differences in numbers were significant at the 95 percent level.

Comparisons also were made of the mean diameters and numbers of mature ova in samples from the central portions of the right and left ovary (table 3). A *t*-test showed no significant difference in mean ova diameters; however, a statistically significant chi-square value ($P < 0.01$) resulted from comparison of the numbers of ova. Inspection of the data showed discrepancies in the 0.82, 1.02, and 1.06 mm. size classes, but since the frequency distributions otherwise ap-

peared similar, it was judged that there were no biological differences in ova from the right and left ovary.

TABLE 3.—Diameter-frequency distributions of maturing ova in samples from the right and left ovary of a single fish (specimen 6.7012)

Diameter	Right ovary	Left ovary
<i>Millimeters</i>	<i>Number</i>	<i>Number</i>
0.73	11	12
.76	11	21
.79	41	57
.82	94	146
.86	138	145
.89	204	219
.92	259	254
.96	255	249
.99	290	241
1.02	154	102
1.06	101	57
1.09	47	28
1.12	21	25
1.16	23	15
1.19	15	9
1.22	4	5
1.25	1	7
Total	1,669	1,595
Mean diameter (mm.)	0.95	0.93

Ova that were measured to establish the maturity stage of the preserved specimens were obtained by cutting a cross section from the central portion of the right ovary and removing a small wedge. The wedge was placed on a glass slide, and the ova were teased from the follicular tissues by dissecting needles with the aid of a binocular microscope. Parallel guidelines etched on the glass minimized the chance of measuring the same

ovum more than once. Diameter measurements were made to the nearest ocular micrometer unit (0.017 mm.). If a specimen contained only immature ova (<0.18 mm.), measurements of about 100 ova were considered adequate to establish this stage of development. If larger ova were present, generally from 200 to 300 of the most mature ova were measured to delineate their size distribution.

DESCRIPTION OF THE OVARIES

Ovaries of Atlantic menhaden are paired, elongated organs suspended from the dorsal wall of the abdominal cavity by the mesovarium. They are elliptical in cross section and separate from each other, except where the two oviducts unite posteriorly before entering the cloaca. The right ovary usually is slightly larger than the left. Ovaries of sexually immature fish are deep red, torpedo-shaped, and may measure no more than several millimeters in length. They are similar in appearance to the testes, but are distinguishable by the oocytes which can be clearly seen under magnification, even in recently metamorphosed juveniles. As females develop to maturity, their ovaries increase in length and girth, and become firm and pale yellow. At the approach of spawning, the ovaries become distended, occupying two-thirds or more of the abdominal cavity; the peripheral blood vessels become enlarged; and the ova are visible through the ovarian membrane. Following spawning, the ovaries are flaccid and bloodshot, and residual ova occur in the follicular tissues and in the lumina.

DEVELOPMENTAL STAGES OF OVARIAN OVA

One or more distinct groups of ova are recognizable in the ovaries of an individual fish at one time or another throughout the year, depending on the proximity of spawning. Based on the appearance and diameters of formalin-preserved material, these may be described as follows:

Immature

Ova which are transparent, irregular in shape, and which contain relatively large, eccentric nuclei. These range from less than 0.02 mm. to approximately 0.22 mm. in diameter and average 0.11 mm. These are present in great numbers and comprise the oocytes from which smaller numbers of ova periodically mature (fig. 2).

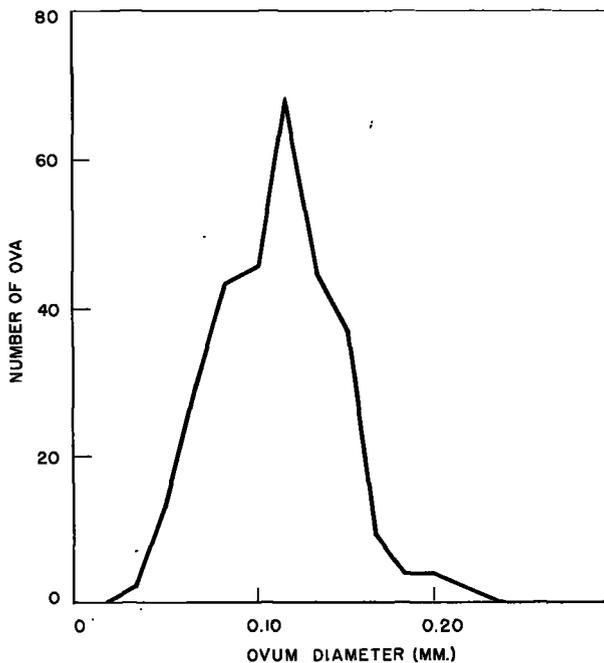


FIGURE 2.—Frequencies of ovum diameter of 300 immature ova from an Atlantic menhaden (specimen 2.1483).

Intermediate

Ova which are semiopaque, spherical, and in which the nuclei have become obscure due to the deposition of yolk granules in the cytoplasm. These range from approximately 0.18 to 0.34 mm. in diameter and are barely visible without magnification.

Maturing

Ova which are opaque and yellow due to abundant yolk material. These range from approximately 0.35 to 0.78 mm. in diameter and are clearly visible within the follicles.

Ripe

Ova which are translucent, each with a single, yellow oil globule, from 0.10 to 0.19 mm. in diameter. Ripe ova range from approximately 0.79 to 1.33 mm. in diameter. They readily burst from the follicles when the ovarian wall is pressed and sometimes are found lying loosely in the lumen of an ovary.

The four developmental groups of ova are present in the ovaries of all near-spawning fish. Development to maturity of ova within the ovaries of a single fish, with no connotation of time, is illustrated in figure 3. The percentage frequencies of ova-diameter measurements of several specimens were grouped into six arbitrary

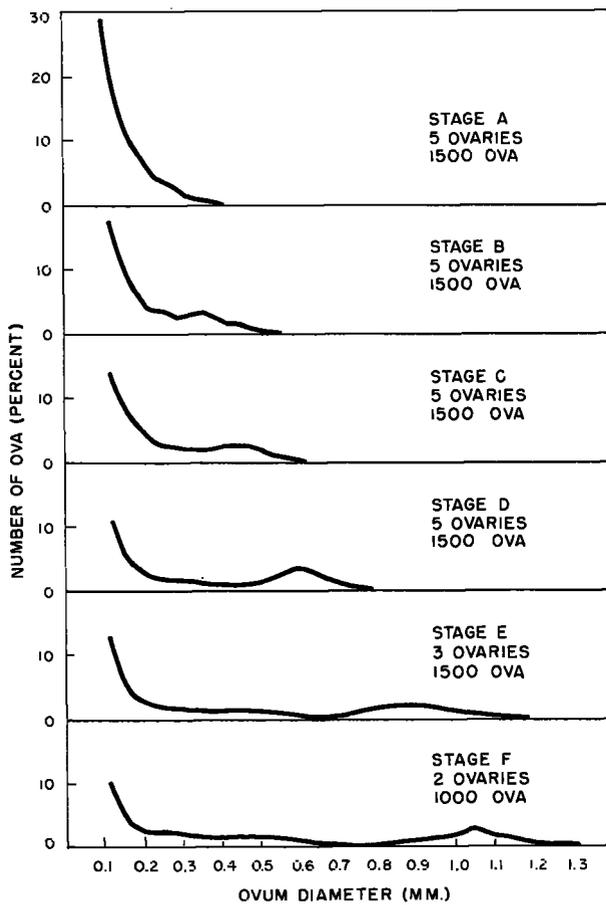


FIGURE 3.—Frequencies of ovum diameter showing the development to maturity. (The data were classified into six arbitrary stages according to the mode of the most mature group of ova. The smallest immature ova were not measured.)

stages, based on the mode of the most mature group, and smoothed twice by a moving average of three. Only ova larger than 0.12 mm. were included. A mode representing ova which eventually would ripen during a single spawning season was first discernible at 0.27 mm. (stage A). It became more sharply defined at 0.36 and 0.48 mm. (stages B and C) and distinct at 0.63 (stage D). The mode at approximately 0.90 mm. (stage E) represented semitranslucent ova which, on the basis of size, had become almost separated from the preceding groups. Ripe ova, ranging from 0.86 to 1.33 mm., with a mode at 1.08 mm. (stage F), constituted a distinct group and were nearly ready to be extruded. A second group of developing ova, between approximately 0.34 and 0.68 mm., was distinguishable by the time that

the most advanced group became semitranslucent (stage E).

OVARY SIZE AS A MEASURE OF MATURITY

Many workers have used ova-diameter measurements to characterize the relative sexual maturity of the ovaries of individual fish (Brock, 1954; Clark, 1934; Thompson, 1915). This method, however, is laborious, and where large numbers of fish are examined, some simpler, objective method usually is desirable. Changes in ovary weight in relation to body size as the ovaries develop to maturity have been used in spawning studies on a number of species (Farran, 1938; Masterman, 1913a and 1913b; Olsen and Merriman, 1946). Later investigators (June, 1953; Schaefer and Orange, 1956; Yuen, 1955) related the size of ovarian ova to the weight of the ovaries and size of the fish and established indices of maturity which ultimately could be computed from ovary weight and fish size.

In the present study, the relation between ova diameters and an "ovary index" was examined in

TABLE 4.—Ovary indices of 1,030 specimens containing ovarian ova in various stages of development

Ovary index	Developmental stage of the most mature ovarian ova				Total Number
	Immature Number	Inter- mediate Number	Matur- ing Number	Ripe Number	
<1.0	150	16			166
1.0-1.9	145	202			347
2.0-2.9	12	82	2		96
3.0-3.9		14	6		20
4.0-4.9			42		42
5.0-5.9			39		39
6.0-6.9			31		31
7.0-7.9			46		46
8.0-8.9			28		28
9.0-9.9			19		19
10.0-10.9			21	1	22
11.0-11.9			20		20
12.0-12.9			24		24
13.0-13.9			16		16
14.0-14.9			9		9
15.0-15.9			18		18
16.0-16.9			14	1	15
17.0-17.9			18	2	20
18.0-18.9			7	1	8
19.0-19.9			13		13
20.0-20.9			9	1	10
21.0-21.9			6	1	7
22.0-22.9			3		3
23.0-23.9			2		2
24.0-24.9			3	2	5
25.0-25.9					1
26.0-26.9					
27.0-27.9			1		1
28.0-28.9					
29.0-29.9				1	1
30.0-30.9					
31.0-31.9					
32.0-32.9					
33.0-33.9				1	1
34.0-34.9					
Total	307	314	398	11	1,030

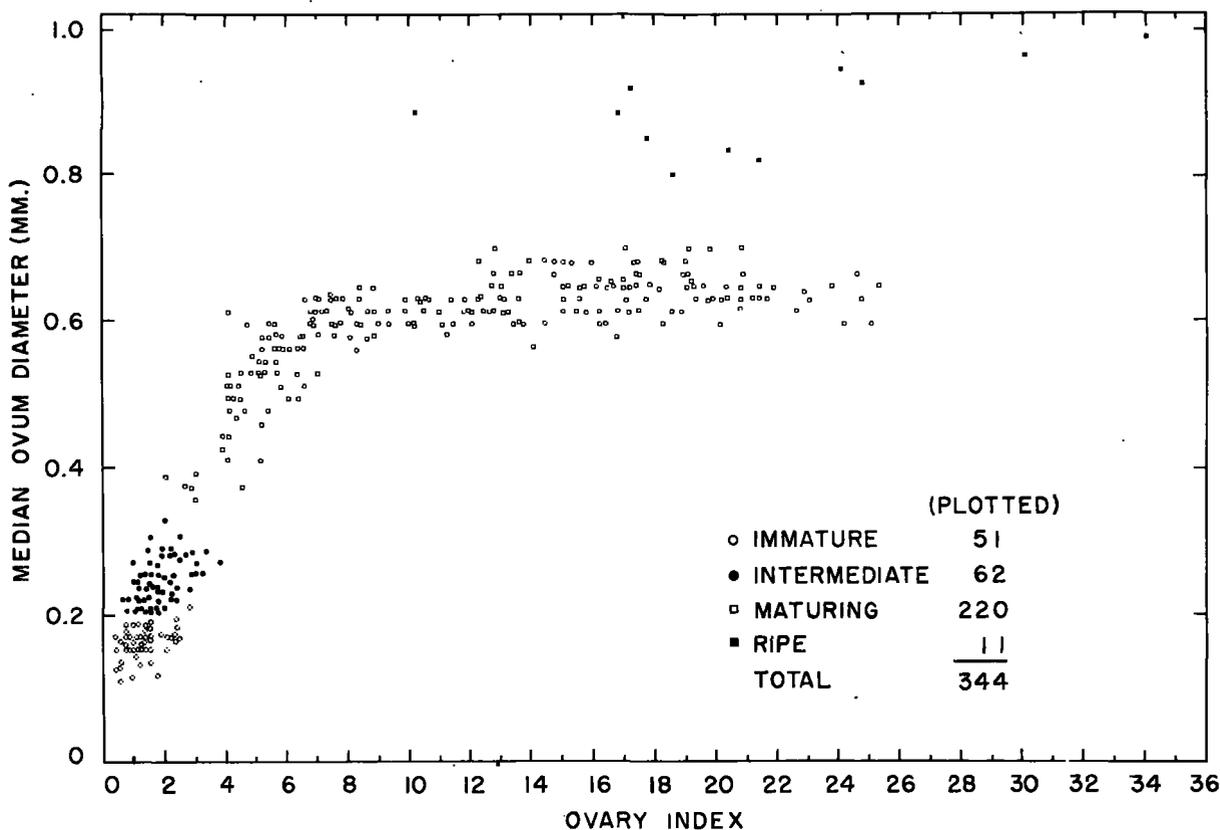


FIGURE 4.—Relation between ovary index and median of diameter frequency distributions of the most mature group of ova in 344 specimens.

1,030 specimens. The index was computed from

$$\text{the formula: } O.I. = \frac{W \times 10^7}{L^3}$$

where $O.I.$ = ovary index

W = weight of both ovaries in grams

L = fork length of the fish in millimeters¹

Of 621 specimens which contained only immature or intermediate ova (<0.34 mm. in diameter), 607 (97.7 percent) had an ovary index of less than 3, and the remainder had an index of less than 4 (table 4). Indices of 409 specimens which contained maturing and ripe ova ranged from 2.9 to 34, and all but eight of these (2.0 percent) had an index greater than 4. In figure 4, the median of the ova-diameter frequency distributions of the most mature ova was plotted against the corresponding ovary index. The

relation increased linearly up to an ovum diameter of about 0.60 mm., changed abruptly, and then tended to level off. The ovary index of 11 specimens which contained ripe ova, however, varied between 10 and 34, and there appeared to be a definite relation between the size of the most advanced ovarian ova and the ovary index.

From the foregoing, it was concluded that there was reasonably good agreement between the ovary index and the size of ovarian ova. Thus, the ovary index provided a simple, objective means of distinguishing ovary specimens which were approaching spawning. Since relatively few ripe and recently spent ovaries were found in the commercial catches, a more precise measure of sexual maturity was superfluous. Ripe ovaries were readily distinguishable by the fact that ova flowed freely from the oviduct with the slightest pressure on the ovaries. Recently spent ovaries also were easily distinguished by their flaccid, bloodshot appearance, and most of these yielded an ovary index of three or less. Verification was

¹ In Atlantic menhaden, body weight is nearly proportional to the cube of the length.

made by the presence of intact, ripe ova in the lumina of the ovaries.

PLACE AND TIME OF SPAWNING INFERRED FROM OVARY INDICES

The geographical and seasonal distribution of spawning was inferred from ovary indices on the assumption that females with an index of 4.0 or more would have actively spawned somewhere in the vicinity of capture. For convenience, those with an index of 4.0 or more were classified as "active" and those with an index of less than 4.0, as "inactive." Females with an index of less than 4.0 whose ovaries were hollow, flaccid, bloodshot, and contained some intact, ripe ova were classified as "spent." The resulting data were summarized by four major geographical areas described by June and Reintjes (1959) and shown in figure 1. The numbers of females classified according to the above criteria are listed by area, month, and year in table 5. In figures 5, 6, and 7 the percentage frequencies of sexually active females are shown

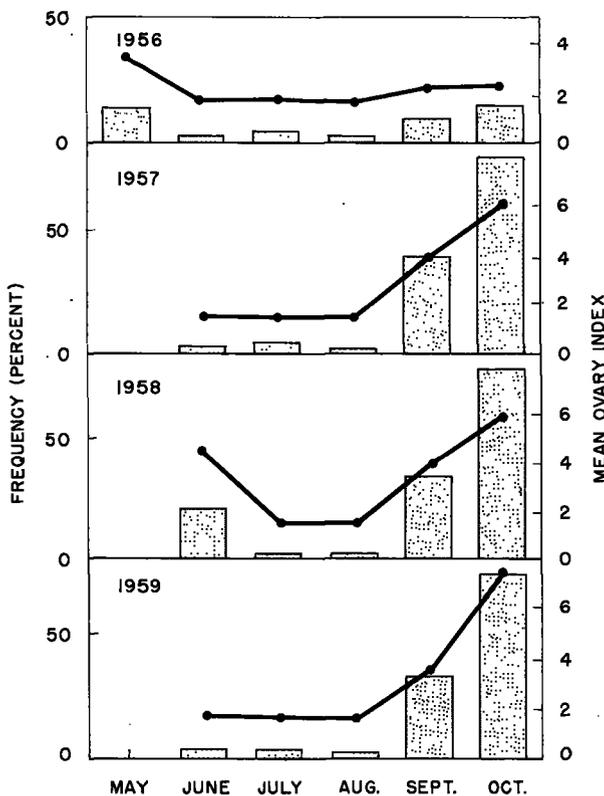


FIGURE 5.—Frequencies of sexually active females and mean ovary indices, by month and year, North Atlantic Area, 1956-59.

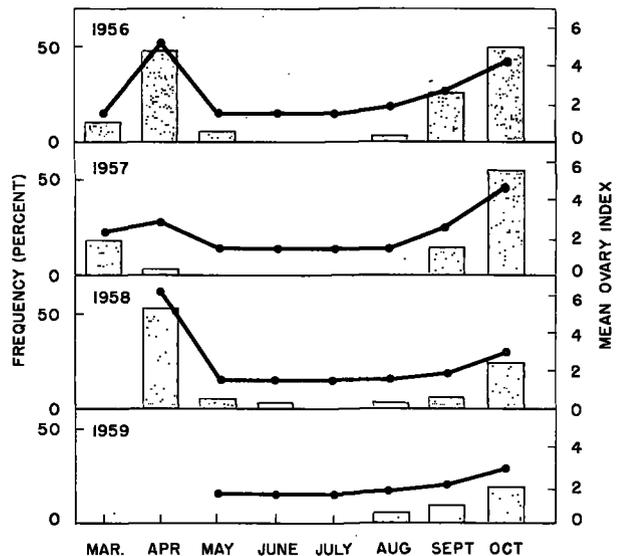


FIGURE 6.—Frequencies of sexually active females and mean ovary indices, by month and year, Middle Atlantic Area, 1956-59.

by month and year for the North, Middle, and South Atlantic Areas. The mean ovary index also is plotted on these figures.

Because so few ripe and recently spent specimens were collected (only 11 specimens containing numerous ripe ova were encountered in the routine field examination of several hundred thousand fish during 4 years of sampling), it was not possible to determine the time required for ova of sexually active fish to become fully ripe and extruded. Hence, it is possible that spawning occurred in some locality other than where sexually active females were caught. The paucity of both ripe and recently spent specimens and the occurrence of numerous collections which consisted entirely of sexually active females suggests, however, that Atlantic menhaden change their habits so as to become unavailable to the fishery prior to and following spawning. Whether spawning fish segregate in schools or in smaller groups is unknown.

NORTH ATLANTIC AREA

Atlantic menhaden were caught by purse seines in northern coastal waters from June to October in every year; consequently most of our collections were limited to this period. A few specimens were obtained from pound nets in May 1956. Ovaries of 6,511 females were ex-

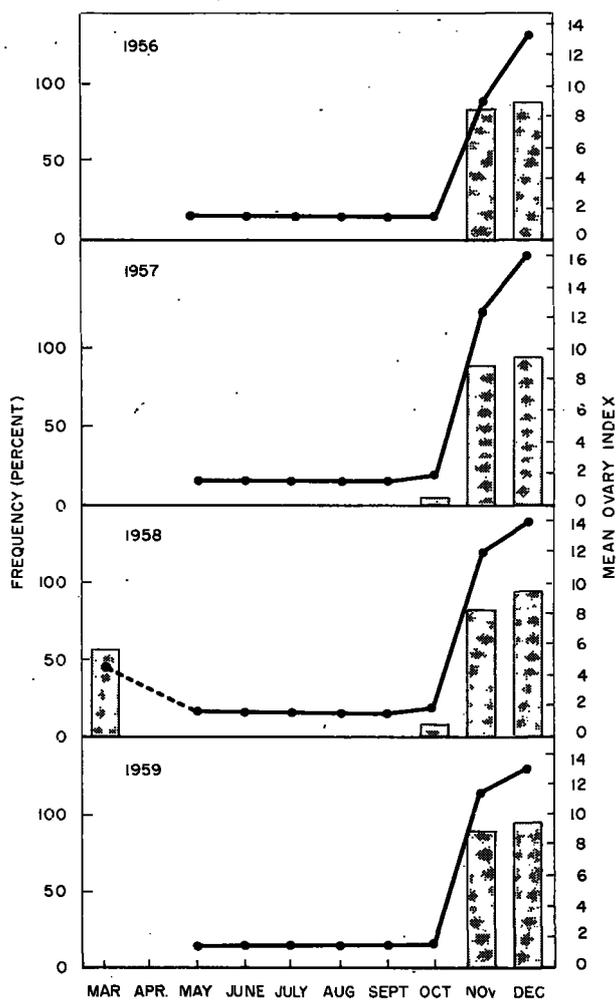


FIGURE 7.—Frequencies of sexually active females and mean ovary indices, by month and year, South Atlantic Area, 1956-59.

amined between 1956 and 1959. Active and/or spent females were represented in every month for which there were data (table 5 and figure 5). Many of the specimens obtained in May 1956 and in June 1958 were active and had high ovary indices. In most years, however, the numbers of active fish in June, July, and August constituted only a small fraction of the monthly totals, and the mean ovary index increased in September and reached a maximum in October. It was concluded from these data that spawning took place in the North Atlantic during the entire period that the fish were available to the fishery, and reached a peak in October.

The above conclusions agree with published reports of the occurrence of planktonic eggs and

larvae. Kuntz and Radcliffe (1917) found both eggs and larvae in the vicinity of Woods Hole, Mass., in June, July, August, and again in October. Herman (1959) reported the occurrence of eggs and larvae in Narragansett Bay from May to August and again in October and concluded that there was a split spawning season in that locality, the autumn spawning being the most productive. Perlmutter (1939) reported eggs and larvae in northern Long Island waters from May to September, and Richards (1959) and Wheatland (1956) concluded that spawning took place in Long Island Sound from May to October, with peaks occurring in early summer and in autumn.

MIDDLE ATLANTIC AREA

A pound net fishery for Atlantic menhaden operates off New Jersey and southern Long Island beginning in April and is followed by the purse seine fishery beginning in May. The purse seine fishery continues until October when the fish disappear from the coastal waters (June and Reintjes, 1959). Except during mild winters, when occasional catches are made by pound nets and otter trawls, the fish are not known to occur in concentrations inshore until the following March or April.

Ovaries of 14,749 females were examined from March to October during the 4-year period (a few specimens were obtained in December 1957). Active and spent females occurred in substantial numbers in April, but abruptly decreased in May (table 5 and figure 6). Only 12 active or spent females appeared in the catches in June, July, and August. In every year, the number of active fish increased in September and generally reached a maximum in October. The mean ovary index was high in April, remained low during the summer, but increased again in September and October. It appears from these data that spawning occurred in spring and again in autumn, with possibly very limited spawning during the summer. The main spawning season was indicated to be in autumn.

There are no published reports of the occurrence of planktonic eggs and larvae within the area; however, evidence that spawning takes place in spring and autumn comes from numerous plankton collections of larvae taken at Indian River Inlet, Del. Routine sampling was conducted at this location

TABLE 5.—Number of sexually inactive, active, and spent female Atlantic menhaden in catch samples, by area and month, 1956-59

Area, year, and ovary condition	Month										Total
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
North Atlantic:											
1956:											
Inactive.....				323	671	573	200	102			1,869
Active.....			6	2	22	8	22	29			89
Spent.....			36	11	21	43	12	53			176
1957:											
Inactive.....				199	600	494	128	19			1,440
Active.....				4	16	9	91	135			255
Spent.....					1	3	2	12			18
1958:											
Inactive.....				65	285	299	166	18			833
Active.....				19	2	1	98	84			204
Spent.....					9		17	3			39
1959:											
Inactive.....				279	427	418	235	17			1,376
Active.....				8	17	9	106	75			215
Spent.....					5	2					7
Subtotal:											
Inactive.....				366	1,983	1,784	729	156			5,518
Active.....			6	33	57	27	317	323			763
Spent.....			36	16	31	48	31	68			230
Middle Atlantic:											
1956:											
Inactive.....				365	484	590	286	211			3,010
Active.....	1	144	429	1		1	92	213			526
Spent.....	9	94	67	4			3	1			178
1957:											
Inactive.....		61	205	765	813	757	407	281		9	3,298
Active.....	5	37	1				51	337			431
Spent.....	24	138	22				1				185
1958:											
Inactive.....		6	179	576	765	810	794	70			3,200
Active.....		61	9	4		3	24	21			122
Spent.....		52	25	2							79
1959:											
Inactive.....			137	813	984	1,056	549	108			3,647
Active.....						4	46	23			73
Spent.....											
Subtotal:											
Inactive.....	1	211	950	3,019	3,046	3,213	2,036	670			13,155
Active.....	6	316	11	4		8	213	594			1,182
Spent.....	33	284	114	6			4	1			442
Chesapeake Bay:											
1956:											
Inactive.....		32	316	369	438	370	166	39			1,720
Active.....											
Spent.....											
1957:											
Inactive.....		310	79	346	436	434	329	156			2,090
Active.....		2									2
Spent.....											
1958:											
Inactive.....			35	428	430	256	374	110			1,633
Active.....											
Spent.....											
1959:											
Inactive.....			72	455	495	448	479	272	39		2,260
Active.....											
Spent.....											
Subtotal:											
Inactive.....		342	502	1,598	1,799	1,508	1,338	577	39		7,703
Active.....		2									2
Spent.....											
South Atlantic:											
1956:											
Inactive.....			359	446	424	524	230	188	52	38	2,261
Active.....									273	251	524
Spent.....											
1957:											
Inactive.....			385	473	339	178	101	80	40	10	1,606
Active.....								4	276	204	484
Spent.....											
1958:											
Inactive.....			279	300	241	93	210	61	39	44	1,267
Active.....	50							4	186	316	556
Spent.....	38										38
1959:											
Inactive.....			262	371	246	213	81	45	33	15	1,266
Active.....									243	347	590
Spent.....											
Subtotal:											
Inactive.....			1,285	1,590	1,250	1,008	622	374	164	107	6,400
Active.....	50							8	978	1,118	2,154
Spent.....	38										38

from 1955 to 1961 as part of an estuarine study conducted by the Menhaden Program. Neither eggs nor larvae were taken in July, August, and September. Larvae appeared in the collections in October, increased in number thereafter, and generally reached a peak of abundance in January. The smallest larvae occurred in the October samples. Their length increased in November, but thereafter remained relatively constant until April when both smaller and larger larvae occurred in the collections (Pacheco, Unpublished Ms.).² These findings suggest the following hypotheses: (1) following a period of no spawning in the area throughout the summer, spawning begins in September or October; (2) larvae from the autumn spawning increase in length through November, but subsequently do not grow appreciably until April or May; and (3) smaller larvae which appear in the collections in April result from a spring spawning in the area, while the larger larvae represent the progeny from the previous autumn spawning. The occurrence of sexually active fish in autumn, their absence in the coastal waters during winter, and their reappearance in spring support these hypotheses.

CHESAPEAKE BAY AREA

In Chesapeake Bay, Atlantic menhaden are caught in quantity by pound nets beginning in April (McHugh, 1960). The purse seine fishery begins in late May and usually continues through October, at which time most of the fish apparently disappear from the Bay (June and Reintjes, 1959). Of 7,705 females examined between April and November, only two active specimens were found, both in April 1957 (table 5). No spent females were found. It was concluded, therefore, that spawning probably did not occur in Chesapeake Bay during the period considered.

Kuntz and Radcliffe (1917) were of the opinion that there were two spawning seasons in the Chesapeake Bay area, but offered no data to support their belief. Hildebrand and Schroeder (1928) reported that females with "well-developed" (although not ripe) ovaries were taken in autumn and that larvae were caught from January to April. These authors concluded that spawning occurred in autumn. Pearson (1941) obtained "a limited number" of eggs in late summer and several 20-24

mm. larvae in April and May plankton samples taken in lower Chesapeake Bay and concluded that some spawning probably occurred outside the area of collection during the winter. McHugh, Oglesby, and Pacheco (1959) found no fully mature fish in samples from pound net and purse seine catches, although some specimens approaching maturity were observed in early spring.³ They further reported that no eggs were found in numerous plankton hauls in Chesapeake Bay; however, larvae 24 to 30 mm. in length were taken as early as April and appeared in greatest abundance in late April and early May. Massmann, Norcross and Joseph (1962) obtained larvae from November to May during monthly offshore plankton cruises in Virginia waters. The smallest specimens were taken in November and ranged between 7 and 10 mm. Those taken during the winter months were fairly uniform in size and ranged from 12 to 29 mm., while those taken in May were larger and ranged between 25 and 33 mm.

The foregoing evidence supports the present conclusion that spawning does not occur in Chesapeake Bay. It is probable that the larvae reported within Chesapeake Bay resulted from an autumn and winter spawning offshore.

SOUTH ATLANTIC AREA

In the South Atlantic Area, Atlantic menhaden are caught exclusively by purse seines, generally from May to December or January.⁴ The summer fishery apparently is based on local stocks and usually lasts from about mid-May to mid-October (June and Nicholson 1964). In November, large, migratory schools appear off the coast of North Carolina and support an intense fishery until mid-December when they disappear off Cape Fear, N.C. (June and Reintjes, 1959).

Examination was made of 8,592 specimens obtained from the purse seine fishery and from incidental catches made by otter trawlers. No active females appeared in the catches from May to September in any year, and only eight active females were found in October (table 5 and figure 7). With the appearance of migrating schools in

³ While no sexually active fish were found in the present study from 1956-59, specimens examined in 1955 showed the presence of 1 sexually active fish in May, 1 in September, and 22 in October. Only inactive fish were found in June, July, and August.

⁴ Catches in January consist almost exclusively of young-of-the-year fish (age 0) which are sexually immature. These were excluded from the study.

² Catches of postlarval Atlantic menhaden, *Brevoortia tyrannus*, at Indian River, Delaware. Unpublished Manuscript, U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.

November and December, the number of active females increased abruptly. Eighty-nine percent of the females examined in November and 95 percent of those examined in December were active. The particularly high ovary indices in November and December also indicated that most of the females in the fishable population were in spawning condition. Among 88 specimens collected on an exploratory fishing cruise in March 1958, 50 were active and 38 were spent.

Reintjes (1961) reported the occurrence of eggs and/or newly hatched larvae, principally in the vicinity of Capes Fear and Lookout, N.C., and Cape Kennedy, Fla., from November to March, but none were found during other months of the year. Based on the known distribution of adults, he believed those taken off the North Carolina coast were Atlantic menhaden, while those taken off central Florida were Atlantic menhaden or yellowfin menhaden (*B. smithi*).

Corroborative evidence of continuous spawning off the North Carolina coast from late fall to early spring is furnished from routine plankton collections taken in the vicinity of Beaufort, N.C., from 1955 to 1961 (Unpublished data, Menhaden Program, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.). Eggs and larvae have been collected in the ocean only during the late fall and winter months; however, eggs have not been taken at any time in samples at Beaufort Inlet. In every year, larvae appeared in Beaufort Inlet samples beginning in November or early December, were present continuously thereafter until early or mid-April, and reached a peak of abundance in late February or early March. Larvae in the early December samples invariably were small, ranging from approximately 10 to 20 mm. in length. Samples throughout the winter contained mixed sizes, indicating successive waves of spawning in nearby waters. The largest larvae usually occurred in the April samples. Larvae were never taken from May to November.

It was concluded that spawning occurred in the South Atlantic Area from mid-November to late March, with a peak probably occurring sometime in mid-winter. Based on the concentrations of sexually active fish and the abundance of newly hatched larvae, it is likely that waters off the North Carolina coast are one of the major spawning grounds for Atlantic menhaden.

AGE AND LENGTH AT FIRST MATURITY

Females were considered immature if their ovaries were in the inactive stage (ovary index <4.0) and ova remnants were not found in the follicular tissues or in the lumina. Fish whose ovaries were either active (ovary index >4.0) or in the spent stage, with intact, ripe ova present in the lumina, were considered sexually mature. On the basis of these criteria, little difficulty was experienced in distinguishing sexually mature individuals.

No sexually active age-0 fish (June and Roithmayr, 1960; June and Reintjes, 1959) were found. This age group, therefore, was not considered further. In most years a few mature females of age 1 occurred in catch samples in the Middle Atlantic Area in October; nine females, ranging from 240 to 265 mm. in length, were found in 1956; two, 215 and 235 mm., in 1957; and one, 210 mm., in 1959 (table 6). Greater numbers were found during the fall fishery in the South Atlantic Area. Between October and December (table 7), 22 mature females, ranging from 205 to 260 mm., were found in 1956; one 190-mm. specimen in 1957; 52 specimens, ranging between 180 and 280 mm., in 1958; and two specimens, 200 and 205 mm., in 1959. No mature females in this age group were found in samples from other areas in any year. From these data, it was concluded that some Atlantic menhaden attained maturity at age 1, and these ranged from approximately 180 to 280 mm. in length. The mean lengths indicate that there was a size difference at which females reached maturity in the two areas. There also was a tendency for the mature females

TABLE 6.—Relation of age, length, and spawning condition of Atlantic menhaden, Middle Atlantic Area, September and October, 1956-59

Year and age group	Number	Inactive		Number	Active	
		Fork length			Fork length	
		Range	Mean		Range	Mean
1956:		<i>Milli-</i>	<i>milli-</i>		<i>milli-</i>	<i>milli-</i>
Age 1.....	158	195-265	225.2	9	240-265	248.4
Age 2.....	127	235-300	260.7	121	235-305	263.2
1957:						
Age 1.....	339	185-255	209.2	2	215-235	225.0
Age 2.....	306	195-305	253.7	98	210-320	266.6
1958:						
Age 1.....	0			0		
Age 2.....	836	215-280	248.4	43	250-280	264.2
1959:						
Age 1.....	437	165-230	194.3	1	210	210.0
Age 2.....	91	210-280	241.5	23	235-285	257.6

TABLE 7.—Relation of age, length, and spawning condition of Atlantic menhaden, South Atlantic Area, October–December, 1956–59

Year and age group	Number	Inactive		Number	Active	
		Fork length			Fork length	
		Range	Mean		Range	Mean
1956:		<i>Milli-</i>	<i>milli-</i>		<i>Milli-</i>	<i>milli-</i>
Age 1.....	270	140-230	169.3	22	205-260	232.5
Age 2.....	8	200-235	220.0	100	225-305	265.0
1957:						
Age 1.....	66	150-210	182.9	1	190	190.0
Age 2.....	58	180-220	196.4	121	185-315	279.8
1958:						
Age 1.....	135	170-280	198.1	52	180-280	217.4
Age 2.....	9	195-240	212.2	253	185-300	261.5
1959:						
Age 1.....	75	130-225	160.7	2	200-205	202.5
Age 2.....	9	185-250	210.6	114	210-290	259.0

of age 1 to be the larger individuals within the age group in both areas.

In every year, mature females of age 2 were found in catch samples in the Middle and North Atlantic Areas beginning in September. By October, 48 percent of all females in this age group examined during the 4-year period had attained maturity, and these ranged between 225 and 320 mm. in length. In the South Atlantic Area, 97 percent of the females examined from October through December during the 4-year period were mature, and these ranged from 195 to 315 mm. in length. Thus it would appear that most females mature by age 2. All females of age 3 and older ages were found to be mature. Ovaries of the latter age groups which were examined microscopically, without exception, contained ova remnants from a previous spawning. These findings, in general, agree with those of Westman and Nigrelli (1955) who stated that all females at age 3 and some at age 2 appeared to be mature.

FREQUENCY OF SPAWNING DURING A SEASON

The frequency distribution of ova diameters in figure 3 showed that, within the ovaries of Atlantic menhaden, there was a progression to maturity of one group of advanced ova, distinguished by a single, well-defined mode. This was followed by a second group of developing ova which became clearly discernible by the time the mode of the first group had advanced to about 0.90 mm. In the lower three panels of the figure (stages D–F), it may be seen that ova constituting the second

group continued to increase in size as the first group advanced to maturity. Thus, it appears that at least two groups of ova develop within a single spawning season, but the question arises as to whether the second matures and is spawned in the same season.

Because so few females in a ripe or near-ripe condition were available in the fishable population, there was no way of determining the fate of the secondary group of ova. A few specimens were collected which had high ovary indices and contained intact, ripe remnants in the lumina. These ovaries were turgid, contained numerous near-ripe ova, and appeared to be ready to spawn in the near future. Recently spent ovaries contained relatively few intermediate and maturing ova in the follicular tissues. Furthermore, the yolk granules of intermediate and maturing ova which remained in the follicular tissues of recently spent ovaries collected in spring were speckled, and the ova were dark, distorted, and appeared to be disintegrating. Yolk granules of the numerous developing ova in specimens taken in late summer and early autumn were globular, and the ova were spherical (cf. Intermediate ova, p. 259). Finally, the absence of remnants within follicular tissues in latent ovaries of sexually mature fish during the summer indicates that residual intermediate and maturing ova are not carried over to the following spawning season. From available evidence, it is impossible to decide conclusively the frequency of spawning by individual fish. We favor, however, the hypothesis of the maturation and fractional spawning of more than one group of ova during a single season.

NUMBER OF OVA SPAWNED

The number of ova assumed to be extruded from the most advanced group of ovarian ova was estimated for 38 fish which ranged in length from 203 to 346 mm. A sample from each ovary specimen was weighed to the nearest 0.001 g. Ova were teased from the follicular tissues and those classified as maturing (p. 259) were counted. The number of maturing ova in both ovaries was estimated by multiplying the number in the sample by the ratio of the weight of both ovaries to the weight of the sample (table 8). The number of ova per female varied widely, but increased with length. Individual estimates ranged from 38,000 to 631,000 ova. A plot of the estimated number

TABLE 8.—Estimated number of ova in the most advanced group in ovaries of fish of different sizes

Fork length	Fish weight	Weight of both ovaries	Sample weight	Number of maturing ova in sample	Estimated number of maturing ova in pair of ovaries
Millimeters	Grams	Grams	Gram		Thousands
203	167	7.1	0.179	1,266	50
204	157	7.3	.178	1,439	59
208	174	6.9	.159	1,036	45
211	174	6.8	.174	1,292	50
216	184	5.6	.189	1,295	38
221	221	12.3	.205	1,525	92
228	234	15.2	.182	1,348	113
240	269	14.5	.237	1,161	71
243	281	19.4	.283	1,642	113
244	280	10.3	.232	1,299	58
246	290	15.5	.222	1,261	88
247	283	7.3	.278	1,852	49
251	295	25.4	.209	1,113	135
258	327	23.6	.390	1,967	160
259	322	14.2	.217	1,715	112
267	346	32.6	.196	1,383	230
270	368	26.3	.165	1,278	204
274	443	41.9	.216	1,135	220
278	368	27.6	.279	1,788	177
278	446	45.1	.113	793	316
285	441	35.2	.412	2,753	235
285	413	37.1	.161	1,194	275
290	536	42.3	.292	2,005	390
299	572	39.9	.118	1,230	416
305	619	54.0	.194	1,485	413
309	661	44.8	.346	2,546	330
313	543	50.0	.189	921	244
313	579	41.1	.356	2,665	308
317	646	62.8	.142	977	432
317	651	46.6	.173	1,012	272
327	750	40.2	.167	1,208	291
328	637	55.4	.334	3,452	573
333	732	74.3	.102	594	433
336	771	68.9	.206	1,536	514
339	910	62.8	.183	1,071	368
343	848	89.0	.174	1,042	533
345	858	78.9	.194	1,551	631
346	786	81.5	.209	1,438	561

of ova on fish length (figure 8) gave a relation which is curvilinear.

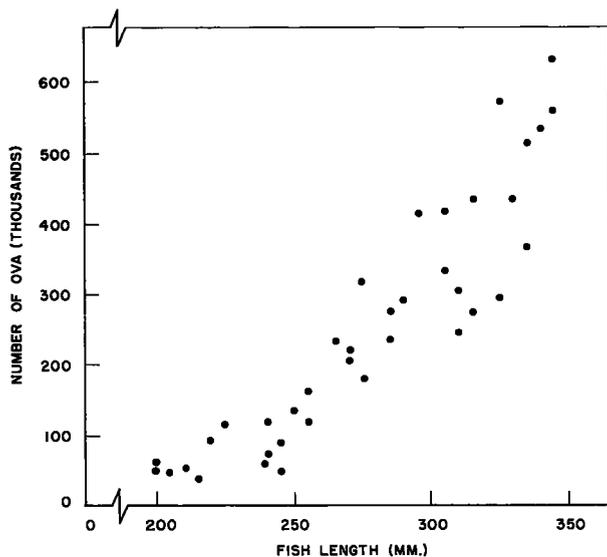


FIGURE 8.—Relation between fish length and the estimated number of maturing ova.

Suttkus and Sundararaj (1961) reported on the fecundity and reproduction of Gulf menhaden, *B. patronus*. This species reaches maturity younger and at a smaller size than *B. tyrannus*. The number of ova produced, for fish of comparable size, is greater in the former species.

DISCUSSION

The seasonal variations in spawning in different areas of the coast may be explained by seasonal variations in the distribution of age and size classes of fish. June (1961), June and Nicholson (1964), and June and Reintjes (1959 and 1960) have shown that during the summer, the purse seine catch in the North Atlantic Area is composed mostly of age-3 and older fish, whereas fish of ages 1 and 2 dominate the catches in other areas. Since all females were found to be sexually mature at age 3, it would be expected that any spawning during the summer would be limited to the North Atlantic Area. Based on the occurrence of dominant length-age groups, June and Nicholson (1964) postulated a cyclic north-south migration of at least a portion of the population north of Chesapeake Bay—southward in autumn and northward in spring. Such a migration pattern would account for the occurrence of the older, sexually mature fish (many of which are in spawning condition) in the Middle Atlantic Area in September and October and again in March, April, and May, and probably accounts for the appearance of sexually mature fish (most of which are in spawning condition, p. 259) in the South Atlantic Area in November and December. Apparently not all fish migrate southward in autumn, however, since numerous inactive and recently spent females occurred in the catches in the North and Middle Atlantic Areas in September and October (table 5). They also are known to have occurred in the latter area during the winter, yet very few inactive, and no spent females appeared in the catches in the South Atlantic Area in November and December. Although the time required for sexually inactive ovaries to become active is unknown, it seems unlikely that maturation would occur over a period of about 2 weeks—the time interval between the disappearance of schools from surface waters in the Middle Atlantic Area and the reappearance of schools off the North Carolina coast. The almost complete absence of inactive females among the older, sexually mature fish

which appear in large schools in the latter area in November and December would suggest that the southward migration in autumn is primarily a spawning migration.

The hypothesis of a cyclic north-south migration of spawning fish would explain the observed variations in the time and space distribution of sexually active fish, eggs, and larvae. According to this hypothesis, spawning during the summer is restricted to the North Atlantic Area where older, sexually mature fish are largely confined. Beginning in September, there is an increase in the number of active fish followed by a general movement southward during which spawning occurs. These migrating schools are joined by other sexually active fish in the Middle Atlantic Area, and spawning continues as the schools move southward. In some seasons, these large schools of sexually active fish are followed as far southward as Delaware and northern Maryland by the purse seine fleet, and the appearance of eggs and larvae in the coastal waters of Delaware and Virginia (p. 265) coincides with the occurrence of such schools in these latitudes. Eventually the schools disappear from the surface waters (sometime in late October), but reappear several weeks later off the coast of North Carolina. Spawning occurs in the South Atlantic Area through the winter. Some individuals continue spawning during the return northward migration in spring as both sexually active and recently spent specimens appear along with sexually inactive specimens in pound net catches along the Middle Atlantic coast in March, April, and May. The older, sexually mature fish finally return to the summer grounds north of Long Island, N.Y. Thus, it is possible that those fish which were sexually inactive in the previous autumn, and which may not have joined in the southward migration, spawn in northern waters during the summer.

The above hypothesis also could account for the variation in meristic characters of juvenile Atlantic menhaden inhabiting estuarine nurseries reported by June (1958) and Sutherland (1963). These authors found that juveniles of five successive year classes were separable into two groups or subpopulations, one occurring north and the other south of Long Island. They also showed that variations in meristic numbers were associated with seasonal differences in water temperatures on the spawning grounds, and Sutherland con-

cluded that the relative stability of the meristic pattern suggested genetic origin. Our data suggest that the fish which spawn in waters north of Long Island in summer constitute a distinct group, which becomes segregated from that which migrates southward and spawns in the South Atlantic Area in winter. If this is indeed the case, it is likely that differences in the physiological condition of individuals, hence differences in the time of year at which their gonads develop to spawning, have a genetic basis. It also would be expected that some overlap in spawning would occur in the vicinity of Long Island where individuals of these two spawning groups apparently segregate in autumn and intermingle again in the following spring during the return migration into northern waters.

Variations in fecundity of females of comparable size (fig. 8) and age suggest that differences in the size and age at attainment of sexual maturity (p. 266) should be explored further, since these may yield further insight into the question of genetic differences in physiology between these two apparent spawning groups. Along these lines, further study of spawning fish in Florida waters is necessary to determine if they differ from those farther northward.

SUMMARY

Ovaries of Atlantic menhaden (*Brevoortia tyrannus*) were obtained during routine sampling of catches at seven ports along the Atlantic Coast of the United States during four fishing seasons, 1956-59. Ovaries were weighed and examined at the time of sampling. Some were preserved for further laboratory study.

Preliminary studies indicated that diameter-frequency distributions of ova sampled in different parts of a pair of ovaries were similar. One or more developmental groups of ova were distinguishable within the ovaries, depending on the nearness of spawning; these were immature, intermediate, maturing, and ripe. Plots of ova-diameter frequency distributions showed the simultaneous development of more than one group of ova within the ovaries of an individual fish.

A relation, called the "ovary index," was calculated between fish length and the weight of both ovaries and compared to the medians of the diameter frequency distributions of the most mature group of ova in 1,030 specimens. Although

the ovary index did not completely correct for the effect of fish length on the weight of ovaries containing ova in the same stage of development, it could be used reasonably well to distinguish inactive ovaries from those which were advancing toward spawning.

Time of spawning in four geographical areas was inferred from ovary indices. Spawning apparently occurred in the North Atlantic Area from May to September; in the Middle Atlantic, from March through May and again in September and October; and in the South Atlantic, from October through March. There was little evidence that spawning occurred inside Chesapeake Bay.

Few females were found to be mature at age 1 (180–280 mm., fork length); most were mature at age 2 (195–320 mm., fork length); and all were mature at age 3 (over 200 mm. fork length).

Simultaneous maturation of two groups of ova within the ovaries suggests that an individual female may spawn more than one group of ova during a single season; however, no conclusions were reached since there was no way of determining the fate of the secondary group. Extrusion of ova appears to be fractional.

Assuming that ova comprising the most advanced group are extruded, estimates of the number of ova spawned during spawning season, ranged from 38,000 to 631,000, depending on the length of the fish.

Variation in times and places of spawning and attainment of first maturity appear to be related to the differential distribution of age and size groups, seasonal migrations, and population structure.

LITERATURE CITED

- BROCK, VERNON E.
1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pacific Science, vol. 8, No. 1, pp. 94–104.
- CLARK, FRANCES N.
1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. California Division of Fish and Game, Fish Bulletin No. 42, 49 pp.
- FARRAN, G. P.
1938. On the size and number of the ova of Irish herrings. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 13, No. 1, pp. 91–100.
- HERMAN, SIDNEY S.
1959. The planktonic fish eggs and larvae of Narragansett Bay. Appendix I. U.S. Fish and Wildlife Service, Sustaining data summary on fishery resources in relation to the hurricane damage control program for Narragansett Bay and vicinity Rhode Island and Massachusetts. (May 1959) Boston, Mass., 24 pp.
- HILDEBRAND, SAMUEL F., AND WILLIAM C. SCHROEDER.
1927. The fishes of Chesapeake Bay. Bulletin of the U.S. Bureau of Fisheries, vol. 43, part 1, (1928) 366 pp.
- JUNE, FRED C.
1953. Spawning of yellowfin tuna in Hawaiian waters. U.S. Fish and Wildlife Service, Fishery Bulletin 77, vol. 54, pp. 47–64.
1958. Variation in meristic characters of young Atlantic menhaden, *Brevoortia tyrannus*. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 143, part 2, No. 4, pp. 26–35.
1961. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1957; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 373, 39 pp.
- JUNE, FRED C., AND WILLIAM R. NICHOLSON.
1964. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1958; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 446, 40 pp.
- JUNE, FRED C., AND JOHN W. REINTJES.
1959. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1952–55; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 317, 65 pp.
1960. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1956; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 336, 38 pp.
- JUNE, FRED C., AND CHARLES M. ROITHMAYR.
1960. Determining age of Atlantic menhaden from their scales. U.S. Fish and Wildlife Service, Fishery Bulletin 171, vol. 60, pp. 323–342.
- KUNTZ, ALBERT, AND LEWIS RADCLIFFE.
1917. Notes on the embryology and larval development of twelve teleostean fishes. Bulletin of the U.S. Bureau of Fisheries, vol. 35, for 1915–16, pp. 87–134.
- MASSMANN, WILLIAM H., JOHN J. NORCROSS, AND EDWIN B. JOSEPH.
1962. Atlantic menhaden larvae in Virginia coastal waters. Chesapeake Science, vol. 3, No. 1, pp. 42–45.

- MASTERMAN, A. T.
1913a. Report on investigations upon the salmon with special reference to age-determination by study of scales. Board of Agriculture and Fisheries. Fishery Investigations, series 1, vol. 1, No. 1, pp. 3-111.
- 1913b. Report on investigations upon the smelt (*Osmerus eperlanus*) with special reference to age-determination by study of scales and its bearing upon sexual maturity. Board of Agriculture and Fisheries. Fishery Investigations, series 1, vol. 1, No. 2, pp. 113-126.
- McHUGH, J. L.
1960. The pound-net fishery in Virginia. Part 2. Species composition of landings reported as menhaden. U.S. Fish and Wildlife Service, Commercial Fisheries Review, vol. 22, No. 2 (February), pp. 1-16.
- McHUGH, J. L., R. T. OGLESBY, AND A. L. PACHECO.
1959. Length, weight, and age composition of the menhaden catch in Virginia waters. Limnology and Oceanography, vol. 4, No. 2, pp. 145-162.
- OLSEN, YNGVE H., AND DANIEL MERRIMAN.
1946. Studies on the marine resources of southern New England. The biology and economic importance of the ocean pout, *Macrozoarces americanus* (Bloch and Schneider). Bulletin of the Bingham Oceanographic Collection, vol. 9, art. 4, 184 pp.
- PEARSON, JOHN C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Fish and Wildlife Service, Fishery Bulletin 36, vol. 50, pp. 79-102.
- PERLMUTTER, ALFRED.
1939. An ecological survey of young fish and eggs identified from tow-net collections. In A biological survey of the salt waters of Long Island, 1938, part 2, pp. 11-71. New York State Conservation Department, supplemental to 28th annual report, 1938.
- REINTJES, JOHN W.
1961. Menhaden eggs and larvae from M/V *Theodore N. Gill* cruises, South Atlantic Coast of the United States, 1953-54. U.S. Fish and Wildlife Service. Special Scientific Report—Fisheries No. 393, 7 pp.
- RICHARDS, SARAH W.
1959. Oceanography of Long Island Sound. VI. Pelagic fish eggs and larvae of Long Island Sound. Bulletin of the Bingham Oceanographic Collection, vol. 17, art. 1, pp. 95-124.
- SCHAEFER, MILNER B., AND CRAIG J. ORANGE.
1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the Eastern Pacific Ocean, by examination of gonads. Bulletin of the Inter-American Tropical Tuna Commission, vol. 1, No. 6, pp. 281-349.
- SUTTKUS, ROYAL D., AND BANGALORE I. SUNDARARAJ.
1961. Fecundity and reproduction in the largescale menhaden, *Brevoortia patronus* Goode. Tulane Studies in Zoology, vol. 8, No. 6, pp. 177-182.
- SUTHERLAND, DOYLE F.
1963. Variation in vertebral numbers of juvenile Atlantic menhaden. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 435, 21 pp.
- THOMPSON, WILLIAM F.
1915. A preliminary report on the life-history of the halibut. Report of the British Columbia Commissioner of Fisheries for 1914, pp. N76-N99.
- WESTMAN, JAMES R., AND ROSS F. NIGRELLI.
1955. Preliminary studies of menhaden and their mass mortalities in Long Island and New Jersey waters. New York Fish and Game Journal, vol. 2, No. 2, pp. 142-153.
- WHEATLAND, SARAH B.
1956. Oceanography of Long Island Sound, 1952-1954. VII. Pelagic fish eggs and larvae. Bulletin of the Bingham Oceanographic Collection, vol. 15, pp. 234-314.
- YUEN, HEENY S. H.
1955. Maturity and fecundity of bigeye tuna in the Pacific. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 150, 30 pp.

AN EXPERIMENTAL EVALUATION OF THE C¹⁴ METHOD FOR MEASURING PHYTOPLANKTON PRODUCTION, USING CULTURES OF *DUNALIELLA PRIMOLECTA* BUTCHER¹

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ABSTRACT

The photosynthetic uptake of radioactive carbon dioxide was compared with net and gross O₂ production, pH changes, and growth in cultures of *Dunaliella primolecta* Butcher. During the logarithmic growth phase of such cultures, C¹⁴ uptake agreed well with net O₂ production and did not differ greatly from gross O₂ production. The logarithmic growth rate of mass cultures (measured by increases in cell concentration, optical density, dry weight, organic carbon and nitrogen) was generally less than a similar logarithmic rate calculated from organic carbon analyses and measurements of photosynthesis in bottles immersed in the culture. This difference was attributed to greater illuminances in the bottles than in the cultures as a whole. In one experiment, when illumination conditions were similar, the two rates were equivalent.

It is commonly accepted that in the open sea the production of all forms of animal life is ultimately dependent upon the production of organic material by phytoplankton. The phytoplankton produce organic material in excess of their metabolic needs, and this excess or "net production" is then available to other forms of life. This excess consists mainly of protein, carbohydrate, and lipid fractions. This material forms the bulk of the food available for incorporation into the cells and tissues of the zooplankton and larval fishes (secondary producers), and also provides an energy source for their activities. Ideally, to study the dynamic aspects of the transfer of food from phytoplankton to secondary producers, it would be desirable to measure changes in the concentra-

When cultures were incipiently nitrogen-deficient, C¹⁴ uptake was similar to net O₂ production and growth was equivalent to photosynthesis. In one experiment, when nitrogen deficiency was extreme, C¹⁴ uptake was larger than net O₂ production, and agreed more closely with gross O₂ production. In another such experiment, C¹⁴ uptake agreed with net O₂ production. Nitrogen deficiency increased the intracellular C/N ratio, and starch became a major storage product. In one experiment, C¹⁴ uptake in an incipiently phosphorus-deficient culture was intermediate between net and gross O₂ evolution; in a similar experiment, C¹⁴ uptake was less than net O₂ production. C¹⁴ uptake in healthy cultures was equivalent to the uptake of CO₂ as measured by pH changes. These results are discussed in relation to other findings and to oceanographic applications.

tions of protein, carbohydrate, and lipid in the sea, or at least, to measure changes in total phytoplankton biomass. Practically, such measurements are very difficult, because present methods are either quite time-consuming or are too insensitive to measure the small changes that occur in the sea.

Since the three major components of phytoplankton all contain carbon, the development of the C¹⁴ method for measuring the production of organic carbon (Steemann Nielsen, 1952), ap-

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peared to provide a sensitive and easy way of measuring changes in the food supply, if the C^{14} method really measures the excess or net production. Intensive investigations of the spatial and temporal variations of C^{14} assimilation that are now in progress should therefore contribute to our understanding of food production in the oceans, and may provide information of practical importance to fishermen. The quantitative determination of phytoplankton production in the sea may also allow a more precise assessment of the effects of various factors on production and of the manner in which it is controlled. Thus, it is rather important that this method be subjected to a detailed evaluation.

To determine phytoplankton photosynthesis with C^{14} , a sample of water containing phytoplankton is placed in a clear, glass-stoppered bottle to which a standard amount of $Na_2C^{14}O_3$ is added as a tracer. The sample is then incubated for a standard length of time either in situ, under known conditions of illumination and temperature, or under conditions which simulate field conditions. Following incubation, the algae are collected on a membrane filter and dried carefully. Their assimilated C^{14} is then counted. The amount of carbon assimilated during the photosynthetic period is calculated from the measured assimilation of tracer carbon, the amount of tracer added, and the total CO_2 content of the water (cf. formula on page 12). The methodology of using C^{14} has been discussed by Steemann Nielsen (1952), Ryther (1956), and Doty and Oguri (1958); and has been reviewed in great detail by Strickland (1960). Thomas (1963) reviewed the various physiological factors which affect the measurement.

So far, the C^{14} method has been tested mainly by comparison of C^{14} uptake with O_2 evolution (Ryther, 1954; Ryther and Vaccaro, 1954; Ryther, 1956; Steemann Nielsen and Al Kholy, 1956; Ichimura and Saijo, 1958). One comparison of the C^{14} method with increases in algal biomass (growth) has been made (McAllister, Parsons, Stephens, and Strickland, 1961). This comparison utilized a natural population enclosed in a plastic bag.

Growth is a net process; for the biomass of algae to increase, material which is produced must be conserved in excess of respiratory requirements. Herbivores utilize the algal material directly for

food. Algal growth measurements provide a direct assay of the increase in available food. Thus, ideally, the C^{14} method should be compared with growth.

The present paper reports comparisons of C^{14} measurements with increases of phytoplankton solids and of organic carbon in rapidly growing cultures of *Dunaliella primolecta* Butcher and also in incipiently nitrogen- and phosphorus-deficient cultures. Further comparisons of O_2 evolution and C^{14} uptake under varying conditions of intracellular nutrient status are presented. CO_2 assimilation by healthy cultures, as measured by pH changes, is also compared with C^{14} uptake.

MATERIALS AND METHODS ²

THE ALGA

The organism used in these studies was *D. primolecta* Butcher, which was obtained from Beatrice Sweeney of the Scripps Institution of Oceanography. According to Luigi Provasoli (personal communication) and to Butcher (1959), this alga was originally isolated by Gross, and is now number 81 in the Culture Collection of the Marine Biological Association at Plymouth, England. According to Robert Guillard (personal communication), *D. euchlora*, which was used by Ryther (1954, 1956), is a separate species.

CULTURE PROCEDURES

Stock cultures were maintained on agar slants made with a medium similar to that of Sweeney and Hastings (1957), which consisted of 75 percent sea water, 0.1 percent Na_3EDTA ,³ 2 percent soil extract, 2,000 $\mu g.$ -at. $KNO_3/1.$, and 200 $\mu g.$ -at. $K_2HPO_4/1.$ Subcultures used in each experiment consisted of 50-ml. liquid cultures of the same medium. Stock cultures and the liquid subcultures were grown routinely at 500 foot-candles (ft.-c.) and 21° C. Culture methods used in the individual experiments are described below.

Growth of cultures in most experiments was measured by cell counting. A 10-ml. aliquot of the suspension was first treated with a few drops of Lugol's iodine solution to kill and stain the cells. Subsamples from this 10-ml. aliquot were then placed in the chambers of a hemocytometer, and the cells were counted until a total of at least

² Reference to a company or product throughout this manuscript does not imply approval by the U.S. Bureau of Commercial Fisheries.

³ Na_3EDTA is the sodium salt of ethylene diamine tetraacetic acid.

200 cells had been counted. The standard error of the mean count of these subsamples ranged from ± 2 to ± 33 percent. The average standard error was ± 13 percent.

In some experiments, growth was also measured by determinations of dry weight and optical density. For dry-weight determinations, aliquots of the cell suspension were filtered through tared HA Millipore® filters (pore size 0.45μ), which were dried at room temperature in a vacuum desiccator. Optical density determinations were made at 600 and 650 $m\mu$ with a Bausch and Lomb Spectronic 20® Spectrophotometer and 1-inch absorption tubes.

Growth is expressed in terms of logarithmic growth rate constants using the formula (Krauss and Thomas, 1954):

$$K_2 = \frac{\log_2 C_2 - \log_2 C_1}{t_2 - t_1}$$

where C_1 and C_2 are cell numbers, dry weights, optical densities, or other growth measurements at times t_1 and t_2 . The reciprocal of K_2 is the time taken for the population to double and is designated the "generation time" in this paper.

CARBON¹⁴ METHODS

The C¹⁴ method used is similar to that described by Steemann Nielsen (1952), Ryther (1956), and others. The radioactive solution was prepared by acidifying BaC¹⁴O₃ in vacuo and absorbing the resulting C¹⁴O₂ in NaOH solution. This solution was then diluted, and the pH was adjusted to pH 9.5–10.0. The diluted solution contained 1 $\mu c./ml.$ and was packaged in ampoules, which were then sterilized in the autoclave.

The solution was standardized by precipitating the C¹⁴ as BaC¹⁴O₃ and filtering portions of the resulting suspension through HA Millipore® filters (pore size 0.45μ). With the standardization procedure described by Steemann Nielsen (1952), it was difficult to obtain reproducible radioactivities at low thickness of precipitate ($< 0.5 \text{ mg./cm.}^2$), although thicker preparations were quite reproducible. Therefore, the following modifications were introduced to make thin samples more reproducible: 1) the amount of carrier sodium carbonate suggested by Steemann Nielsen was reduced by one-half; 2) the filters were washed with 0.001 molar BaCl₂ to avoid losses of precipitate; 3) the BaC¹⁴O₃ suspension was stirred with a magnetic

stirrer during precipitation and sampling; and 4) the filter was shaken during filtration to distribute the precipitate uniformly on the surface of the filter.

Self-absorption curves obtained using these modifications are shown in figure 1. For window-

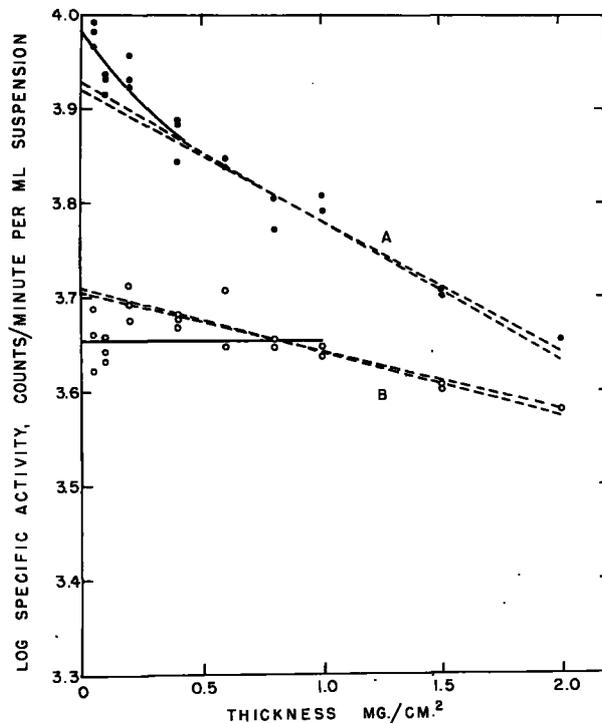


FIGURE 1.—BaC¹⁴O₃ self-absorption curves: (A) Samples counted with a windowless flow chamber; and (B) samples counted with a chamber fitted with a Mylar window of approximately 1 mg./cm.^2 thickness. Broken lines show the extrapolation to zero thickness using thick samples ($\geq 0.4 \text{ mg./cm.}^2$ in curve A; $\geq 0.2 \text{ mg./cm.}^2$ in curve B). Solid lines show the empirical extrapolations that were actually used to determine zero-thickness activity.

less counting, the values were empirically extrapolated to zero thickness (solid line in curve A, fig. 1) and the error of this value was approximately ± 5 percent. Thicknesses of BaC¹⁴O₃ as low as 0.05 mg./cm.^2 were used in the extrapolation. Jitts and Scott (1961) have criticized on various grounds our extrapolation from thicknesses below 0.4 mg./cm.^2 . Though their criticisms may be valid, an empirical extrapolation to zero thickness activity using low thicknesses ($< 0.4 \text{ mg./cm.}^2$) results in a value that is about 13 percent higher than that found by using thick samples alone (dashed lines in curve A, fig. 1). Their

liquid scintillation method results in a zero-thickness value that is 17–26 percent higher than that obtained by extrapolation from thick pads. Thus, our empirical method of extrapolation gives zero-thickness activities which do not differ greatly from the liquid scintillation values obtained by Jitts and Scott.

Using a counting chamber fitted with a Mylar window, we found a slight decrease in specific activity (cpm/ml.) as the thickness approached zero (open circles, fig. 1). This decrease was observed in three separate standardizations and may be due to a decrease in "self-scattering" of the beta radiation, as suggested by Steinberg and Udenfriend (1957). Since this effect does not occur when the same pads are counted with a windowless chamber, it is probably related to scattering of those beta particles having energies great enough to allow them to pass the window. Despite the downward trend of specific activity at very low thicknesses, at thicknesses below 1 mg./cm.² these specific activities do not differ significantly from each other. Thus, a mean of specific activities obtained at thicknesses below 1 mg./cm.² was taken to be that added to the experimental bottles. This mean had a standard error of ± 4 percent and is shown by the solid line of curve B, figure 1. It was about 11 percent less than that obtained by extrapolation from thick samples (dashed lines in curve B).

For C¹⁴ measurements of photosynthesis in laboratory cultures, 50-ml. portions of the cell suspension were placed in 67-ml. bottles. In some experiments where the cell suspension was very dense, 10-ml. portions of the suspension were diluted to 50 ml. with sterile sea water. The bottles were then inoculated with 1 ml. of C¹⁴ solution. They were prepared in duplicate and incubated for periods not exceeding 6 hours (generally 1–2 hours). Darkened bottles and illuminated bottles were always incubated together. Bottles were darkened by wrapping them with aluminum foil.

Following incubation, the contents of the bottles were filtered through membrane filters (pore size 0.45 μ), and the filters were washed four times with 10- to 20-ml. portions of nonradioactive sea water. The filters were then dried in a vacuum desiccator at room temperature.

The radioactivity on the filters was measured with a proportional flow counter using either a

windowless chamber or a similar chamber having a Mylar window interposed between the center wire and the filter. Using the windowless chamber, we observed a progressive decrease in sample counting rates. This decrease in the counting rate was avoided by counting the sample for 1 minute, removing it from the chamber, and counting it again at least one-half hour later. This decrease was apparently due to electrostatic charging of the nonconducting filter pads and was a troublesome problem in the dry atmosphere of California. Similar difficulties in counting samples on membrane filters in a windowless chamber were reported by Setter, Hagee, and Straub (1958). The Mylar window completely prevented this charge effect, and reduced the count of a standard C¹⁴ source by only one-half.

The determinations of algal activity were corrected to zero-thickness by means of empirical algal self-absorption curves. Different volumes of suspensions of radioactive *Dunaliella* cells were filtered to obtain varying thicknesses of algae. These samples were then counted, and the specific activity plotted against thickness (fig. 2). With

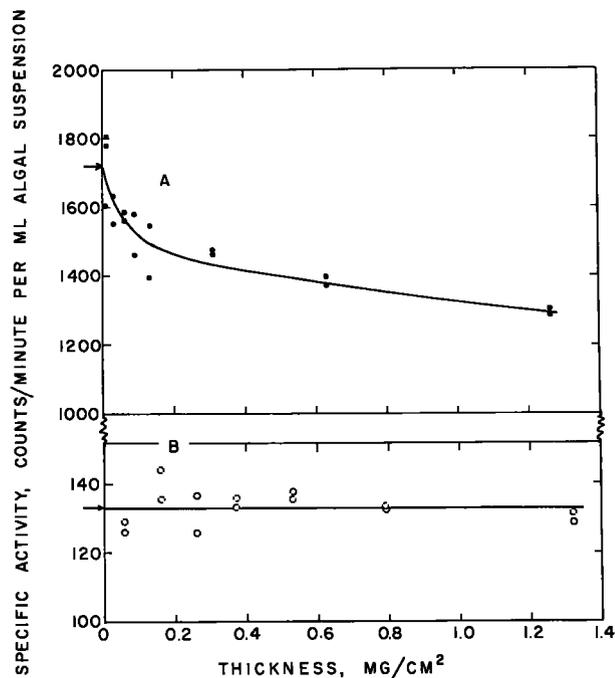


FIGURE 2.—Algal self-absorption curves: (A) Samples counted with a windowless flow chamber; (B) samples counted with a chamber fitted with a Mylar window of approximately 1 mg./cm.² thickness. Solid lines show the empirical extrapolations to zero-thickness activity.

the windowless chamber (curve A), considerable difficulty was experienced in extrapolating from very thin pads (<0.2 mg./cm.²) to zero thickness, and the estimated error of corrections made from curve A is ± 6 percent. With the Mylar window, as is shown in curve B, self-absorption corrections appeared to be unnecessary at thicknesses below 1.3 mg./cm.² The standard deviation of the mean of all values for specific activity was ± 3 percent. In the experiments reported below, algal thicknesses were never this large.

The radioactivity used in calculating production by the C¹⁴ method was the mean value obtained by filtering duplicate light bottles minus the mean value from duplicate darkened bottles. The overall precision of the incubation, filtration, and counting procedure was determined by incubating 10 replicate cultures under uniform conditions of illumination and temperature. The standard error of the mean radioactivity taken up in these bottles was ± 7 percent.

Total CO₂ in the experimental C¹⁴ bottles was measured by the excess acid method of Anderson and Robinson (1946), and the equations and factors given by Harvey (1955). A pH meter having a reproducibility of ± 0.02 pH unit was used for this determination. An error of ± 0.02 units in measuring the final pH after the addition of standard acid results in an error in the total CO₂ concentration of approximately ± 6 percent.

Production was calculated from the following equation:

$$\text{Photosynthesis} = \frac{\text{cpm (light)} - \text{cpm (dark)}}{\text{cpm added}} \\ \times 1.06 \times \text{total CO}_2/\text{time}$$

The factor 1.06 corrected for the isotope discrimination effect (Steemann Nielsen, 1952). No corrections were made for the respiration of labeled carbon during the incubation nor for excretion of labeled organic matter.

The total experimental error of the C¹⁴ method in our hands was estimated by pooling all the various sources of error. This was accomplished by taking the square root of the sum of the squares of each error. For windowless counting, the error in the amount of activity added was ± 5 percent; the error for incubation, filtration, and counting of activity taken up in replicate bottles was ± 7 percent for both light and dark bottles; the error for algal self-absorption was ± 6 percent; and the

error in total CO₂ was ± 6 percent. The pooled total error was thus ± 14 percent. With Mylar window counting, some of these individual errors were decreased and the pooled total error was ± 13 percent. The windowless counter was used in experiments 1, 2, 4, and 5; the counting chamber fitted with the Mylar window was used in experiments 3, 6, 7, 8, and 9.

OXYGEN METHODS

Oxygen production was measured by filling 67-ml. bottles with the cell suspension. The initial amount of oxygen was measured in one pair of bottles, another pair was darkened with aluminum foil, and the third pair was illuminated. Light and dark bottles were incubated under the same conditions as the C¹⁴ bottles for periods not exceeding 6 hours. Dissolved oxygen was measured with the Winkler technique using 0.01 normal sodium thiosulfate for the final titration.

A test of the precision of the technique in our hands was made by filling 22 such bottles, measuring the oxygen content in 6 initial bottles, and incubating 6 dark bottles and 10 light bottles. The determinations and their standard errors were as follows: initial oxygen, 5.35 ± 0.03 ml. O₂/l.; dark bottles, 5.08 ± 0.07 ml. O₂/l.; light bottles, 11.51 ± 0.42 ml. O₂/l. The relative errors of each measurement are small, ± 1 percent for the initial and dark bottles and ± 4 percent for the light bottles. This test showed the relative experimental errors that might be expected when photosynthesis was intense, i.e., using cultures that were still in the logarithmic period of growth and incubating the bottles at high illuminances. Since the amounts of oxygen produced or consumed varied with the conditions prevailing during each experiment, the mean of duplicate bottles was used to determine production and the experimental error of each measurement was determined from the deviation from this mean.

The production of oxygen was converted to carbon production by use of a photosynthetic quotient (O₂/CO₂) of 1.25 as suggested by Ryther (1956). The problem of choosing a correct quotient has been reviewed by Ryther. Under the conditions of our experiments—cells grown with nitrate as an N-source, cells grown at high illuminances, N-deficient cells, etc.—the correct quotient probably lies within ± 12 percent of this value. This error is pooled with the experimental

error for each oxygen measurement. Pooling of these errors was done in the same manner as with the C¹⁴ measurements.

ORGANIC CARBON DETERMINATIONS

In experiments 1 and 2, the method of Kay (1954) was used for determining organic carbon in aliquots of the culture suspension. While the combustion mixture, glassware, and the train were similar to those of Kay, absorption of the resulting CO₂ was carried out in the sidearm of a 125-ml. Erlenmeyer flask containing the Ba(OH)₂ absorbing solution. This modification was suggested by George Bien of the Scripps Institution of Oceanography. Our mean recovery of 0.5–2.0 mg. of carbon in the form of glucose, methionine, or tryptophane by this method was 98±8 percent. Similar amounts of algal carbon were measured.

In experiment 3, a much less complex method (Strickland and Parsons, 1960) was used to determine algal carbon. Aliquots of the culture suspension containing 1–2 mg. of carbon were filtered on fiber glass filter papers covered with 40 mg. of MgCO₃ powder. The filters were then frozen until the analyses could be done. The filters were placed in 30-ml. beakers, and 1 ml. concentrated phosphoric acid was added, followed by 1 ml. of distilled water. The beakers were heated in a boiling water bath for 30 minutes to remove residual chloride ion, and then were cooled. Two ml. distilled water was added, followed by 10 ml. of a dichromate-sulfuric acid oxidizing reagent. After the beakers were heated for an additional 60 minutes and cooled, the solution was decanted into 1-cm. absorption cells. The optical density was measured at 650 mμ against a distilled water blank which was carried through the whole procedure. This procedure differed slightly from that of Strickland and Parsons; instead of measuring the disappearance of dichromate ion (at 440 mμ), the procedure measured the formation of trivalent chromium ion (at 650 mμ). Furthermore, no final dilution was made; thus, a maximum extinction would be measured.

The method was calibrated by analyzing a set of glucose standards with each set of unknown samples. Recovery of tryptophane was 100 percent, but that of methionine was only 50 percent. Thus, some part of the algal carbon may not be completely determined by this method, but this fraction is believed to be quite small (Strickland

and Parsons, 1960). The extinction of the samples was corrected by subtracting a blank value obtained by taking a glass filter with MgCO₃ through the whole procedure.

The correspondence between the two methods for measuring organic carbon was tested by comparing values for the mean carbon per cell as measured by each method during the logarithmic phase of growth. In experiment 2, with Kay's method, the mean carbon per cell was 35.8 ± 6.7 μμg.C/cell; in experiment 3, with the Strickland and Parsons method, it was 41.2 ± 7.9 μμg.C/cell. The difference between these experiments was not statistically significant, and a mean value of 39.0 μμg.C/cell was used in converting cell concentration to organic carbon in experiments in which organic carbon was not measured directly.

ORGANIC NITROGEN DETERMINATIONS

In experiments 3 and 4, algal nitrogen was determined by a micro-Kjeldahl method. The cell sample was digested for four hours with a salicylic acid-sulfuric acid mixture (Ranker, 1927) and a copper sulfate-selenium catalyst. Ammonia in the digest was then distilled into boric acid solution and titrated with 0.01 normal sulfuric acid.

LIGHT MEASUREMENTS

Incident illumination was measured with an International Rectifier Corporation B2M selenium photocell. This cell had a spectral sensitivity of 300 to 760 mμ with a peak at 580 mμ. It was calibrated against a Weston foot-candle meter with the same type of light source (a bank of daylight fluorescent tubes) that was used for illuminating the cultures and photosynthetic bottles.

STATISTICAL METHODS

"Student's" parametric *t* test was used to determine statistically significant differences between means of various measurements (Snedecor, 1956). Where sample numbers were small, the nonparametric Mann-Whitney *U* test was also used (Siegel, 1956).

RESULTS

COMPARISONS OF C¹⁴ UPTAKE, O₂ EVOLUTION, AND GROWTH DURING THE LOGARITHMIC GROWTH PHASE

Experiment 1

In an initial experiment, several 1,500-ml. cultures of *Dunaliella* were grown at 21° C. and

550 ft.-c. in sea water enriched with 500 $\mu\text{g.}$ -at. $\text{NO}_3\text{N/l.}$, 50 $\mu\text{g.}$ -at. $\text{PO}_4\text{-P/l.}$ and 0.25 p.p.m. Fe (as the citrate, Rodhe, 1948). These cultures were not aerated or shaken. When the cultures were visibly green, aliquots were transferred to sterile 67-ml. bottles for C^{14} and O_2 measurements of photosynthesis. Photosynthesis bottles were incubated under the same conditions as the cells were grown. The remainder of the cell suspension was harvested for organic carbon and other growth measurements. The measurements were repeated on 4 successive days. At the end of this period, the pH had risen from 8.0 to 9.2 and growth had ceased.

Table 1 reports corresponding measurements of photosynthesis and increase in organic carbon during this 4-day period. During the first 3 days, C^{14} uptake agreed with net O_2 evolution within the experimental error. This was not the case on the fourth day when C^{14} uptake was probably limited by a decrease in the amount of free CO_2 in solution. The increase in organic carbon was calculated by dividing the difference in organic carbon by the time between samplings. Thus the increase was measured for a longer experimental period than the photosynthetic measurements. This increase was similar to photosynthesis, but was not exactly equivalent to it.

TABLE 1.—Comparative photosynthesis and organic carbon measurements of cultures of *Dunaliella primolecta*

[Experiment 1]

Days	C^{14} uptake	Net O_2 evolution	Gross O_2 evolution	Increase in organic carbon
	$\mu\text{g. C/l. hour}$	$\mu\text{g. C/l. hour}$	$\mu\text{g. C/l. hour}$	$\mu\text{g. C/l. hour}$
1	18.1 ± 2.5	23.4 ± 9.6	24.0 ± 9.6	
2	158 ± 22	182 ± 24	212 ± 26	
				208.0
3	124 ± 17	125 ± 15	187 ± 22	
				47.9
4	36.2 ± 5.1	72.2 ± 8.3	107 ± 20	

Visual observations of these flask cultures showed that they did not all grow to the same extent, i.e., that they were not exactly parallel cultures. Differences between flasks were probably the result of uneven illumination at subsaturating light intensities. In the next experiment a 40-liter mass culture was used instead of several flasks, so that many samples could be taken for an extended period of time from the same culture, and so that CO_2 limitations could be avoided by stirring and aeration.

EXPERIMENTAL EVALUATION OF C^{14} METHOD

Experiment 2

For this experiment, twenty 2-liter cultures, containing sea water enriched as in the previous experiment, were inoculated with *Dunaliella*. After 4 days of growth in the culture room at an illuminance of 550 ft.-c. and a temperature of 21°C. , during which the cell concentration increased from 3,000 cells/ml. to 118,000 cells/ml., the cell suspension from all twenty cultures was mixed in a plastic-lined aquarium. The aquarium culture was placed in a water bath thermostated at 26°C. and was illuminated from below at an illuminance of 800 ft.-c. The culture was stirred with a glass stirrer coupled to a motor mounted above the aquarium, and 5 percent CO_2 -in-air was supplied to the culture through a fritted glass dispersion tube at approximately 300 ml./min. The aquarium was covered with plate glass to reduce evaporation from the culture and contamination by laboratory dust.

After incubation for 24 hours, growth and photosynthesis measurements were started. Seven such sets of measurements were made during the following 48 hours. Photosynthesis bottles were incubated on the bottom of the aquarium and within the culture itself. During the 48-hour period, the pH of the culture was 7.06 to 7.30 and the total CO_2 concentration was 40.2 to 49.7 mg. $\text{CO}_2\text{-C/l.}$

Table 2 gives comparative C^{14} uptake and O_2 evolution measurements for this culture. During the first 29 hours of this experiment O_2 evolution (gross and net) generally agreed with C^{14} uptake within experimental error. At zero time, however, C^{14} uptake was somewhat lower than O_2 production. At 35 hours and 48 hours, both net and gross O_2 production were much less than C^{14} uptake. Photosynthesis was probably so intense that the water in the light bottles became supersaturated with O_2 to such an extent that the

TABLE 2.—Comparative photosynthesis measurements in a 40-liter mass culture of *Dunaliella primolecta*

[Experiment 2]

Time	C^{14} uptake	Net O_2 evolution	Gross O_2 evolution
	$\mu\text{g. C/l. hour}$	$\mu\text{g. C/l. hour}$	$\mu\text{g. C/l. hour}$
0	558 ± 78	789 ± 100	862 ± 100
5	847 ± 120	$1,090 \pm 130$	$1,200 \pm 150$
10	$1,440 \pm 200$	$1,500 \pm 190$	$1,630 \pm 210$
24	$2,160 \pm 300$	$1,820 \pm 220$	$1,980 \pm 240$
29	$2,160 \pm 300$	$1,930 \pm 230$	$2,170 \pm 260$
35	$3,610 \pm 510$	$2,600 \pm 240$	$2,330 \pm 280$
48	$5,200 \pm 730$	$1,820 \pm 240$	$2,220 \pm 280$

production could not be measured as a change in dissolved O₂.

The growth of this culture was measured by increases in cell concentration, dry weight, and organic carbon, and was plotted on a logarithmic scale (fig. 3). From these data, mean logarithmic

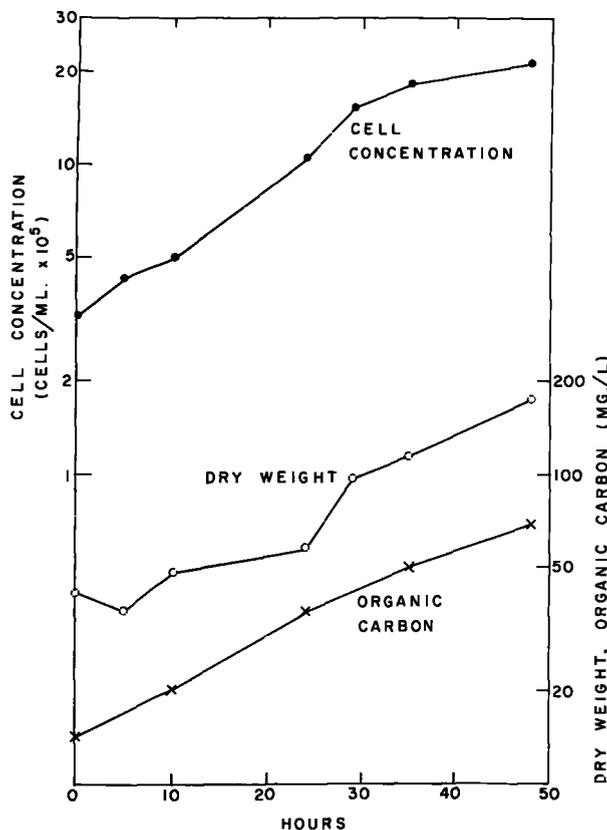


FIGURE 3.—Growth of a mass culture of *Dunaliella primolecta*.

growth constants (K_2) for each type of measurement were calculated by averaging K_2 values obtained between each sampling time.

In experiment 1, linear increases in organic carbon were compared with photosynthesis determinations. Obviously, a more meaningful comparison could be made if photosynthesis measurements were converted to logarithmic K_2 values. In the present experiment, the organic carbon measurements provided an initial concentration (C_1) from which photosynthetic K_2 values could be calculated. A sample calculation of a photosynthetic K_2 value is shown in table 3.

TABLE 3.—Sample calculation of a photosynthetic K_2 value¹

$$\begin{aligned}
 C_1 &= 20.5 \text{ mg.C/l.} & \text{Photosynthesis (C}^{14}\text{)} &= 1.4 \text{ mg.C/l./hour} \\
 C_2 &= 20.5 + 1.4 = 21.9 \text{ mg.C/l.} \\
 t_1 &= 0 \\
 t_2 &= 1 \\
 K_2 &= \frac{3.32 \log_{10} 21.9 - 3.32 \log_{10} 20.5}{1} \\
 &= \frac{3.32 (1.34044 - 1.31175)}{1} \\
 &= 0.09525 \text{ hours}^{-1} \\
 \text{Generation time} &= 1/0.09525 = 10.5 \text{ hours}
 \end{aligned}$$

¹ Data at 10-hour sampling time, experiment 2.

TABLE 4.—Mean K_2 values and generation times calculated from growth and photosynthesis measurements in a mass culture of *Dunaliella primolecta*

[Experiment 2]

Type of measurement	Mean K_2	Generation time
Growth:		
	Hours ⁻¹	Hours
Cell concentration.....	0.0613	16.3
Dry weight.....	.0492	20.3
Organic carbon concentration.....	.0470	21.3
Mean of growth values.....	.0532	18.8
Photosynthesis:		
C ¹⁴ uptake.....	.0866	11.5
Net O ₂ production.....	.0665	15.0
Mean of photosynthesis values.....	.0765	13.1

Table 4 gives mean K_2 values and generation times for the three types of growth measurements and two types of photosynthesis measurements in experiment 2. Statistical analysis showed that the K_2 values for the three types of growth measurements did not differ significantly; similarly K_2 values for C¹⁴ uptake did not differ significantly from those calculated from net O₂ measurements. Also given in table 4 are the overall means for growth and for photosynthesis. This mean growth rate was about 70 percent of the mean photosynthetic rate, and the difference was highly significant ($p < 0.01$). Thus, growth in the culture was significantly less than photosynthesis in bottles placed at the bottom of the culture.

Further comparisons of C¹⁴ uptake, O₂ evolution, and growth were made during the initial logarithmic phases of mass cultures in which growth was eventually limited by nitrogen deficiency (experiments 3 and 4) and by phosphorus deficiency (experiment 6).

EFFECTS OF NITROGEN DEFICIENCY

Experiment 3

This experiment was similar to the previous one, except that the amount of added nitrate was halved, so that growth would be limited by

nitrogen deficiency, and the light intensity incident to the bottom of the aquarium culture was increased to alleviate possible light limitations. Two-liter cultures were incubated for 2 days in the culture room at 550 ft.-c. and 21° C. Then they were mixed in the aquarium, supplied with air for 10 hours, and with 5 percent CO₂-in-air thereafter, at a rate of 300 ml./min. Growth and photosynthesis were measured every 10 hours for the next 100 hours and also at 120 hours. Growth was measured by determinations of cell concentration, organic carbon, organic nitrogen, dry weight, and optical density. C¹⁴ uptake and O₂ evolution were determined as in the previous experiment by placing the photosynthesis bottles in the bottom of the aquarium. At the beginning of these measurements, the pH of the culture was 8.68, at 10 hours it was 6.55, and then increased to a maximum of 7.82 at 120 hours. The total CO₂ concentration was 20.5 mg. CO₂-C/l. at the beginning of the experiment, and thereafter it was 33.1 to 37.9 mg. CO₂-C/l.

Photosynthesis and cell composition measurements are given in table 5; and growth is shown in figure 4. During the first 50 hours, growth in the culture proceeded in a logarithmic fashion

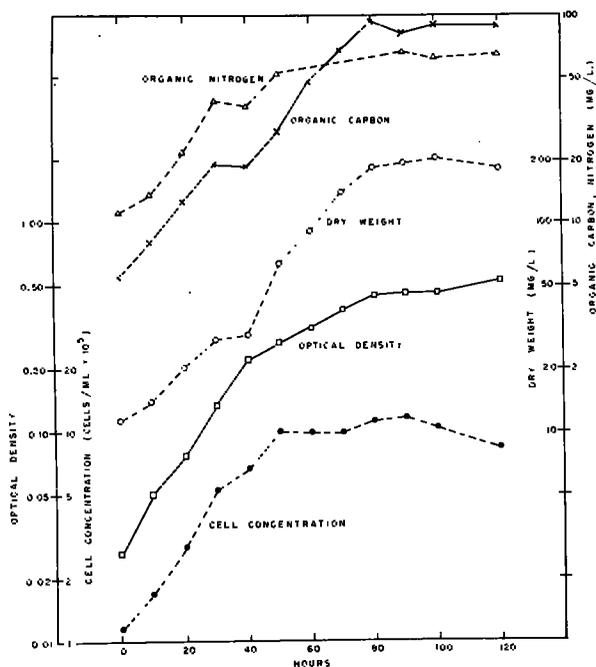


FIGURE 4.—Growth of a mass culture of *Dunaliella primolecta* containing a limiting concentration of nitrogen.

EXPERIMENTAL EVALUATION OF C¹⁴ METHOD

and the concentration of nitrogen in the cells was higher than that found in the last three measurements. The C/N ratio was lower. During this period of logarithmic growth, C¹⁴ uptake agreed well with both net and gross O₂ production.

Mean K₂ values and generation times for the first 50 hours were calculated from the five types of growth measurements (table 6); also reported are the K₂ values and generation times calculated from photosynthesis measurements (C¹⁴ uptake and net O₂ evolution) and the measured amounts of organic carbon (table 6). The mean growth rate is about 65 percent of the mean K₂ value calculated from photosynthesis measurements. This difference is statistically highly significant (p < 0.01). As in the previous experiment, growth in the culture was significantly less than photosynthesis in the bottles.

TABLE 5.—Comparative photosynthesis and cell composition measurements in a mass culture of *Dunaliella primolecta* [Experiment 3]

Time	Photosynthesis			Cell composition	
	C ¹⁴ uptake	Net O ₂ evolution	Gross O ₂ evolution	N	C/N ratio
<i>Hours</i>	<i>μg. C/l./hour</i>	<i>μg. C/l./hour</i>	<i>μg. C/l./hour</i>	<i>Percent</i>	<i>Atoms</i>
0.....	447±58	399±48	447±54	10.00	5.4
10.....	541±70	564±70	644±80	9.79	6.8
20.....	772±100	818±100	956±120	10.83	6.8
30.....	873±110	1,030±130	1,190±140	11.90	5.8
40.....	1,320±170	1,220±150	1,460±180	9.44	5.9
50.....	2,830±370	1,870±230	2,380±290	8.20	8.3
60.....	3,240±420	2,620±330	3,150±390		
70.....	2,160±280	2,290±270	2,840±340		
80.....	1,900±250	2,030±240	2,580±320		
90.....	1,550±200	1,580±190	2,210±260	3.36	14.4
100.....	1,220±160	1,390±180	1,700±240	3.05	16.8
120.....	338±44	429±51	880±110	3.64	15.4
123.....	(2,000 μg.-at./l. N added)				
144.....	1,350±180	1,200±160	1,670±220	9.48	6.2

TABLE 6.—Mean K₂ values and generation times during the logarithmic growth phase as calculated from growth and photosynthesis measurements in a mass culture of *Dunaliella primolecta*

[Experiment 3]		
Type of measurement	Mean K ₂	Generation time
Growth:	<i>Hours⁻¹</i>	<i>Hours</i>
Cell concentration.....	0.0629	15.9
Dry weight.....	.0490	20.4
Organic carbon concentration.....	.0583	17.1
Organic nitrogen concentration.....	.0430	23.3
Optical density.....	.0657	15.2
Mean of growth values.....	.0553	17.9
Photosynthesis:		
C ¹⁴ uptake.....	.0877	11.4
Net O ₂ production.....	.0841	11.9
Mean of photosynthesis values.....	.0859	11.6

In the present experiment, optical densities and illuminances at the bottom of the culture were measured. From these measurements, rough calculations could be made of the illuminance at the midheight in the bottles and at midheight in the culture (table 7). The calculations indicate that the culture as a whole received less light than photosynthesis bottles placed on the bottom of the culture. The values given in table 7 refer to measurements made in the center of the aquarium. Although no detailed study was made of the horizontal distribution of light in the aquarium, a few measurements taken near the ends were less than those taken in the center. Thus the culture as a whole may have received even less light than is indicated in table 7.

TABLE 7.—Illuminance at the bottom of a mass culture of *Dunaliella primolecta*; illuminance at the midheight of 67-ml. photosynthesis bottles placed on the bottom of the culture; and illuminance at the midheight of the culture itself

[Experiment 3]

Time	Illuminance		
	At culture bottom	At bottle midheight	At culture midheight
<i>Hours</i>	<i>Ft.-c.</i>	<i>Ft.-c.</i>	<i>Ft.-c.</i>
0.....	2,070	1,785	1,650
10.....	1,850	1,500	1,220
20.....	1,850	1,580	1,280
30.....	1,750	1,170	720
40.....	1,620	900	350
50.....	1,750	880	300
60.....	1,800	795	310
70.....	1,850	700	426
80.....	1,900	610	220
90.....	1,850	590	200
100.....	1,850	560	200
120.....	1,850	495	155

If growth and photosynthesis are proceeding at subsaturating illuminances, the rates of these processes will be dependent upon the light received. Photosynthesis in bottles containing about 10^5 cells per ml. is saturated at an incident illuminance of about 1,200 ft.-c. at 26° C., the temperature of the culture (Thomas, unpublished data). This cell concentration approximates that at zero time in experiment 3. Values close to or less than 1,200 ft.-c. were found in the culture after 10 hours and in the bottles at 30 hours and thereafter (table 7). Thus light probably limited the rate of growth in the culture during most of the initial 50-hour period. At least it seems certain that the culture received less light than the bottles and that this is the reason that K_2 values for growth were less than those for photosynthesis. Probably growth and photosynthesis would have agreed very well if

illumination conditions were exactly the same for both types of measurements (see experiment 6).

After 50 hours, cell division ceased in the culture. The amount of nitrogen added to the culture was only half the amount added in the previous experiment, and only about half as many cells were produced. Cells taken at the next three sampling times (60, 70, and 80 hours) were probably in the beginning stages of nitrogen deficiency. Unfortunately, the samples for organic nitrogen taken at these times were lost, but it is unlikely that the organic nitrogen concentration was greater than that found at 70 hours and thereafter.

During this period of incipient deficiency, organic carbon continued to accumulate and the dry weight also increased (fig. 4). Photosynthesis reached a maximum at 60 hours and decreased thereafter (table 5). At 60 hours both gross and net O_2 evolution were less than C^{14} uptake, probably because of supersaturation of the water in the O_2 bottles. At 70 and 80 hours, C^{14} uptake agreed most closely with net O_2 production. During this 60- to 90-hour period, K_2 values for growth, as calculated from organic carbon, optical density, and dry-weight measurements, did not differ significantly from K_2 values calculated from C^{14} uptake and net O_2 production and the measured organic carbon concentration. The mean K_2 value for the growth measurements was 0.0123 hours⁻¹ (generation time=24.6 hours), while that for the photosynthesis measurements was 0.0196 hours⁻¹ (generation time=15.4 hours).

At 90 hours and thereafter, the effects of nitrogen deficiency were quite marked. The nitrogen in the cells was only 3 to 3.5 percent of the dry weight, the C/N ratio was high, and growth had ceased in the culture (table 5 and figure 4). Photosynthesis continued to decrease and C^{14} uptake agreed well with net O_2 evolution. At 120 hours net O_2 evolution was only half of the gross O_2 evolution, and C^{14} uptake was close to the net O_2 value.

At 123 hours, the culture was brought up to a volume of 28 l. and KNO_3 was added to bring the N concentration to 2,000 $\mu\text{g.}-\text{at.}/\text{l.}$ At 144 hours, growth and photosynthesis measurements were made. During this 21-hour period of recovery from N deficiency, the cell nitrogen increased and the C/N ratio decreased (see table 5). The culture took up nitrogen at a high rate; the K_2 value for increase in organic N was 0.0926 hours⁻¹.

The cell concentration did not increase, but K_2 values for increases in organic carbon, dry weight, and optical density were 0.0303 hours⁻¹, 0.0268 hours⁻¹, and 0.0122 hours⁻¹, respectively. All photosynthesis values were over twice the amounts recorded at 120 hours, even though the culture had been diluted. Net O₂ evolution was 72 percent of gross O₂ evolution. C¹⁴ uptake was intermediate between net and gross O₂ evolution. K_2 values calculated from organic carbon concentration at 144 hours and photosynthesis measurements at that time were 0.0329 hours⁻¹ (C¹⁴ uptake) and 0.0294 hours⁻¹ (net O₂ evolution).

Experiment 4

In a further investigation of the effects of nitrogen deficiency on photosynthesis, two 20-liter bottles, each containing 6 liters of sea water medium, were inoculated with *Dunaliella*. One bottle was enriched with 2,000 μg.-at.N/l., 200 μg.-at. P/l. and 0.5 p.p.m.Fe, and served as a control culture for comparison with the other bottle, which contained sea water enriched with the same amount of P and Fe, but an amount of N (250 μg.-at./l.) that would limit the final population. Also efforts were made to keep the cultures bacteria-free and to keep the volume of medium in the bottles more constant than in previous experiments. Each bottle was fitted with an air inlet tube extending below the surface of the culture, through which 5 percent CO₂-in-air was supplied at 500 ml./min. The gas was filtered through cotton wool to avoid bacterial contamination. Each bottle was also fitted with a tube for adding fresh sterile medium after each sampling, and with a siphon tube for taking the sample. A final tube was added for the egress of air.

After inoculation, the bottles were placed side by side on a reciprocating shaker which agitated them gently throughout the experiment. The cultures were continuously illuminated from below at an incident illumination of 1,500 ft.-c, and they were incubated at 22° C. in an air-conditioned room. In the control culture (+N), the pH was 6.30 to 6.95, and the total CO₂ concentration was 43.9 to 59.9 mg.CO₂-C/l. In the deficient culture, the pH was 6.28 to 6.69 and the total CO₂ concentration was 39.5 to 51.1 mg.CO₂-C/l.

Samples were taken for growth and photosynthesis measurements at intervals over a period of 8 days. Growth was measured only by cell

counts and is expressed in K_2 units and generation times as previously described. Samples for cell nitrogen analyses were centrifuged at 4,400 g. for 20 minutes. The cells were resuspended in distilled water and recentrifuged; they were then transferred to tared glass cups and dried in vacuo at 50° C. Measurement of growth by dry-weight determinations was attempted from these samples, but unavoidable losses of cell material occurred during centrifugation and resuspension. Thus, these samples could only be used to determine the percent N in the cells. After each sample was taken from the cultures, equivalent volumes of fresh media were added, but no nitrogen was added to the N-deficient culture until after 138 hours of incubation.

Photosynthesis bottles were incubated separately from the cultures at 1,250 ft.-c. illuminance and 22° C. These measurements were carried out with portions of the undiluted culture during the first seven samplings; 10-ml. aliquots were diluted with sterile sea water for the last three measurements. Thus, in these latter determinations, light limitations due to mutual shading of the cells were avoided, as were errors due to supersaturation of the suspension with oxygen.

The results of this experiment are given in tables 8 and 9. To compare data from different sampling times, photosynthesis is expressed as the photosynthetic capacity or photosynthesis per cell, as well as in terms of photosynthesis per liter. The condition of the cells in relation to nitrogen is shown by the figures for percent nitrogen in the cells. These nitrogen values are less than those reported in the previous experiment for cells in the same condition. Probably some N was lost during the washing procedure.

During the first 42 hours, mean growth constants, generation times, and photosynthetic capacities were similar in both cultures, but there was considerable variation in these values from sampling time to sampling time in each culture. Mean photosynthesis per cell, from all determinations in both cultures was 2.10 μμ g.C/cell/hour, for C¹⁴ uptake; 2.02 μμ g.C/hour, for net O₂ production; and 2.88 μμ g.C/cell/hour, for gross O₂ production.

The mean growth constant (K_2) of the -N culture was 0.1058 hours⁻¹ (9.5 hours generation time) and 0.1354 hours⁻¹ (7.4 hours generation time) in the +N culture. These mean K_2 values

TABLE 8.—Growth and comparative photosynthesis measurements of *Dunaliella primolecta* cells containing sufficient nitrogen

[Experiment 4]

Time, (hours)	Growth		Photosynthesis			Photo-synthetic capacity			Ni-trogen
	Growth constant between samples K_2 (hours ⁻¹)	Generation time (hours)	C ¹⁴ uptake $\mu\text{g. C/l./hr.}$	Net O ₂ production $\mu\text{g. C/l./hr.}$	Gross O ₂ production $\mu\text{g. C/l./hr.}$	C ¹⁴ uptake $\mu\text{g. C/cell/hr.}$	Net O ₂ production $\mu\text{g. C/cell/hr.}$	Gross O ₂ production $\mu\text{g. C/cell/hr.}$	
0	0.1281	7.8	347±49	342±61	622±90	2.99	2.95	5.36	6.50
8	0.1203	8.3	565±79			2.90			8.15
24	0.0912	11.0	1,400±200	1,480±190	1,730±220	2.48	2.61	3.04	9.47
32	0.2021	4.9	991±140	1,570±220	2,620±310	1.24	1.97	3.28	11.13
42	0.0411	24.3	1,900±270	2,950±440	3,120±270	1.38	2.15	2.27	9.23
66	0.0428	23.6	2,620±370	2,980±390	3,400±490	1.05	1.19	1.36	---
90	0.0443	22.6	2,410±340	2,770±360	3,510±460	0.82	0.94	1.19	6.12
114	0.0053	188.0	918±130	931±150	980±150	1.34	1.35	1.43	8.87
138	0.0031	328.0	697±98	727±90	779±97	1.28	1.34	1.43	8.55
163			583±82	686±96	774±100	1.31	1.44	1.62	6.78

TABLE 9.—Growth and comparative photosynthesis measurements in nitrogen-deficient cells of *Dunaliella primolecta*

[Experiment 4]

Time, (hours)	Growth		Photosynthesis			Photo-synthetic capacity			Ni-trogen
	Growth constant between samples K_2 (hours ⁻¹)	Generation time (hours)	C ¹⁴ uptake $\mu\text{g. C/l./hr.}$	Net O ₂ production $\mu\text{g. C/l./hr.}$	Gross O ₂ production $\mu\text{g. C/l./hr.}$	C ¹⁴ uptake $\mu\text{g. C/cell/hr.}$	Net O ₂ production $\mu\text{g. C/cell/hr.}$	Gross O ₂ production $\mu\text{g. C/cell/hr.}$	
0	0.0716	14.0	429±60	333±80	554±99	2.12	1.64	2.74	7.75
8	0.1330	7.5	404±57	601±87	787±110	1.62	2.40	3.07	8.77
24	0.1247	8.0	2,410±340	1,740±220	2,080±260	2.84	2.05	2.45	9.47
32	0.0937	10.7	3,390±490	2,530±320	3,810±460	2.34	1.75	2.63	3.86
42	0.0307	32.6	1,210±170	797±110	1,190±160	1.06	0.69	1.04	---
66	0.0077	130.4	383±54	472±74	891±130	0.21	0.27	0.51	1.77
90	0.0107	83.3	138±19	171±21	353±42	0.12	0.13	0.28	1.79
114	0.0317	31.6	40.4±5.6	16.4±5.7	8.2±3.5	0.28	-0.11	0.06	2.22
138	0.0249	40.2	6.3±0.9	7.9±3.6	15.9±2.3	0.08	-0.11	0.21	1.65
163			69.3±9.7	66.3±10.3	91±11	1.66	1.59	2.18	6.86

¹ 2,000 $\mu\text{g. at. N/l}$ added after samples were taken.

did not differ statistically. Photosynthesis bottles were incubated at an illuminance of 1,250 ft.-c., whereas the cultures were incubated at 1,500 ft.-c. Thus, K_2 values calculated from photosynthesis

and organic carbon estimations would not be exactly comparable. However, such K_2 values were calculated. In these calculations, the initial organic carbon (C_1) was estimated by multiplying the mean value for carbon per cell (obtained from the logarithmic phases of experiments 2 and 3) by the cell concentration, and C^{14} uptake or net O_2 evolution values were added to the initial organic carbon estimate to obtain C_2 . For cells from the -N culture, the mean of such photosynthetic K_2 values were 0.0800 hours⁻¹ (C^{14}) and 0.0706 hours⁻¹ (net O_2); respective generation times were 12.5 and 14.1 hours. Cells from the +N culture gave mean K_2 values of 0.0872 hours⁻¹ (C^{14}) and 0.0897 hours⁻¹ (net O_2), and the generation times were 11.5 and 11.1 hours, respectively. These mean values did not differ statistically. The mean growth constant for both cultures was 0.1200 hours⁻¹; the mean photosynthetic K_2 value calculated from all photosynthesis measurements and organic carbon estimates in both cultures was 0.0810 hours⁻¹. The growth rate was 48 percent greater than the photosynthetic rate and this difference was statistically significant. This difference may be attributed to different illuminances in the culture and in the photosynthesis bottles.

In the control (+N) culture, after 42 hours, photosynthetic capacities were somewhat reduced. C^{14} uptake agreed most closely with net O_2 production, but neither C^{14} nor net O_2 production differed from gross O_2 production by an amount greater than the experimental error of the measurements. Although the growth rate decreased and growth eventually ceased, photosynthesis and photosynthetic capacity were not strongly inhibited. The reduction in growth rates and in photosynthetic capacities was probably due to light limitations in the very dense culture. The culture retained its bright green appearance, and the concentration of N in the cells did not change greatly.

After 42 hours, N deficiency was very marked in the -N culture, which was pale green in color. Much less nitrogen was found in the cells. During the next 48 hours, growth continued at a reduced rate and the photosynthetic capacity was greatly reduced. Net oxygen production fell from the usual 70 to 90 percent of gross production to 50 percent of gross production. C^{14} uptake agreed with net production during this period. N-deficient cells stained more heavily with Lugol's

iodine solution and more of them were nonmotile than cells in the +N culture.

After 90 hours, growth constants were negative in the -N culture. Net photosynthesis was negative, and C¹⁴ uptake agreed more closely with gross O₂ evolution.

After 138 hours, 2,000 µg.-at.N/1. were added to the -N culture. Although the cell concentration did not increase during the next 23 hours, the photosynthetic capacity increased greatly. C¹⁴ uptake agreed closely with net O₂ production. No measurements were made beyond this point, but the culture was very much more green and dense on the following day.

In this experiment on nitrogen deficiency, aseptic technique was employed to keep the culture bottles bacteria-free. This point was checked at each sampling time by adding a portion of the sample to a tube of sea water enriched with 1 percent dextrose and 5 percent peptone. These tubes became turbid with bacterial growth in 3 days at room temperature. Thus, bacteria were undoubtedly present, although contamination was probably not great, since turbidity did not develop in less than 3 days.

Experiment 5

To study the effects of N deficiency on photosynthesis in the absence of bacteria, small-scale, bacteria-free cultures containing limiting and sufficient amounts of nitrogen were inoculated with *Dunaliella*. One-liter Erlenmeyer flasks containing 700 ml. of the same +N and -N media used in experiment 4 were incubated on the reciprocating shaker at 1,000 ft.-c. illuminance and 22° C. No aeration was provided, and after 8 days the pH had risen from 8.1 to 9.2 in both cultures, and growth had ceased. Then 15 millimoles of sodium bicarbonate were added aseptically to each culture. After 3 more days, the pH had risen again to 9.1. The -N culture was pale green, while the +N culture was bright green in appearance. For photosynthesis measurements, 10-ml. portions of each culture were then added to 50 ml. sterile sea water containing 0.2 ml. 0.5 molar NaHCO₃ in 67-ml. bottles. Bottles for O₂ measurements were filled with sterile sea water, and C¹⁴ bottles received 1 ml. of C¹⁴ solution. The pH in these bottles was 8.6. The bottles were incubated on the shaker under the same conditions of illuminance and temperature that were used to grow the cells.

EXPERIMENTAL EVALUATION OF C¹⁴ METHOD

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Peptone-dextrose sterility test tubes showed that bacteria were absent from these cultures. The results of these photosynthesis measurements are shown in table 10.

TABLE 10.—Photosynthesis in N-deficient and N-sufficient bacteria-free cultures of *Dunaliella primolecta*

[Experiment 5]

Measurements	Culture	
	-N	+N
Photosynthesis:		
C ¹⁴ uptake (µg.C/1./hour).....	300±42	834±120
Net O ₂ production (µg.C/1./hour).....	309±37	933±110
Gross O ₂ production (µg.C/1./hour).....	380±46	1,010±120
Photosynthetic capacity:		
C ¹⁴ uptake (µµg.C/cell/hour).....	1.33	2.77
Net O ₂ production (µµg.C/cell/hour).....	1.37	3.09
Gross O ₂ production (µµg.C/cell/hour).....	1.68	3.35

The ratio of net O₂ evolution to gross O₂ evolution in the N-deficient culture was 81 percent, while that in the control (+N) culture was 91 percent. Thus the effects of deficiency were not as pronounced as those shown by measurements taken after 40 hours in the previous experiment. In both cultures, C¹⁴ uptake agreed most closely with net O₂ production.

EFFECTS OF PHOSPHORUS DEFICIENCY

Experiment 6

To study the effects of phosphorus deficiency on photosynthesis and growth, the mass culture apparatus (aquarium) was again used. Forty liters of sterilized sea water were placed in the aquarium and enriched with 2,000 µg.-at. N/1., 1 p.p.m. Fe, and a limiting concentration of P (20 µg.-at./1.). The culture was inoculated with *Dunaliella* and incubated for 19 hours before growth and photosynthesis measurements were begun. During this period no CO₂ was supplied, but the culture was stirred with a glass stirrer. The aquarium was incubated at 26° C. and continuously illuminated from below at an illuminance of 800 ft.-c.

After the 19-hour preliminary period, 5 percent CO₂-in-air was supplied at 300 ml./min. for the rest of the experiment. Temperature, illumination, and stirring conditions were maintained at the level previously set. When the initial sample was taken, the pH of the culture was 8.05 and varied from 6.22 to 6.89 thereafter. Similarly, the initial CO₂ concentration was 23.0 mg. CO₂-C/1. and varied from 33.7 to 44.6 mg. CO₂-C/1. for

the rest of the experiment. Growth was measured by cell concentration and by optical density measurements. Photosynthesis was measured as previously described by placing the bottles on the bottom of the culture.

The growth of the culture is depicted in figure 5

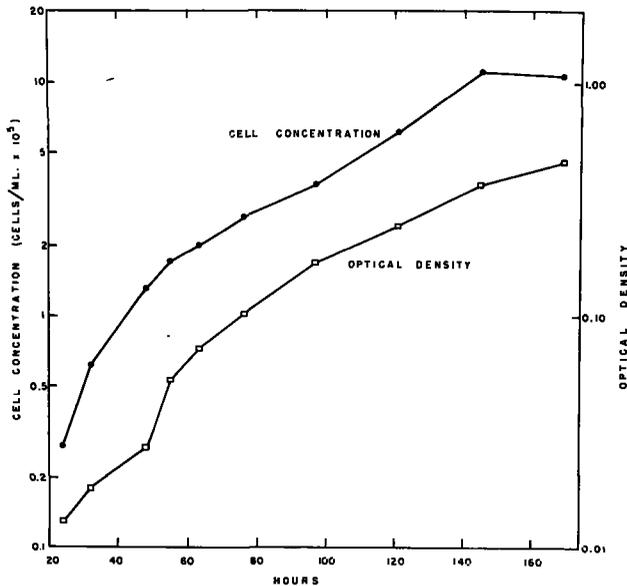


FIGURE 5.—Growth of a mass culture of *Dunaliella primolecta* containing a limiting concentration of phosphorus.

and photosynthesis measurements are given in table 11. The initial cell concentration and optical density were too low to measure. Initial photosynthesis rates were correspondingly low; C^{14} uptake agreed with net O_2 evolution within the experimental error at this low phytoplankton concentration.

TABLE 11.—Comparative photosynthetic measurements at 800 ft.-c. during the development of phosphorus deficiency in a mass culture of *Dunaliella primolecta*

[Experiment 6]

Time (hours)	Photosynthesis			Photosynthetic capacity		
	C^{14} uptake $\mu\text{g. C/l./hour}$	Net O_2 production $\mu\text{g. C/l./hour}$	Gross O_2 production $\mu\text{g. C/l./hour}$	C^{14} uptake $\mu\text{g. C/cell/hour}$	Net O_2 production $\mu\text{g. C/cell/hour}$	Gross O_2 production $\mu\text{g. C/cell/hour}$
0.....	11±1	19±8
24.....	112±15	135±27	154±20	4.06	4.88	5.58
32.....	126±16	157±20	188±24	2.07	2.56	3.06
48.....	231±30	279±36	423±51	1.77	2.13	3.24
55.....	371±48	367±60	449±67	2.18	2.16	2.64
63.....	475±62	541±70	678±82	2.41	2.73	3.42
76.....	764±99	667±110	864±130	2.88	2.50	3.24
97.....	1,350±180	1,060±160	1,210±180	3.69	2.88	3.31
121.....	1,580±210	1,470±160	1,640±200	2.58	2.41	2.67
145.....	1,320±170	1,090±150	1,740±230	1.19	0.98	1.56

During the period from 24 to 55 hours, rapid logarithmic growth occurred in the culture. C^{14} uptake agreed most closely with net O_2 production. The mean growth rates (K_2) were 0.0884 hours⁻¹ and 0.0781 hours⁻¹, as determined by cell concentrations and optical density measurements, respectively. Cell concentrations were converted to an estimated organic carbon concentration which was used in calculating photosynthetic K_2 values from C^{14} uptake and net O_2 production measurements. These mean photosynthetic K_2 values were 0.0843 hours⁻¹ and 0.1048 hours⁻¹, as calculated from C^{14} uptake and net O_2 production respectively. The overall mean K_2 for growth was 0.0835 hours⁻¹, while that for photosynthesis was 0.0945 hours⁻¹. Statistical tests showed that these mean K_2 values did not differ significantly. Rough calculations of illuminances in the bottles and at midheight in the culture showed that at 24, 32, and 48 hours these illuminances did not differ by more than 10 percent, and at 55 hours, illuminance in the bottles was 25 percent greater than illuminance at the midheight of the culture. Thus during this period before the culture became too dense, illumination conditions were nearly equivalent in the culture and in photosynthesis bottles placed on the bottom of the culture, and photosynthesis was equivalent to growth.

The growth rate of the culture was much reduced during the period from 55 to 145 hours. The mean growth constant K_2 , as calculated from increases in cell concentration, was 0.0291 hours⁻¹; that calculated from increases in optical density was 0.0344 hours⁻¹. K_2 values calculated from photosynthesis determinations and estimated organic carbon concentrations were 0.0892 hours⁻¹ (C^{14}) and 0.0761 hours⁻¹ (net O_2). The overall mean photosynthetic constant was 0.0827 hours⁻¹; that for growth was 0.0317 hours⁻¹. Statistical tests showed that this difference was significant. Growth in the culture proceeded at only about 40 percent of the rate of photosynthesis in bottles placed on the bottom of the culture. Rough calculations of light intensities showed that the intensity at midheight in the culture was only 45–75 percent of that in the bottles.

During this 90-hour period, C^{14} uptake corresponded to both net or gross O_2 evolution, which did not differ greatly from each other. Further indications that light was limiting in the culture, were found by incubating a duplicate set of photo-

synthesis bottles at 1,800 ft.-c. These photosynthesis measurements are shown in table 12. Photosynthetic capacities were greatly increased by incubation at this light intensity, and C^{14} uptake was similar to both net and gross O_2 production.

TABLE 12.—Comparative photosynthesis determinations at 1,800 ft.-c. during the development of phosphorus deficiency in *Dunaliella primolecta*

[Experiment 6]

Time (hours)	Photosynthesis			Photosynthetic capacity		
	C^{14} uptake $\mu\text{g. C/l./hour}$	Net O_2 production $\mu\text{g. C/l./hour}$	Gross O_2 production $\mu\text{g. C/l./hour}$	C^{14} uptake $\mu\text{g. C/cell/hour}$	Net O_2 production $\mu\text{g. C/cell/hour}$	Gross O_2 production $\mu\text{g. C/cell/hour}$
76.....	1,440±190	1,170±140	1,370±170	5.44	4.39	5.13
97.....	2,010±260	1,810±220	1,970±240	5.48	4.93	5.36
121.....	2,330±300	2,360±290	2,520±310	3.82	3.85	4.12
145.....	2,310±300	1,880±230	2,520±310	2.08	1.68	2.26

At 145 hours, cell division ceased, but optical density continued to increase for an additional 24 hours. To test for phosphorus deficiency, 50-ml. aliquots of the cell suspension were placed in four 125-ml. flasks at 153 hours. Two flasks were enriched with phosphorus at a concentration of 20 $\mu\text{g. -at. P/l.}$ Two others received no addition. The flasks were incubated for 16 hours at 1,500 ft.-c and 22° C. on a reciprocal shaker. The initial optical density was 0.409; after 24 hours the optical density of cultures to which phosphate was added was 0.561, while that of the control (–P) cultures was 0.481. Thus, the increase in optical density was greater in cultures which contained added phosphate than in control cultures. The cells were undoubtedly phosphorus-deficient, but only in the beginning stages of deficiency, since some growth (increase in optical density) occurred in the culture and in the flasks to which no phosphorus was added. At 145 hours, for bottles placed in the culture and incubated at an incident illuminance of 800 ft.-c, net O_2 production was 62 percent of the gross value. These net gross ratios are generally less than those found earlier in this experiment, and are also indicative of the beginning stages of phosphorus deficiency. At 145 hours, C^{14} uptake was intermediate between, but did not differ significantly from, net and gross O_2 evolution. Photosynthesis was not measured at 169 hours.

EXPERIMENTAL EVALUATION OF C^{14} METHOD

Experiment 7

Another experiment on the effects of phosphorus deficiency was performed with small-scale, bacteria-free cultures containing limiting and sufficient amounts of phosphate. One-liter Erlenmeyer flasks containing 700 ml. of media were inoculated with *Dunaliella* and incubated on the reciprocal shaker at 1,600 ft.-c. and 26° C. The complete (+P) medium consisted of sea water enriched with 2,000 $\mu\text{g. -at. NO}_3\text{-N/l.}$, 200 $\mu\text{g. -at. PO}_4\text{-P/l.}$ and 1 p.p.m. Fe. In the phosphorus-deficient culture the sea water was enriched with only 20 $\mu\text{g. -at. PO}_4\text{-P/l.}$

After 188 hours, the –P culture contained 7,700,000 cells/ml., while the +P culture contained 9,500,000 cells/ml. Sixty-seven-ml. bottles containing 50 ml. sea water and 0.1 millimole of NaHCO_3 were inoculated with 10-ml. portions of each culture. Bottles for O_2 measurements were then filled with sterile sea water, those for C^{14} measurements received 1 ml. C^{14} solution. They were incubated at 1,400 ft.-c. and 25° C.

Table 13 shows the results of this experiment with bacteria-free cultures. In the control (+P) culture, C^{14} uptake agreed quite well with net O_2 production. In the phosphorus deficient culture, it was much less than either net O_2 production or gross O_2 production.

TABLE 13.—Photosynthesis in P-deficient and P-sufficient bacteria-free, cultures of *Dunaliella primolecta*

[Experiment 7]

Measurements	–P Culture	+P Culture
Photosynthesis:		
C^{14} uptake ($\mu\text{g. C/l./hour}$).....	165±21	511±66
Net O_2 production ($\mu\text{g. C/l./hour}$).....	272±33	504±61
Gross O_2 production ($\mu\text{g. C/l./hour}$).....	318±39	542±66
Photosynthetic Capacity:		
C^{14} uptake ($\mu\text{g. C/cell/hour}$).....	1.07	2.69
Net O_2 production ($\mu\text{g. C/cell/hour}$).....	1.77	2.65
Gross O_2 production ($\mu\text{g. C/cell/hour}$).....	2.06	2.85

COMPARATIVE MEASUREMENTS OF PHOTOSYNTHESIS BY pH CHANGES, C^{14} UPTAKE, AND O_2 EVOLUTION

Experiments 8 and 9

In previous experiments, C^{14} uptake was compared with O_2 evolution and with growth. It appeared desirable to compare C^{14} uptake with measurements of CO_2 assimilation that were more direct than determinations of O_2 evolution and growth. By using cultures where the rate of photosynthesis was high (cultures in the logarithmic growth phase, and incubated at high illuminances), it was feasible to measure CO_2

assimilation directly from pH changes and to compare CO₂ assimilation with C¹⁴ uptake and O₂ evolution.

Cells for these comparisons were grown in sea water enriched with 2,000 µg.-at. NO₃-N/l., 200 µg.-at. PO₄-P/l. and 1 p.p.m. Fe. After 6 days of growth at 500 ft.-c. and 26° C., 25 ml. of the cell suspension was added to 25 ml. of sterile sea water containing 0.1 ml. of 0.5 molar NaHCO₃ in 67-ml. bottles. Bottles for O₂ and pH measurements were filled with sterile sea water; those for C¹⁴ measurements received 1-ml. C¹⁴ solution. All bottles were incubated at 23° C. and 1,450 ft.-c.

The results of these experiments are shown in table 14. The pH changed in the first experiment from 8.66 to 8.88 during 3¼ hours of incubation; in the second experiment it changed from 8.15 to 8.98 during four hours. From these changes and the carbonate alkalinity, the amount of CO₂ taken up was calculated. The total (pooled) error of the pH method was ±8.5 percent—±6 percent for each measurement, beginning and final. In both experiments CO₂ assimilation as measured by pH changes agreed with that measured by C¹⁴. O₂ measurements were also equivalent to both CO₂ measurements within the experimental error.

TABLE 14.—*Photosynthesis in Dunaliella primolecta as measured by pH changes, C¹⁴ uptake, and O₂ evolution*

Type of measurement	Experiment 8	Experiment 9
pH change (µg. C/l./hour).....	1,380±120	2,770±240
C ¹⁴ uptake (µg. C/l./hour).....	1,720±220	2,670±350
Net O ₂ production (µg. C/l./hour).....	1,300±180	2,230±280
Gross O ₂ production (µg. C/l./hour).....		2,350±280

DISCUSSION

Under conditions of adequate nutrition and illuminance, the difference between total or "gross" O₂ evolution and net O₂ evolution is not large. Commonly the difference is only 5–20 percent. To compare such measurements with C¹⁴ uptake it is necessary to calculate the equivalent carbon production using a photosynthetic quotient (O₂/CO₂) which may vary nearly as much (±12 percent, Ryther, 1956) as the experimental error of the C¹⁴ method. The present results show that, under these ideal conditions, C¹⁴ uptake agrees well with net O₂ evolution, but does not differ greatly (and often not significantly) from gross O₂ evolution either. This was shown

by experiments using cells taken from the logarithmic phases of growth in the aquarium cultures (experiments 1, 2, 3, and 6) and in control cultures (+N and +P) of the experiments on N and P deficiency (experiments 4, 5, and 7). These results agreed with those of other investigators who have used healthy cultures to compare O₂ evolution and C¹⁴ uptake (Ryther, 1954; Ryther and Vaccaro, 1954; Steemann Nielsen and Al Kholi, 1956; Ichimura and Saijo, 1958).

The growth of an algal culture is also a net process, and such growth is more representative of an increase in the food which would be available to zooplankton, for instance, than is net O₂ evolution. In the present experiments, growth was measured in several ways and logarithmic growth constants were calculated from these growth measurements. Organic carbon determinations provided a way of converting photosynthesis measurements to similar K₂ values, so that photosynthesis could be compared with growth.

In experiments 2 and 3, growth was somewhat less than photosynthesis as measured by C¹⁴ uptake and net O₂ evolution. This difference was attributed to differences in the illumination of cells in photosynthesis bottles placed within the culture and that reaching the culture itself. At low cell densities (experiment 6), when illuminance in the bottles was similar to that in the culture, growth and photosynthesis did not differ. In experiment 4, when the illuminance in the culture was greater than that in the bottles, growth was greater than photosynthesis. These results indicate that during the logarithmic phase of growth, if conditions are the same for the two measurements, growth and photosynthesis are similar, and that C¹⁴ measurements are equivalent to increase in algal biomass. It would have been more desirable to compare C¹⁴ uptake and growth in the same vessel, but a frequent sampling routine could not have been maintained. Furthermore, glass-stoppered bottles are used as containers for photosynthesizing cells in field C¹⁴ measurements, and it was desired to approximate field conditions as much as possible.

Using a natural phytoplankton population enclosed in a large plastic bag, McAllister et al. (1961) have recently compared several methods of measuring production. During the logarithmic phase of growth in the bag, measurements

made with the C^{14} method were approximately equivalent to those calculated from O_2 changes, pH changes, increases in organic carbon, and increases in cell volume (see their fig. 7). This equivalence between growth and photosynthesis was confirmed by our results with *Dunaliella* cultures.

In the sea, rapid logarithmic phytoplankton growth is probably not common. It occurs mainly during the spring outburst in temperate waters, and during the development of "red tides." In most tropical and subtropical seas, at least, incipient nutrient deficiency is probably a more common condition, a condition under which phytoplankton grow and produce organic matter at a rate which is limited by the rates of such processes as the remineralization of nutrients in the surface layers or slow diffusion from subsurface supplies.

Incipient nitrogen deficiency in *Dunaliella* was studied in experiments 3 and 4. Under such conditions, C^{14} uptake was similar to net O_2 evolution. During the period of incipient deficiency, K_2 values for increases in organic carbon calculated from photosynthesis measurements did not differ significantly from those calculated for growth.

It is also interesting to note that incipient nitrogen deficiency resulted in a change in metabolism—a "shunt" in which cell material is formed which is low in nitrogen. During logarithmic growth, some 8 to 10 percent of the dry weight was nitrogen. During incipient deficiency, nitrogen made up only 3 percent of the dry weight and carbon continued to accumulate. Thus, the C/N ratio shifted from approximately six during the logarithmic growth period to approximately 15 when the cells became deficient (see table 5). The main product of this shunt metabolism was probably starch, since deficient cells were stained more heavily by iodine. Similar shifts in metabolism from predominantly protein formation to carbohydrate or lipid formation have been reported for other green algae when nitrogen was deficient (Spoehr and Milner, 1949; and others).

Extreme nutrient deficiency is probably of more academic than oceanographic significance. When deficiency becomes extreme, net O_2 production falls below 50 percent of gross O_2 production. Steemann Nielsen and Al Kholy (1956) pointed out

that a phytoplankton population would not persist in nature under such conditions. During the night, respiration would presumably continue at the same rate as during the day, and, assuming a 12-hour day-length, gross photosynthesis must be at least twice the amount of respiration. This point was reiterated by Strickland (1960). Extreme nitrogen deficiency was achieved in one of the present experiments (experiment 4); C^{14} uptake agreed most closely with gross O_2 production under this condition. At this time, the photosynthetic capacity was much reduced; and growth constants and net O_2 evolution were negative.

Ryther (1954), using a related alga, *D. eucchlora*, presented data on the effects of nutrient deficiency on C^{14} and O_2 measurements. He gave no details about the culture conditions used in growing the alga, so that one cannot tell whether his results were due to nitrogen or to phosphorus deficiency. After 15 days of growth, however, net O_2 production was 50 percent of gross O_2 production; after 30 days, net production was only about 5 percent of gross production. In both cases, C^{14} uptake agreed well with net O_2 production. On the other hand, Steemann Nielsen and Al Kholy (1956), using the fresh-water green alga, *Chlorella pyrenoidosa*, showed that C^{14} uptake in nitrogen- and phosphorus-deficient cultures did not differ greatly from gross O_2 production. The conditions of their cultures appear to approach those of Ryther after 30 days of growth, since net O_2 production was only a small fraction of gross O_2 production.

Results given in experiments 3 and 4 indicate that C^{14} uptake agrees closely with net O_2 production during a period of incipient nitrogen deficiency. These data agree with those obtained by Ryther in 15-day cultures. Furthermore, the agreement between growth and photosynthesis under these conditions also suggests that the C^{14} method measures a net increase in algal biomass.

The effects of extreme nitrogen deficiency were less clear. In the latter stages of experiment 4, when the cells were extremely deficient, net O_2 evolution was negative, and C^{14} uptake corresponded more closely with gross O_2 production. This result is more in agreement with the comparisons of Steemann Nielsen and Al Kholy than those of Ryther. However, the low values for net O_2 evolution in experiment 4 may be erroneous

due to bacterial contamination. Cells from an older, bacteria-free culture (experiment 5), which may also have been extremely nitrogen-deficient, assimilated C^{14} at a rate which corresponded to net O_2 evolution. Obviously, further studies of the effects of extreme nitrogen deficiency in bacteria-free culture would be of interest but would be less significant than investigations of incipient deficiency.

Phosphorus deficiency was not studied in as great detail as nitrogen deficiency. In the latter stage of experiment 6 (tables 11 and 12), with cells that were probably in a stage of incipient deficiency, C^{14} uptake did not differ significantly from either net or gross O_2 production, and was intermediate between the two O_2 values. In another phosphorus-deficient culture (experiment 7), which was also bacteria-free and was older than that of experiment 6, C^{14} uptake was much less than net O_2 evolution. Phosphorus deficiency in this experiment may have been more extreme than in experiment 6, and, under such conditions, soluble, C^{14} -labelled, organic matter might have been excreted by *Dunaliella* cells. Such material would not have been collected on the membrane filter and included in the measurement of C^{14} uptake.

In another test of the general validity of the C^{14} method, C^{14} uptake was shown to be equivalent to the uptake of CO_2 as measured by pH changes. These experiments (8 and 9) were carried out with healthy cells.

To relate studies with laboratory cultures to C^{14} measurements carried out in the open sea, it would be necessary to use cultures of representative oceanic phytoplankton species in experiments such as these. *D. primolecta* may only be representative of the phytoplankton of British coastal waters, from which it was isolated (Butcher, 1959), and caution is necessary in applying the results of the present experiments to measurements of oceanic photosynthesis.

To the extent that *Dunaliella* is a representative alga, however, these experiments indicate that the C^{14} method provides a reliable measure of net photosynthesis and of increase in phytoplankton biomass, under good conditions for phytoplankton growth and under conditions of incipient nitrogen deficiency. Fortunately, cultures of representative oceanic phytoplankton are becoming available

(Thomas, 1959), and could be used for further studies of the C^{14} method.

SUMMARY

1. During the logarithmic phase of growth of cultures of *D. primolecta*, photosynthetic C^{14} uptake agreed well with net O_2 production, but also did not differ greatly from gross O_2 production.

2. During this growth phase, the growth rate of mass cultures was generally less than the photosynthetic rate (C^{14} uptake and net O_2 production) in bottles of the cell suspension placed within the culture. This difference was attributed to different illumination conditions between the bottles and the culture. In one experiment, when illumination conditions were similar, growth in the culture was equivalent to photosynthesis in the bottles.

3. In cultures that were incipiently nitrogen-deficient, C^{14} uptake was similar to net O_2 production and growth was equivalent to photosynthesis.

4. In one experiment, under conditions of extreme nitrogen deficiency, C^{14} uptake was greater than net O_2 evolution, and more closely approximated gross O_2 evolution. In another such experiment, C^{14} uptake agreed well with net O_2 evolution.

5. Nitrogen deficiency in *Dunaliella* suppresses the formation of protein and a carbohydrate, probably starch becomes a major component of the cells.

6. In one experiment, C^{14} uptake in an incipiently phosphorus-deficient culture was intermediate between net and gross O_2 evolution; in another experiment, C^{14} uptake was less than net O_2 production in a phosphorus-deficient culture.

7. C^{14} uptake in healthy cultures of *Dunaliella* was equivalent to the uptake of CO_2 as measured by pH changes.

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LITERATURE CITED

- ANDERSON, DON H., with REX J. ROBINSON.
1946. Rapid electrometric determination of the alkalinity of sea water using a glass electrode. *Industrial and Engineering Chemistry (Analytical Edition)*, vol. 18, No. 12, pp. 767-769.
- BUTCHER, R. W.
1959. An introductory account of the smaller algae of British Coastal waters. Part I: Introduction and Chlorophyceae. Ministry of Agriculture, Food, and Fisheries (U.K.), Fisheries Investigations, series IV, pp. 1-74.
- DOTY, MAXWELL S., and MIKIHICO OGURI.
1958. Selected features of the isotopic carbon primary productivity technique. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 144, pp. 47-55.
- HARVEY, H. W.
1955. The chemistry and fertility of sea water. Cambridge University Press, Cambridge, 224 pp.
- ICHIMURA, SHUN-EI, and YATSUKA SAIGO.
1958. On the application of C^{14} method to measuring organic matter production in the lake. *The Botanical Magazine, Tokyo*, vol. 71, No. 839, pp. 174-180.
- JITTS, H. R., and B. D. SCOTT.
1961. The determination of zero-thickness activity in Geiger counting of C^{14} solutions used in marine productivity studies. *Limnology and Oceanography*, vol. 6, No. 2, pp. 116-123.
- KAY, HANS.
1954. Eine Mikromethode zur chemischen Bestimmung des organisch gebundenen Kohlenstoffes im Meerwasser. Institut für Meereskunde an der Universität Kiel. *Kieler Meeresforschungen*, Band 10, Heft 1, pp. 26-36.
- KRAUSS, ROBERT W., and WILLIAM H. THOMAS.
1954. The growth and inorganic nutrition of *Scenedesmus obliquus* in mass culture. *Plant Physiology*, vol. 29, No. 3, pp. 205-214.
- MCALLISTER, C. D., T. R. PARSONS, K. STEPHENS, and J. D. H. STRICKLAND.
1961. Measurements of primary production in coastal sea water using a large volume plastic sphere. *Limnology and Oceanography*, vol. 6, No. 3, pp. 237-258.
- RANKER, EMORY R.
1927. A modification of the salicylic-thiosulfate method suitable for the determination of total nitrogen in plants, plant solutions, and soil extracts. *Journal of the Association of Official Agricultural Chemists*, vol. 10, No. 2, pp. 230-251.
- RODHE, WILHELM.
1948. Environmental requirements of fresh-water plankton algae. *Botaniska Institutionerna i Uppsala. Symbolae Botanicae Upsalienses*, vol. 10, No. 1, pp. 1-149.
- RYTHER, JOHN H.
1954. The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. *Deep-Sea Research*, vol. 2, No. 2, pp. 134-139.
- RYTHER, JOHN H.
1956. The measurement of primary production. *Limnology and Oceanography*, vol. 1, No. 2, pp. 72-84.
- RYTHER, J. H., and R. F. VACCARO.
1954. A comparison of the oxygen and C^{14} methods of measuring marine photosynthesis. Conseil Permanent International pour l'Exploration de la Mer, *Journal du Conseil*, vol. 20, No. 1, pp. 25-34.
- SETTEE, L. R., G. R. HAGEE, and C. P. STRAUB.
1958. Analysis of radioactivity in surface waters—practical laboratory methods. *American Society for Testing Materials Bulletin No. 227*, pp. 35-40.
- SEIGEL, SIDNEY.
1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York, N. Y., 312 pp.
- SNEDECOR, GEORGE W.
1956. *Statistical methods*. 5th ed. Iowa State College Press, Ames, Iowa, 534 pp.
- SPOEHR, H. A., and HAROLD W. MILNER.
1949. The chemical composition of *Chlorella*; effect environmental conditions. *Plant Physiology*, vol. 24, No. 1, pp. 120-149.
- STEMMANN NIELSEN, E. and R. F. VACCARO.
1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. Conseil Permanent International pour l'Exploration de la Mer, *Journal du Conseil*, vol. 18, No. 2, pp. 117-140.
- STEMMANN NIELSEN, E., and A. A. AL KHOLY.
1956. Use of C^{14} -technique in measuring photosynthesis of phosphorus or nitrogen deficient algae. *Physiologia Plantarum*, vol. 9, No. 1, pp. 144-153.
- STEINBERG, DANIEL, and SIDNEY UDENFRIEND.
1957. The measurement of radioisotopes. In Sidney P. Colowick and Nathan O. Kaplan, eds., *Methods in Enzymology*, vol. 4, pp. 425-472. Academic Press, New York.
- STRICKLAND, J. D. H.
1960. Measuring the production of marine phytoplankton. *Fisheries Research Board of Canada Bulletin No. 122*, 172 pp.
- STRICKLAND, J. D. H., and T. R. PARSONS.
1960. A manual of sea water analysis. *Fisheries Research Board of Canada Bulletin No. 125*, 185 pp.

SWEENEY, BEATRICE M., AND J. WOODLAND HASTINGS.

1957. Characteristics of the diurnal rhythm of luminescence in *Gonyaulax polyedra*. *Journal of Cellular and Comparative Physiology*, vol. 49, No. 1, pp. 115-128.

THOMAS, WILLIAM H.

1959. The culture of tropical oceanic phytoplankton. *In International Oceanographic Congress Preprints*, Mary Sears, ed., pp. 207-209.

THOMAS, WILLIAM H.

1963. Physiological factors affecting the interpretation of phytoplankton production measurements. *In Maxwell S. Doty, editor, Proceeding of the Conference on Primary Productivity Measurement, Marine and Freshwater*. U.S. Atomic Energy Commission. TID-7633, Biology and Medicine, pp. 147-162.

DENTITION OF THE NORTHERN FUR SEAL

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ABSTRACT

Gross morphology and development of deciduous and permanent teeth of *Callorhinus ursinus* are described. The deciduous teeth are essentially nonfunctional; two-thirds of them are usually shed in fetal life. The permanent teeth begin to calcify very early; all have erupted from the jaw, though not all from the gum, at birth. Root growth continues through life, especially in teeth which retain an open pulp canal for 20

years. The 1st premolar and all molars in each quadrant are primary permanent teeth. A "lower 1st incisor" was presumably lost in the evolution of the seal. Cusplets and a double root on certain teeth suggest that modern teeth are derived from more complex ones. In 11 percent of specimens, supernumerary or prenatally absent teeth are recorded.

Purpose

Since 1867 the U.S. Government has managed the Alaska fur seal herd. The seals breed on the Pribilof Islands, and their population in mid-summer is about 1,800,000. To improve the management of the herd, the Government obtains zoological information about the animals in its care. In 1949, in the course of exploratory research, Fish and Wildlife Service biologists found that fur seal teeth have layers which correspond in number to the age of the individual in years (Scheffer, 1950). This finding has proved to be useful, and biologists now engaged in applied research have identified the ages of more than 50,000 seals killed during the past decade.

The study of fur seal dentition has continued so that we could gain a better understanding of variation in the teeth and jaws with age and sex. One purpose of the present paper is to trace the origin, growth, and disappearance of the deciduous (milk) teeth which erupt from the bony alveolus in early fetal life. Another purpose is to trace the origin and growth of the permanent teeth which normally erupt from the bony alveolus in late fetal life.

Previous Research

While the dental formula for the fur seal *Callorhinus ursinus* has been known for nearly a century, the ontogeny of the dentition has not been well described. The young fur seal is extremely precocious, and its dentition is determined and developed in utero during winter and spring when the pregnant female is at sea. Because of prohibitions against killing seals at sea, biologists were unable, until 1950, to obtain fetuses. Between 1958 and 1962 they took annually for research purposes about 900 pregnant females along the oceanic migration routes.

Certain papers have contributed to our understanding of the teeth of *Callorhinus*. Allen and Bryant (1870) presented drawings of the skulls of young and adult *Callorhinus* and the first description of fur seal permanent dentition.

Allen (1880) stated that the teeth of *Callorhinus* are weaker than those of the southern fur seal *Arctocephalus*, the Steller sea lion *Eumetopias*, or the California sea lion *Zalophus*.

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Kükenthal (1894) reviewed the literature on deciduous teeth of seven phocids and one otariid (the southern fur seal). In all he reported three deciduous premolars antecedent to the 2d, 3d, and 4th permanent premolars in each quadrant.

Lucas (1899) gave the deciduous and permanent dental formulas of *Callorhinus* as known today. He examined only one fetus younger than full term and identified as premolars the first four postcanines in each quadrant, after observing that the three deciduous premolars are adjacent to the alveoli of the 2d, 3d, and 4th permanent premolars.

Osborn (1907, p. 143) believed that "the teeth of the . . . Pinnipedia are so much modified secondarily that until we trace their ancestral history we cannot feel any confidence in attempts either to homologize the cusps or to trace these teeth back to a tritubercular or triconodont stage."

Todd (1918, p. 175) stated that "it does not take very long, geologically speaking, for a tritubercular molar to retrogress into a simple conical tooth." His remarks on the California sea lion *Zalophus* apply also to *Callorhinus*: "The premolars and molar of the maxilla are secondarily simple teeth, each with a well-marked cingulum surrounding the base of the crown. Their single cusps probably represent the paracone. The mandibular cheek teeth are also simple but the basal cingulum rises into a small cusp in front and behind the apex [crown tip] of the tooth, which may be the homologue of the protoconid" (p. 186).

Kellogg (1922) concluded that the terrestrial ancestors of the Pinnipedia may have had six more teeth than has modern *Callorhinus*. They may have had, on each side, one more upper posterior molar, one more lower medial incisor, and one more lower posterior molar. "In studying the dentition of the Otariidae," wrote Kellogg (p. 64, 100), "the fact is gradually forced upon one that the earliest otarids slowly retrogressed from the complex, flesh-tearing dentition of the land carnivores and reverted back toward a simple, conical tooth most favorable for the capture of elusive prey. . . . The evidence shows that the reduction of the true molars was very rapid in the Otariidae, at least."

Howell (1929) gave a dental formula for otariids which included one, two, or three lower molars on each side. Reference to three lower molars is puzzling. While the Miocene pinniped *Allodesmus*

had two lower molars, no modern pinniped normally has more than one on each side.

Simpson (1945, p. 233) stated that "probably the pinnipeds are an early offshoot of the little differentiated late Eocene and early Oligocene canoid ancestry, paralleled by the otters, which had the same ultimate origin and a similar adaptive trend, and in other features by the bears, also with the same remote origin." The oldest known pinniped remains are from Miocene beds, perhaps 35 million years old. The remains are fossil skulls and skeletons, and are obviously those of pinnipeds. Their progenitors are completely unknown (Scheffer, 1958).

Rand (1950) studied the dentitions of 42 pups of the southern fur seal *Arctocephalus*. The teeth are like those of *Callorhinus*, although deciduous canines may persist for 5 months and deciduous premolars for 4 months after birth.

Gregory (1951, p. 405) stated that the teeth of seals "are usually 'simple' pegs, with a basal cingulum, a small basal cusp and conical, slightly recurved crowns adapted for fish-catching. Very probably this is a retrogressive, secondarily simplified dentition." He stated that there are four premolars in each quadrant, and he supposed that all have deciduous predecessors.

In a random sample of 38 female fur seal skulls, Chiasson (1955) found 6 that lacked one or more upper teeth, usually including the posterior upper molar. He stated (p. 564) "due to the fact that fur seals may replace the 6th upper postcanine [m2], this deciduous tooth might, upon accidental extraction, be replaced by the permanent tooth."

In 1957 Chiasson presented a discussion of the dentition of the fur seal. He emphasized the "double-rooted tooth development" of the posterior postcanines, stating that it "appears in the alligator and perhaps in other reptiles but not, to my knowledge, in any other mammal." Chiasson implied that the fur seal can have only three premolars in each half of each jaw since it has only three deciduous postcanines. He surmised that pinnipeds could not have evolved from creodont (precarnivore) stock because the creodonts had complicated teeth and modern seals do not.

Sergeant (1959) and Laws (1962) discussed the rhythmic deposition of dentin and cementum on the teeth of seals and cetaceans. The result is often a series of annual growth layers or ridges, useful as indicators of age (see page 308).

An Interim Convention on Conservation of North Pacific Fur Seals was signed in 1957 by representatives of four nations. The Convention resulted in anatomical studies by biologists of Canada, Japan, and the United States. The studies have produced six recent reports on dentition, namely, theses by Bokstrom (1961), Takano (1961), and Lamb (1962), written with the guidance of Kraus; and three publications by Kubota, Komura, Nagasaki, Tsuboi, and Matsumoto (1961a, b) and Kubota, Nagasaki, Matsumoto, and Tsuboi (1961). We shall discuss these later.

In critically reviewing previous research, the following points are important: (1) The number of permanent premolars in each quadrant has been given, variously, as three and four; four is correct. (2) In the southern fur seal, the deciduous canines may persist for 5 months, as against 3 months in the northern genus (p. 300). (3) While fossil evidence is lacking, the teeth of pre-Miocene seals were presumably more numerous and were more elaborately cusped than those of Recent seals. (4) One author has emphasized the evolutionary importance of the simple crown of all postcanines, and the double root of certain postcanines. In our opinion, there has been ample time—at least 35 million years—for the development of both features. (5) From six recent reports issued in 1961 and 1962, pertinent data have been extracted and will be used in the present paper as supplementary and comparative material, with appropriate citations.

MATERIALS AND METHODS

Numbers of Specimens

The specimens of the present study were collected on the Pribilof Islands, or at sea along the northwest coast of North America. They include material in formalin, dry skulls, dental arches only, isolated teeth, and photographs only, as follows:

	<i>Number</i>
Fetal and prematurely born (aborted).....	20
Newborn and full-term fetal.....	18
Pups older than newborn.....	34
Yearling, pelagic.....	5
Yearling, autumn (on land).....	4
Ages 2 to 10 years.....	62
Over 10 years.....	24
Total.....	167

Of these, about half are represented by skulls in the permanent collection of the National Museum or in the Bureau of Commercial Fisheries Marine Mammal Biological Laboratory. The others are represented by specimens which have been dissected, photographed in the field, or otherwise treated as temporary study materials.

We have also examined, in order to estimate the incidence of anomalous teeth, the skulls of 42 seals taken pelagically in 1952, and several hundred isolated teeth (right upper canines) taken in the course of fur seal population studies.

Dr. Tadahiro Ohe (Tokyo Medical and Dental University), while studying at the University of Washington School of Dentistry in 1962, made special preparations of several early fetuses and has generously allowed us to use certain of his unpublished findings. These are noted at appropriate places.

With minor exceptions, the specimens represent seals killed at random from a normal population. They do not represent a pathological group or a group of individuals found dead and salvaged for scientific use. The demonstrated variability in dentition is believed to be typical of the population at large.

Ages of Specimens

The exact ages of the fetal specimens are not known. From embryological evidence, however, it is possible to estimate for a fetus of given weight, its implanted age and its progress toward full-term size. The evidence is sketched below.

Date of implantation.—Pearson and Eunders (1951) examined the genital tracts of 99 adult female seals killed on a Pribilof breeding ground on October 27, 1949. The seals were 4 years old or older. In each of 10 tracts the investigators found a single blastocyst, and they noted that around 6 of the blastocysts an implantation pocket was beginning to form. The general conclusion may be drawn that, by late October at least, no embryo of macroscopic size is present.

Scheffer (1960) examined another collection of adult female tracts obtained on the same breeding ground, though later in the year, as follows: four tracts on November 18, 1958, three tracts on 28 November 1951, and five tracts on December 3, 1958. Only in the December sample did he find embryos of macroscopic size: three embryos 10, 10, and 20 mm. in crown-rump length.

Douglas G. Chapman (in letter of October 15, 1957) analyzed the weights of 398 fetuses collected between mid-January and the end of June. The weights "were plotted on arithmetical probability paper (time versus percent of final value). This is essentially equivalent to assuming that the growth curve follows the logistic form." Extrapolation suggested a fetal weight of 10 g. for both male and female on November 21. Considering all the evidence available, we tentatively conclude that the mean date of implantation is in mid-November.

Fetal growth rate.—The weights of the 398 fetuses have been published (Scheffer, 1962). A chart of the weights up to the 10-day period centering on June 28 is shown in figure 1. During this last period, the mean weight of four males was 5.6 kg., and of seven females was 5.5 kg.

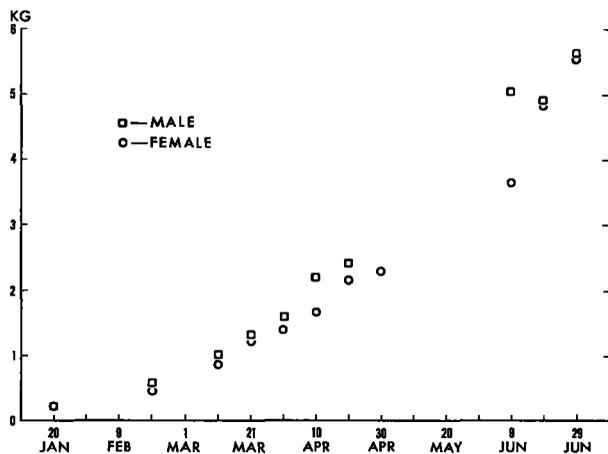


FIGURE 1.—Body weight of the fetal male and female, January to June. (Based on the weights of 209 males and 189 females (Scheffer, 1962, tables 1 and 2).)

Date of birth and weight of the newborn pup.—On a breeding ground where at least 782 pups were born in the summer of 1951, Bartholomew recorded the number born per day (Bartholomew and Hoel, 1953). The mean birth date was July 13.

At various times in summer on the breeding grounds, a total of 39 newborn and full-term fetal pups have been weighed (Scheffer and Wilke, 1953). The mean weight of 23 males was 5.4 kg., and of 16 females, 4.8 kg. These values are slightly less (7 percent) than those obtained for 11 fetal seals collected at sea in late June (see above). The discrepancy is probably a small-

sample effect, though perhaps it may also be due to natural variation, from one year to the next, in newborn size. For purposes of the present paper, mean newborn weight (MNW) is 5.4 kg. for males and 4.8 kg. for females.

Ages of postnatal specimens.—From the time it is born in midsummer to the time it departs from land in late autumn, a pup, or individual in the calendar year of its birth, is identifiable as such. At birth it wears a distinctive black pelage. By age 3 months, the black coat has been replaced by a silvery, adult-type pelage. At this stage the pup can be distinguished in the field from a yearling by its smaller size and less prominent canine teeth. We will show (table 15) that the length of the upper canine root is only 3 mm. in the late autumn pup as against 9 mm. in the yearling. Between the pup and the yearling there may be some overlap in body weight and length, but apparently none in erupted length of the canines.

The ages of many specimens older than pups have been estimated quite closely from counts of annuli on the roots (Scheffer, 1950). The exact ages are known for other specimens which had been captured, marked, and released during their first summer and recaptured in later years. Through 1962, about 527,000 pups had been marked on the Pribilof Islands by a permanent metal tag clamped to a flipper.

Dental Terminology

Dental terminology for the fur seal and, indeed, for many mammals including man, is still controversial. The terminology used in the present paper is described below.

Primary tooth (indicated by small letter).—A tooth without a fetal antecedent.

Secondary tooth (indicated by large letter).—A tooth which develops near the locus of, and eventually replaces, a primary tooth.

Deciduous tooth.—A tooth which is exfoliated in utero or before age 14 weeks. All deciduous teeth are primary.

Permanent tooth.—A tooth which is normally retained through life. Most permanent teeth are secondary; certain ones are primary. During perinatal life while certain teeth of both deciduous and permanent series are present in the oral cavity the dentition is referred to as mixed.

Classified on the basis of their position in the dental arch, the permanent teeth are of four types.

Starting with the midline, the following teeth are present in each quadrant:

Incisors (I).—The most anterior teeth; rooted in the premaxillary bone (=intermaxillary bone=incisive bone) or mandibular bone; aligned approximately in a right-and-left (transverse) direction.

Canine (C).—The large tooth at the anterolateral corner of the jaw; rooted in the maxillary or mandibular bone.

Premolars (p and P).—The first four postcanines; rooted in the maxillary or mandibular bone.

Molars (m).—The most posterior teeth, being the 5th and 6th upper postcanines and the 5th lower postcanine; rooted in the maxillary or mandibular bone.

The deciduous teeth bear the names of the teeth which replace them.

The surfaces of the teeth are designated as:

Lingual.—That surface which is in contact with the tongue.

Labial.—That surface of the incisors which is in contact with the lips.

Buccal.—That surface of the canines and postcanines which is in contact with the cheek.

Occlusal.—That surface which comes into contact with the opposing teeth.

Mesial.—That surface which contacts (or nearly contacts) the tooth anterior to it in the dental arch.

Distal.—That surface which contacts (or nearly contacts) the tooth posterior to it in the dental arch.

The crown is the exposed, enamel-covered portion of the tooth. Near the gingival line, the enamel may form a shelf-like ridge or cingulum around the base of the crown. The neck is the region of the cemento-enamel junction. The root is normally the hidden, cementum-covered portion of the tooth. The basal or apical end of the tooth is the attached end; the opposite end is usually referred to as the tip of the crown. The tooth is rooted in a socket, the bony alveolus.

Height of tooth is measured from the tip of the crown to the midpoint of the buccal or labial rim of the bony alveolus (=alveolar height=morphological height) or to the rim of the gingiva (=gingival height), along the outer surface of the tooth. Special cases are: (1) on upper incisors I1 and I2, the tip of the crown is considered to be the more anterior of the two cusps; (2) for each canine, the measurement line is along the anterolateral "prow"; (3) where the root of the molar is longitudinally furrowed, a small peak of bone may extend into the furrow, toward the crown, from the bony alveolar rim, particularly on old seals; this peak is ignored in measuring alveolar

height. A value given for "height" is the mean height of right and left teeth of a pair.

Length of root is measured on the extracted tooth, on the lingual surface from the cemento-enamel junction to the base (apex). If the tooth is double-rooted, the mean length of the two roots is given. On canines, especially, the lingual surface is identified by a distinct "keel" that runs the length of the crown.

Condylbasal length (CBL) is measured from a transverse line touching the most posterior points on the occipital condyles to a transverse line touching the most anterior points on the premaxillary bones. In other words, it is a midline measurement between a tangent to the most posterior points of the condyles to the most anterior points of the midsagittal plane of the premaxilla. On fetal skulls having a CBL of less than 75–80 mm., the condyles slope into the parietal region and the "most posterior points" are difficult to identify.

Cranial width (CW) is calvarial width, or the greatest transverse width of the brain case posterior to the zygomatic arches. In males, it exceeds mastoid width until ages 4 to 6 years, when mastoid width overtakes it. Thus, in fully adult males, cranial width equals mastoid width. In females, cranial width is always greater than mastoid width. Scheffer and Wilke (1953) defined and illustrated mastoid width as the greatest width of the skull across, "or near," the mastoid processes. Modern opinion is that the term mastoid width should be restricted to the width across the processes.

Length of postcanine series is measured on a straight line along the axis of the tooth row from the distal (posterior) margin of the bony alveolus of the posterior molar to the mesial (anterior) margin of the bony alveolus of the anterior premolar.

The principal events that we shall be concerned with in the development of the dentition are as follows: Crown calcification, or formation of enamel and dentin, begins in deciduous and permanent teeth in early fetal life. Root formation begins in each tooth before crown calcification has ceased. Growth of the root is accompanied by alveolar eruption, when the tip of the crown rises above the bony alveolar rim, and later by gingival eruption (=clinical eruption) when the tip cuts the gum and enters the oral cavity. Root

closure, or closure of the apical foramen, is followed by exfoliation (=shedding) in the deciduous teeth. Root closure in the permanent teeth is apparently followed by slow deposition of cementum; the teeth remain in place. (In the development of the deciduous dentition of the fur seal a curious and unexplained sequence is observed. In all teeth except the canines, root closure takes place a week or more in advance of gingival eruption.)

DECIDUOUS TEETH

Morphology of Deciduous Teeth

The deciduous formula (plates 1 and 2) is:

$$\frac{i1-i2-i3}{i2-i3} \quad \frac{c}{c} \quad \frac{p2-p3-p4}{p2-p3-p4}$$

The deciduous teeth are small and, excepting the canines, are nonfunctional. They are haplodont (with simple crown), though the premolars have small anterior and posterior bulges suggesting cusps. All are weakly rooted; some occasionally do not erupt from the gum; none remains after the first 13 weeks of the 3- to 4-month suckling period. Excepting those of the canines, the roots attain full size in utero. In the dentitions of two fetal males and two fetal females, ranging in body weight from 1.36 to 2.27 kg. (25 to 42 percent MNW), the following teeth are found to be double-rooted; upper p2, upper p4, and lower p4. The others are single-rooted. Kubota et al. (1961b) reported a similar finding.

Calcification, Alveolar Eruption, and Root Closure of Deciduous Teeth

Calcification.—Takano (1961), who studied stained sections and radiographs, found that the lower deciduous teeth "begin calcifying after 1 percent MNW (mean newborn weight). All of the [lower] deciduous teeth showed calcification before 2.1 percent MNW in the female and 2.4 percent MNW in the male" (p. 25).

Lamb (1962) determined the time of appearance of both dentin and enamel in the deciduous teeth of the lower jaw (table 1). His findings agree with Takano's, that calcification of all lower deciduous teeth is initiated before or soon after the fetus has attained 2 percent MNW.

As for the upper deciduous teeth, the radiographs of Kubota et al. (1961b) show that the teeth calcify at about the same time as the lower ones. Those authors, however, did not give the

TABLE 1.—Presence of dentin and enamel in the mandibular dentition of the fetus¹

[For dental terminology used in this and subsequent tables, see pages 296 to 298]

Teeth	Weight of fetus, as percentage of mean newborn weight				
	1 percent	2 percent	3 percent	4 percent	5 percent
Presence of dentin and enamel ²					
Deciduous:					
i2-----	—	DE	DE	DE	DE
i3-----	—	D	DE	DE	DE
c-----	—	D	DE	DE	DE
p2-----	D	DE	DE	DE	DE
p3-----	D	DE	DE	DE	DE
p4-----	D	DE	DE	DE	DE
Permanent:					
I2-----	—	—	—	—	—
I3-----	—	—	—	—	—
C-----	—	—	D	—	D
p1-----	—	—	—	D	D
p2-----	—	—	—	—	—
P3-----	—	—	—	—	—
P4-----	—	—	—	—	—
m1-----	—	—	—	—	—

¹ After Lamb (1962, p. 35) based on five male fetuses.

² D=dentin, E=enamel, identified by radiography and examination of stained frontal sections.

weights of the fetuses nor did they indicate the sequence of calcification of the upper deciduous teeth, beyond stating that calcification starts in the incisors.

Takano (1961, p. 25) stated that "the deciduous . . . teeth do not form completely enclosed within bone" but, rather, "crown formation takes place within a soft tissue mass which is directly connected to the gingival tissue." In other words, all deciduous teeth except the canines develop in shallow depressions rather than in true bony alveoli. Lamb (1962) concluded that histodifferentiation during tooth formation in the seal is essentially the same as in man.

In summary, we conclude that crown calcification of the deciduous teeth is progressing while the fetus is increasing in weight from about 100 g. (2 percent MNW, implanted age about 7–8 weeks) to 150 g. (3 percent MNW, implanted age about 8–9 weeks), in January.

Alveolar eruption.—Alveolar eruption of the deciduous teeth has no distinct beginning, for the smallest teeth, the medial incisors, begin to calcify at the level of the bony alveolar rim. In our smallest specimen preserved as a cleaned skull, all deciduous teeth have erupted beyond the bony alveolar rim. This is a female of 438 g. (9.1 percent MNW). Here the tooth with least alveolar height (0.5 mm.) is the upper 4th premolar, and with the greatest alveolar height (2.2 mm.) is the upper 3d incisor.

TABLE 2.—Alveolar height of deciduous teeth

Teeth	Specimen catalog number ¹						
	39	40	34	41	36	37	29
	Alveolar height (mm.)						
Upper:							
i1.....	1.0	1.0	1.0	0.5	lost	1.3	1.0
i2.....	1.0	1.2	1.0	1.0	1.6	1.3	1.0
i3.....	2.6	1.6	2.6	2.0	1.9	2.2	2.7
c ²	4.2	4.3	4.3	5.0	4.8	4.6	4.6
p2.....	2.0	2.1	2.3	3.1	2.6	2.6	2.9
p3.....	1.7	1.8	2.5	2.2	2.2	3.0	2.2
p4.....	1.8	2.2	2.6	2.5	2.1	2.2	2.5
Lower:							
i2.....	1.0	1.9	0.8	1.0	3.0	1.5	lost
i3.....	1.0	2.2	1.0	2.0	2.7	1.5	3.0
c ²	3.3	3.2	3.0	3.5	3.4	3.1	4.1
p2.....	2.7	2.1	2.6	2.9	2.6	3.0	3.1
p3.....	2.0	2.2	2.5	1.9	3.0	2.8	2.5
p4.....	2.3	2.2	2.3	2.3	2.3	2.4	2.5
Total tooth heights.....	28.6	27.5	28.5	29.9	30.2	30.5	32.1
Specimen data							
Sex.....	Male.....	Female.....	Male.....	Male.....	Male.....	Female.....	Female.....
Date.....	Mar. 30.....	Apr. 1.....	Mar. 28.....	Apr. 1.....	Mar. 30.....	Mar. 30.....	Mar. 28.....
Condylbasal length, mm.....	72.....	79.....	85.....	80.....	81.....	84.....	85.....
Body length, cm.....	40.....	41.....	42.....	47.....	42.....	42.....	43.....
Body weight, kg.....	1.4.....	1.4.....	1.8.....	2.3.....	1.8.....	1.6.....	1.8.....
Percent MNW.....	25.....	28.....	33.....	42.....	33.....	33.....	38.....

¹ All specimens are in the "Sitka 50" series; all are fetal and are listed according to increasing total tooth height.

² The canines continue to grow in perinatal life. Maximum recorded heights are: upper, 8.2 mm; lower, 5.5 mm.

In a slightly larger fetus (female, 660 g., 13.7 percent MNW) alveolar eruption of the deciduous teeth is also complete. For seven still larger specimens, the alveolar height of each tooth is shown in table 2.

We conclude that alveolar eruption begins shortly after crown calcification in the fetus of 200 g. (4 percent MNW, implanted age about 10 weeks), and has begun in all teeth in the fetus of 400 g. (8 percent MNW, implanted age 12-13 weeks), in January and February.

Root closure.—In a fetal male of 1.36 kg. (25 percent MNW) the root of upper c is open; the roots of upper i1, i2, and p4 are nearly closed; the roots of upper i3, p2, and p3 are closed; the roots of lower c and p4 are open; the roots of lower i2, i3, p2, and p3 are closed. In two fetal females of 1.36 and 1.59 kg. (28 and 33 percent MNW) all roots are closed except those of upper and lower c (plate 2).

We conclude that, in certain deciduous incisors and premolars, the roots close when the fetus has attained a weight of about 1.0 kg. (20 percent MNW). In the remaining incisors and premolars, the roots close when the fetus has attained a weight of about 1.50 kg. (30 percent MNW), when the first teeth are about to erupt from the gum.

In the canines, the roots close near time of birth, earlier in the lower pair than in the upper.

Gingival Eruption of Deciduous Teeth

In two fetuses similar in appearance, both 1.35 kg. (27 percent MNW), no teeth have erupted from the gum, though the site of each tooth is evident as a mound. Two larger fetuses present a similar picture, with teeth unerupted, though by now the upper medial incisors (i1) show through the gingival tissue as slender dark lines, and in a 1.70 kg. specimen (34 percent MNW) lower i2 is about to erupt (plate 3).

The next fetus in size (2.3 kg., 45 percent MNW) is the first-listed of table 3. Here 9 teeth out of 26 have erupted. The specimens of table 3, collected between April 21 and July 5, suggest, but do not show clearly, the sequence of eruption. We have, therefore, rearranged the data of Kubota et al. (1961a, p. 330-333), based on 25 fetal specimens, mainly collected in April when eruption is most active. The sequence of eruption is as follows:

Upper:	i1	i2	i3	c	—	p2	p3	p4
Sequence:	7	11	3	1	—	2	6	8
		4	13	5		10	12	9
Lower:	—	i2	i3	c	—	p2	p3	p4

TABLE 3.—Gingival eruption of deciduous teeth

Teeth	Specimen catalog number ¹			
	NWC 52 3119	NWC 52 3122	NWC 52 3121	US 58 790 R
	Stage of eruption ²			
Upper:				
i1.....	(x)	(x)	(x)	(x)
i2.....	/	(x)	(x)	(x)
i3.....	x	o	x	(x)
c.....	/	x	x	x
p2.....	/	x	x	x
p3.....	—	—	x	x
p4.....	—	—	o	x
Lower:				
i2.....	o	(x)	(x)	(x)
i3.....	(x)	(x)	(x)	(x)
c.....	—	o	x	x
p2.....	—	—	x	x
p3.....	—	—	—	x
p4.....	—	—	x	x

Specimen data

Age.....	Fetal.....	Fetal.....	Fetal.....	Fetal.....
Sex.....	Female.....	Female.....	Male.....	Fetal, Female.....
Date.....	April 21.....	April 21.....	April 21.....	May 9.....
Condylobasal length, mm.....	97.....	96.....	105.....	108.....
Body length, cm.....	46.....	50.....	51.....	54.....
Body weight, kg.....	2.3.....	2.4.....	2.7.....	3.4.....
Percent MNW.....	45.....	50.....	50.....	71.....

TABLE 3.—Gingival eruption of deciduous teeth—Con.

Teeth	Specimen catalog number ¹				
	26-6-60 A	5-7-60 A	BDM 549	NWC 52 3214	29-6-60 A
	Stage of eruption ²				
Upper:					
i1.....	(x)	(x)	(x)	(x)	(x)
i2.....	(x)	(x)	(x)	(x)	(x)
i3.....	(x)	(x)	(x)	x	(x)
c.....	x	x	x	x	x
p2.....	(x)	(x)	(x)	x	(x)
p3.....	(x)	(x)	(x)	x	(x)
p4.....	/	x	x	x	x
Lower:					
i2.....	(x)	(x)	(x)	(x)	(x)
i3.....	(x)	(x)	(x)	(x)	(x)
c.....	x	/	x	x	(x)
p2.....	(x)	(x)	(x)	x	(x)
p3.....	(x)	(x)	(x)	x	(x)
p4.....	(x)	/	x	x	x

Specimen data

Age.....	Newborn.....	Newborn.....	Days?.....	Fetal.....	Fetal.....
Sex.....	Female.....	Male.....	Male.....	Male.....	Female.....
Date.....	June 26.....	July 5.....	July.....	June 20.....	June 29.....
Condylobasal length, mm.....	122.....	124.....	135.....	132.....	133.....
Body length, cm.....	65.....	—.....	—.....	69.....	69.....
Body weight, kg.....	4.4.....	—.....	6.5.....	6.8.....	7.1.....
Percent MNW.....	92.....	—.....	120.....	126.....	147.....

¹ Specimens are listed in order of increasing weight or condylobasal length.
² Symbols: Dash (—)=tooth not erupted; o=tooth about to erupt; /—one tooth of a pair erupted; x=both teeth of a pair erupted; (x)=erupted but exfoliated.

We conclude that gingival eruption of the deciduous teeth is progressing while the fetus is increasing in weight from 1.65 kg. (33 percent MNW, implanted age about 20 weeks) to 3.0 kg.

(60 percent MNW, implanted age about 25 weeks), in April and May. Eruption does not proceed in an anterior to posterior direction, as in the permanent teeth. The upper deciduous teeth tend to erupt slightly in advance of the lower ones. For reasons undetermined, all of the teeth except the canines erupt after root closure has taken place.

Exfoliation of Deciduous Teeth

Table 3, which shows gingival eruption, also indicates when certain teeth exfoliate.

The incisors, first to exfoliate, are usually shed before birth, perhaps as a result of "mouthing" movements of the fetus. They begin to exfoliate soon after the onset of gingival eruption. However, in the jaws of a fetal individual of 3.4 kg. (71 percent MNW) one incisor (left upper i2) is still attached to the gum. In the jaws of a newborn male, one lower i3 is persistent. In the jaws of a male a few days old, upper i1 can be seen as a white speck on the surface of the gum, most of its length buried.

The premolars (p2, p3, and p4) disappear just before or soon after the pup starts to nuzzle and suck. In six specimens including late-term fetuses and newborn young, only one, a large full-term fetus, has retained all of its deciduous premolars. A male several days old has retained only the posterior pair (p4) in upper and lower jaws.

The canines are far more deeply rooted than are other deciduous teeth and are functional after birth, the upper ones for a longer period than the lower ones. In our sample, the maximum alveolar height of upper c is 8.2 mm. in a male about 2 weeks old. Maximum height of lower c is 5.5 mm. in a full-term fetal male. One or more deciduous canines are present in 5 out of 14 skulls of known-age pups ranging in age from 23 to 103 days, as follows:

Age in days	Deciduous canines present (X)			
	Upper right	Upper left	Lower right	Lower left
23.....	X	X	X	X
23.....	X	X	X	X
25.....	—	—	—	—
32.....	—	—	—	—
39.....	—	—	—	—
50.....	—	—	—	—
63.....	—	—	—	—
66.....	—	—	—	—
66.....	—	—	—	—
66.....	—	—	—	—
73.....	X	X	—	—
73.....	—	—	—	—
82.....	—	—	—	—
92.....	X	—	—	—
103.....	—	—	—	—

walrus calves, Fay¹ noted the frequency of occurrence of permanent incisors:

Incisors	I1	I2	I3
	Percent 56	Percent 78 22	Percent 100 66
Upper.....			
Lower.....			

In the skulls of 24 adults, however, he found no upper I1 and no lower incisors. He concluded that upper I3, the caniniform, is the only incisor consistently present in the adult, and that, in the evolution of the walrus, there has been a tendency toward absence of the medial rather than the lateral incisors.

Evidence for evolutionary loss of the lower medial incisors in *Callorhinus* is weaker. Unlike the walrus, the fur seal retains all of its permanent incisors through life. In the fur seal, however, in both deciduous and permanent dentitions and in both upper and lower arches, there is a gradient of incisor size decreasing in the direction of the midline. We agree with Kubota et al. (1961b, p. 393) that "the lower tooth opposite to the most rudimentary upper central incisor . . . has been lost."

The first two upper incisors (I1 and I2) on each side are notched transversely to accept the crown tips of the two lower incisors, which are chisel-shaped (plate 7). To the best of our knowledge, no members of the Order Carnivora have notched incisors, whereas all members of the Family Otariidae of the Order Pinnipedia do. When the seal's mouth is closed, the incisors, as well as other teeth, interlock to form a tight-fitting trap from which small fish or squid would have difficulty in escaping. The lower medial incisors (I2) are essentially tricuspidate (plate 8, A). The cusps become worn within a few weeks after birth and are not conspicuous in the adult. The incisors are usually single-rooted. We have seen only one specimen in which upper I1 and I2 are double-rooted (plate 9, A).

The canines.—The canines are like those of the Carnivora, with simple pointed crown and single root. We will discuss later (p. 308) the protracted growth period of the canine roots.

The postcanines.—The permanent molariform teeth, six postcanines in each upper quadrant and five in each lower, are superficially alike. We designate the most anterior four above and below as premolars, the rest as molars, for these reasons: (1) On histological evidence there is a discontinuity between the 4th and 5th postcanines, above and below, in the sense that the 4th is a secondary tooth while the 5th is a primary. (2) In eruptive sequence the upper first four (p1, P2, P3, and P4) fall in one group, the fifth (m1) in another. That is, in each upper quadrant the first four postcanines erupt from the gum in regular order, from anterior to posterior, but the 5th erupts out of turn, earlier than the 4th. (3) In the Superfamily Canoidea, nearest relatives of the Pinnipedia, the first four postcanines have long been regarded as premolars (Frechkop, 1955; Grassé, 1955; Gregory, 1951; Weber, 1928).

To elaborate on point 1 (above), the first upper and lower postcanine (p1), the 5th and 6th upper postcanines (m1 and m2), and the 5th lower postcanine (m1) are primary teeth. They have no surviving (functional) successors, though during fetal development each is paired for a short time on its lingual margin with the anlage of a secondary tooth (Tadahiro Ohe, in a letter of July 25, 1962).

Each postcanine may have a small anterior and a small posterior cusp or cusplet (plate 8, B). A carnassial (shearing) cusp is never found as on certain posterior teeth, usually the 5th upper and 4th lower postcanines, of Carnivora. A cingulum is conspicuous only on the postcanines of the seal, especially on the lingual side of the teeth.

The roots of the first three premolars (p1, P2, and P3), upper and lower, have a vertical groove which tends to be deeper in the posterior series of teeth. Upper m1 is nearly always double-rooted; lower m1, usually; upper m2 and upper and lower P4, occasionally (tables 4 and 5; plate 9, B). There is no apparent sex difference in shape of root of the postcanines. (Tables 4 and 5 are based on specimens 8 years old or younger. Above 6 to 8 years, unless the root is distinctly bifurcated, cementum deposition tends to obscure the original shape.)

The posterior upper tooth, m2, is consistently the smallest of the molariform teeth, and it has no antagonist. It may be absent without trace from adult skulls (p. 311). The root of m2 turns

¹ Investigations of the Pacific walrus. Terminal report, Project No. 26, Arctic Institute of North America, March 1960, 3+72 typewritten pages.

TABLE 4.—*Shape of root in permanent posterior postcanines, male*

Catalogue No.	Age of specimen	Upper teeth			Lower teeth	
		P4	m1	m2	P4	m1
		Shape of root ¹				
BDM 417.....	9 months.....	D	C	D	D	D
BDM 476.....	14 months.....	D	A	A	D	C
BDM 230.....	14 months.....	C	A	C	C	C
BDM 552.....	2 years.....	D	A	A	C	A
27-7-60A.....	2 years.....	D	A	B	D	C
BDM 50.....	3 years.....	C	A	D	D	A
BDM 53.....	3 years.....	C	B	C	D	C
BDM 51.....	4 years.....	C	A	B	D	A
BDM 68.....	4 years.....	A	A	C	A	A
BDM 107.....	5 years.....	C	A	C	C	B
BDM 149.....	6 years.....	C	A	B	D	B
Mean score ²		3.2	1.3	2.5	3.4	2.2

¹ Symbols: A=root double and distinctly bifurcated; B=root double but not distinctly bifurcated; C=root deeply furrowed but not double; D=root single, not furrowed.

² The tooth which is most consistently double-rooted has the lowest score, based on a system where A=1, B=2, C=3, and D=4.

TABLE 5.—*Shape of root in permanent posterior postcanines, female*

Catalogue No.	Age of specimen	Upper teeth			Lower teeth	
		P4	m1	m2	P4	m1
		Shape of root ¹				
BDM 545.....	7 months.....	D	A	B	D	C
BDM 16.....	15 months.....	C	A	B	D	B
BDM 407.....	2 years.....	C	A	D	D	A
NWC 52-3097.....	3 years.....	C	B	C	C	A
BDM 405.....	3 years.....	C	A	A	D	B
NWC 52-3632.....	5 years.....	B	A	B	C	A
BDM 460.....	5 years.....	C	A	B	B	B
NWC 52-3661.....	7 years.....	B	A	D	B	A
BDM 463.....	7 years.....	B	A	D	A	A
NWC 52-3272.....	8 years.....	B	A	D	B	C
Mean score ²		2.7	1.1	2.8	2.9	1.9

¹ Symbols: A=root double and distinctly bifurcated; B=root double but not distinctly bifurcated; C=root deeply furrowed but not double; D=root single, not furrowed.

² The tooth which is most consistently double-rooted has the lowest score, based on a system where A=1, B=2, C=3, and D=4.

anteriorward, perhaps thereby securing a better hold in the thicker part of the maxillary bone.

Calcification and Alveolar Eruption of Permanent Teeth

Calcification.—Calcification of the permanent teeth starts in the lower canine at fetal weight of 150 g. (3 percent MNW, about 9 weeks implanted age), in January. This is remarkably early compared with man. Kraus (1959) found that the first human permanent tooth begins to calcify at about time of birth, or 40 weeks implanted age, much later than in the seal. The permanent 1st mandibular molar of the rhesus monkey begins to calcify after the first three-quarters of prenatal development (Swindler and Gavan, 1962). Possibly this indicates a trend toward delayed calcification of permanent teeth in human evolution.

Initial calcification in the permanent dentition overlaps that in the deciduous, though is much more prolonged. That is, initial calcification is occurring in deciduous teeth at fetal stages of 2 to 3 percent MNW, while it is occurring in permanent teeth at fetal stages of 3 to 70 percent MNW. Initial calcification is last to start in the posterior upper molar, m2, in the fetus of about 3.5 g. (70 percent MNW, implanted age about 27 weeks) (Bokstrom, 1961; Takano, 1961; Kubota et al., 1961b; Lamb, 1962).

The sequence of calcification as described by Bokstrom, Takano, and Lamb was given separately for upper and lower teeth. We are unable to coordinate the sequence for the dentition as a whole, except to state that the lower teeth tend to calcify before their upper counterparts. Thus calcification has started in all of the lower teeth by fetal weight 0.9 kg. (18 percent MNW) as compared with 3.5 kg. (70 percent MNW) for the uppers. The sequence is as follows:

<i>Maxillary</i>	<i>Mandibular</i>
1. C and p1.....	C and p1.
2. I3 and m1.....	I2 and m1.
3. I1 and I2.....	P3.
4. P2, P3, and P4.....	I3 and P2.
5. m2.....	P4.

Alveolar eruption.—The sequence of alveolar eruption of the permanent teeth is difficult to demonstrate in our specimens, which are skulls cleaned by beetle larvae. In many skulls which ought to show the sequence of eruption, beetles have eaten the periodontal membranes around the partly formed teeth, allowing the loose teeth to sink into the alveoli. In the skull of a fetus of 660 g. (13 percent MNW), however, the following permanent teeth can be seen: upper canines and first three postcanines (p1, P2, and P3), lower canines and all five postcanines (p1, P2, P3, P4, and m1). All upper and lower incisors are hidden beneath dried remains of the gingiva. The last three upper postcanines (P4, m1 and m2) cannot be seen.

In a sample of seven older skulls taken from fetuses ranging in size from 1.36 to 2.27 kg. (25 to 42 percent MNW) all of the permanent teeth, except the posterior upper molar m2, are visible within their alveoli. The tips of their crowns are white, hard, and well calcified. From the stage of advancement of the tips we conclude that the first teeth—the incisors—erupt from the jaw

when the fetus has attained a weight of about 2.5 kg. (50 percent MNW, implanted age about 24 weeks), in early May.

The status of alveolar eruption near time of birth is shown in table 6 and plates 10 and 11. All of the permanent teeth have usually erupted in utero to the level of, or beyond, the bony alveolar rim.

Alveolar eruption evidently continues through life. Increase in alveolar height between ages 5 and 10-plus years is shown in table 7. Table 7 suggests that, in the female, most of the teeth grow less than 1 mm. in root length after age 5 years. Exceptions are the large caniniform incisor (upper I3) and the canines. Alveolar height of the permanent teeth in fully adult skulls of both sexes is shown in table 8 and figure 2. The causes of increase in alveolar height during adult life are not clear, though cementum deposition on the roots is quite certainly one of them. Resorption of the bony alveolar rim is perhaps another (plate 20, A).

TABLE 6.—Alveolar height of permanent teeth in fetal and newborn pups

Teeth	Specimen catalog number ¹				Alveolar height (mm) ²
	BDM 325	BDM 547	BDM 225	BDM 450	
	Upper:				
I1.....	2.0	5.8	5.1	5.3	
I2.....	2.0	5.8	5.5	6.0	
I3.....	1.2	8.0	8.2	8.4	
C.....	2.0	4.0	6.8	7.8	
p1.....	1.9	4.7	6.9	6.9	
P2.....	—	3.9	6.1	4.7	
P3.....	—	3.9	4.0	4.6	
P4.....	—	.8	3.5	2.4	
m1.....	.2	3.6	4.3	4.1	
m2.....	—	.8	—	2.0	
Lower:					
I2.....	3.9	6.3	5.9	6.2	
I3.....	2.9	6.3	6.2	7.0	
C.....	.1	.1	7.0	6.9	
p1.....	3.3	6.7	6.3	7.0	
P2.....	1.0	6.6	6.0	6.6	
P3.....	.2	7.0	6.2	6.4	
P4.....	—	1.0	3.5	3.5	
m1.....	.5	2.0	2.0	4.1	
Total tooth heights.	21.2	77.1	93.5	99.9	

Specimen data

Age.....	Fetal.....	Fetal.....	Days?.....	Days?.....
Sex.....	Female.....	Male.....	Female.....	Female.....
Date.....	July 18.....	July 31.....	July 23.....	August 11.....
Condylbasal length, mm.....	99.....	122.....	123.....	121.....
Body length, cm.....	49.....	67.....	67.....	67.....
Body weight, kg.....	2.3.....	6.0.....	4.3.....	5.2.....
Percent MNW.....	56.....	111.....	99.....	109.....

¹ Specimens are listed by increasing total tooth height.
² A dash indicates an unerupted tooth.

TABLE 7.—Alveolar height of permanent teeth in the female at ages 5 and 10+ years

Teeth	Six specimens age 5 years			Seven specimens age 10+ years ¹			Difference between means (increase)
	Alveolar height (mm)			Alveolar height (mm)			
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	
Upper:							
I1.....	6.3	7.7	6.95	7.0	8.6	7.85	0.90
I2.....	7.2	8.0	7.88	7.0	9.0	7.98	.55
I3.....	9.4	10.5	10.08	10.1	14.0	11.62	1.54
C.....	19.0	19.5	19.20	21.0	27.0	24.30	5.10
p1.....	7.8	9.8	8.78	8.7	10.9	9.47	.69
P2.....	7.3	9.0	8.33	8.3	9.7	8.94	.61
P3.....	6.7	8.5	7.77	7.4	9.2	8.21	.44
P4.....	6.3	8.0	7.43	7.2	8.6	8.09	.61
m1.....	6.1	8.0	7.03	6.2	9.0	7.81	.78
m2.....	6.3	7.0	6.73	5.5	9.0	7.27	.54
Lower:							
I2.....	6.4	7.3	6.95	6.5	7.9	7.18	.23
I3.....	6.9	8.2	7.35	7.0	9.0	7.63	.38
C.....	15.0	18.0	16.75	20.0	22.0	21.00	4.25
p1.....	7.0	8.8	7.77	7.6	9.3	8.58	.79
P2.....	6.2	8.8	7.90	7.6	9.1	8.40	.50
P3.....	7.1	9.1	8.57	8.2	10.0	9.34	.77
P4.....	7.1	9.1	8.25	7.8	9.3	8.67	.42
m1.....	6.3	8.1	7.42	7.7	9.6	8.63	.21

¹ For these old specimens, the height of the canine teeth has been "restored" by small amounts, averaging 1.1 mm, to eliminate the factor of crown-wear. The aim has been to show alveolar height as an indirect measure of root increase.

TABLE 8.—Alveolar height of permanent teeth in the adult

Teeth	Mean alveolar height of tooth (mm)	
	In seven males ¹	In seven females ²
Upper:		
I1.....	9.9	8.5
I2.....	10.2	8.5
I3.....	15.1	12.2
C.....	36.0	24.5
p1.....	12.7	10.7
P2.....	11.6	9.4
P3.....	11.6	8.8
P4.....	10.4	8.6
m1.....	10.4	8.8
m2.....	9.9	8.3
Lower:		
I2.....	8.3	7.4
I3.....	8.3	7.5
C.....	32.2	20.7
p1.....	10.3	9.0
P2.....	9.7	8.9
P3.....	10.9	9.5
P4.....	10.7	9.0
m1.....	10.7	9.0

¹ The sample included one 9-year-old, three 10-year-olds, and three older than 10, though the value shown for each tooth is the mean of the highest three. By this expedient, an attempt is made to show the height of the fully grown, but yet unworn, tooth.

² The sample included three 9-year-olds, one 10-year-old, and three older than 10, though the value shown for each is the mean of the highest three.

Gingival Eruption of Permanent Teeth

We have measured the height of the teeth above the gum in the jaws of 9 male and 10 female pups ranging in age from full-term fetal to 103 days (tables 9 and 10). We have also measured gingival height in five fully adult males and five fully adult females (table 11). As a basis for estimating the sequence of gingival eruption (table 12), we have analyzed the data for the six youngest specimens listed in table 9.

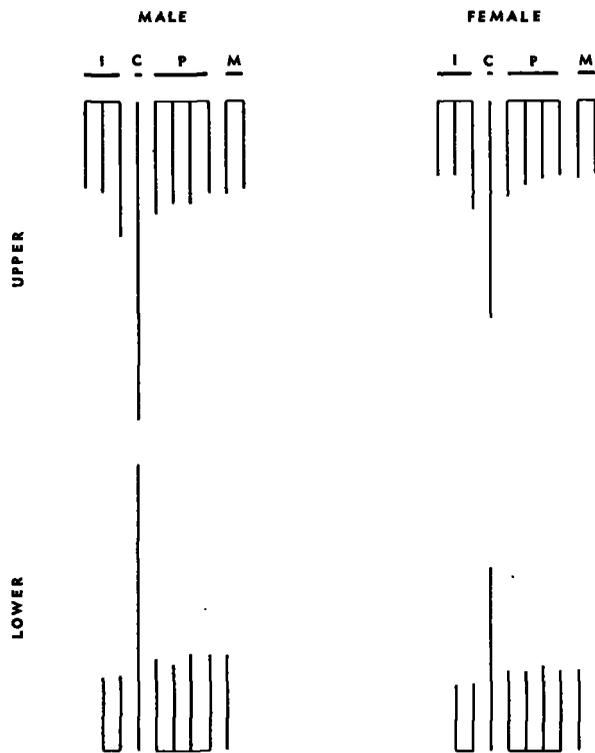


FIGURE 2.—Relative alveolar height of permanent teeth in the adult male and female. The length of each vertical bar represents the height of the tooth above the bony alveolar rim. The upper teeth are represented as pointing downward, the lower teeth as pointing upward. I=incisors, C=canines, P=premolars, M=molars. (Data from table 8.)

These represent an important perinatal period ending when the last tooth (upper m2) is about to erupt. One clue to the sequence is the number of specimens, in an age-graduated series, in which a particular tooth is present in the oral cavity. That is, a particular tooth present in six out of six specimens is assumed to have erupted earlier than another which is present in only four out of the same six specimens. A second clue is the eruptive maturation, or progress of a particular tooth toward its adult height. That is, a tooth which has already attained 80 or 90 percent of its estimated ultimate height is assumed to have erupted earlier than one in the same specimen which has attained only 60 percent of its estimated ultimate height. The estimated sequence of eruption is as follows:

	Upper:	I1	I2	I3	C	p1	P2	P3	P4	m1	m2
Sequence:		2	4	7	16	6	9	12	13	14	18
			1	3	15	5	8	10	11	17	
	Lower:		I2	I3	C	p1	P2	P3	P4	m1	

TABLE 9.—Gingival height of permanent teeth in the pup, male

Teeth	Specimen catalog number ¹				
	BDM 549	5-7-60 A	NWC 52 3214	24-7-60 A	23-8-60 A
	Gingival height (mm) ²				
Upper:					
I1-----	2.8	2.7	3.5	3.5	4.3
I2-----	2.8	2.8	3.2	3.7	4.4
I3-----	—	3.8	3.3	4.7	7.1
C-----	—	—	—	—	.2
p1-----	—	2.4	2.9	3.4	4.7
P2-----	—	.2	.2	.2	4.1
P3-----	—	—	—	—	3.0
P4-----	—	—	—	—	1.5
m1-----	—	—	—	—	2.0
m2-----	—	—	—	—	—
Lower:					
I2-----	2.3	2.2	3.4	2.5	3.2
I3-----	3.5	2.7	4.3	4.0	4.3
C-----	—	1.5	—	—	—
p1-----	2.4	.4	2.6	2.6	4.1
P2-----	.6	—	1.0	.8	4.7
P3-----	.2	—	.1	.3	4.6
P4-----	—	—	—	.8	1.8
m1-----	—	—	—	—	—
Total tooth heights.....	14.6	18.7	24.5	26.5	53.0

Specimen data					
Age.....	Days?.....	Newborn.....	Fetal.....	Newborn.....	Days?.....
Date.....	July.....	July 5.....	June 20.....	July 24.....	August 23.....
Body length, cm.....	66.....
Body weight, kg.....	6.5.....	6.8.....
Percent MNW.....	120.....	126.....

¹ Specimens are listed by increasing total tooth heights.
² A dash indicates an unerupted tooth.

Teeth	Specimen catalog number ¹			
	15-8-60 A	D 3 62	D 2 62	D 7 62
	Gingival height (mm) ²			
Upper:				
I1-----	3.0	4.5	4.0	5.0
I2-----	3.7	4.7	4.5	5.5
I3-----	7.0	8.3	7.6	6.5
C-----	3.3	.3	4.0	7.2
p1-----	5.8	5.9	5.9	5.4
P2-----	3.3	5.0	5.8	6.9
P3-----	2.7	5.0	5.4	5.3
P4-----	1.2	4.3	5.6	4.5
m1-----	2.0	5.7	5.0	6.5
m2-----	—	.1	.5	1.0
Lower:				
I2-----	3.2	3.5	3.7	4.1
I3-----	4.1	5.0	5.0	5.6
C-----	3.9	.1	1.6	3.8
p1-----	3.8	4.2	4.3	4.2
P2-----	3.6	5.9	6.0	6.3
P3-----	2.7	5.3	6.2	6.0
P4-----	.9	2.5	3.0	3.9
m1-----	.2	2.6	1.0	1.7
Total tooth height.....	54.4	72.9	79.1	88.4

Specimen data				
Age.....	Days?.....	73 days.....	66 days.....	103 days.....
Date.....	Aug. 15.....	Sept. 9.....	Sept. 2.....	Oct. 9.....
Body length, cm.....	72.....	69.....	80.....
Body weight, kg.....	7.4.....	7.9.....	11.6.....
Percent MNW.....	137.....	146.....	215.....

¹ Specimens are listed by increasing total tooth heights.
² A dash indicates an unerupted tooth.

TABLE 10.—Gingival height of permanent teeth in the pup, female

Teeth	Specimen catalog number ¹				
	26-6-60 A	15-8-60 C	23-8-60 B	15-8-60 B	23-8-60 C
	Gingival height (mm) ²				
Upper:					
I1.....	2.7	5.0	4.0	3.5	3.5
I2.....	3.3	5.0	4.4	3.6	3.8
I3.....	5.0	7.2	6.2	6.3	7.0
C.....	—	—	3.1	6.0	4.8
pl.....	3.6	5.5	4.2	5.5	5.1
P2.....	2.0	3.3	3.2	4.4	4.4
P3.....	.1	3.2	2.0	2.9	3.2
P4.....	—	1.6	1.9	.2	2.6
m1.....	—	2.0	3.6	3.5	4.8
m2.....	—	—	—	—	—
Lower:					
I2.....	2.3	2.7	3.2	3.0	2.9
I3.....	2.7	3.7	4.3	3.8	3.7
C.....	3.0	—	2.7	5.3	5.6
pl.....	2.8	4.0	4.3	3.5	3.5
P2.....	2.9	4.4	4.1	4.4	4.4
P3.....	2.5	4.2	3.5	4.1	4.4
P4.....	—	1.4	1.3	1.5	3.0
m1.....	—	—	.1	—	1.9
Total tooth heights.....	33.1	53.2	56.1	61.5	68.6

Specimen data

Age.....	Newborn	Days?...	Days?...	Days?...	Days?...
Date.....	June 26.....	Aug. 15.....	Aug. 23.....	Aug. 15.....	Aug. 23.....
Body length, cm.....	65.....	—	—	—	—
Body weight, kg.....	4.4.....	—	—	—	—
Percent MNW.....	92.....	—	—	—	—

¹ Specimens are listed by increasing total tooth heights.
² A dash indicates an unerupted tooth.

Teeth	Specimen catalog number ¹			
	D6 62	D1 62	D5 62	D4 62
	Gingival height (mm) ²			
Upper:				
I1.....	4.5	3.6	4.0	4.1
I2.....	5.0	3.8	4.1	4.1
I3.....	8.3	6.5	6.8	6.4
C.....	3.0	7.2	6.4	9.5
pl.....	6.5	5.7	6.6	7.0
P2.....	4.8	5.7	6.6	6.8
P3.....	4.2	5.0	7.0	6.2
P4.....	4.2	4.0	6.0	6.0
m1.....	6.0	5.2	5.5	7.0
m2.....	—	—	—	.5
Lower:				
I2.....	3.6	3.7	3.9	4.0
I3.....	4.8	3.8	4.5	4.2
C.....	2.0	7.4	7.0	9.0
pl.....	4.7	3.9	5.0	4.8
P2.....	5.9	4.0	5.5	5.0
P3.....	5.0	4.8	5.0	5.5
P4.....	3.3	3.0	3.7	4.3
m1.....	.6	.5	3.2	3.3
Total tooth heights.....	75.9	77.8	90.8	97.7

Specimen data

Age.....	92 days.....	66 days.....	83 days.....	73 days.....
Date.....	Sept. 28.....	Sept. 2.....	Sept. 19.....	Sept. 9.....
Body length, cm.....	67.....	73.....	73.....	73.....
Body weight, kg.....	8.4.....	6.8.....	8.0.....	8.5.....
Percent MNW.....	175.....	142.....	167.....	177.....

¹ Specimens are listed by increasing total tooth heights.
² A dash indicates an unerupted tooth.

TABLE 11.—Gingival height of permanent teeth in the adult

Teeth	Five males, age 10 years or older			Five females ages 6 to 15 years (mean 11)		
	Gingival height (mm)			Gingival height (mm)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Upper:						
I1.....	3.0	4.8	3.94	2.7	4.3	3.54
I2.....	3.7	6.0	5.18	2.8	4.8	3.96
I3.....	7.7	13.4	10.24	6.0	8.3	7.20
C.....	27.0	36.0	30.60	13.0	20.5	16.88
pl.....	6.2	7.2	6.66	4.4	8.2	6.68
P2.....	5.8	8.6	6.72	3.8	7.3	5.90
P3.....	4.1	7.1	5.66	4.0	6.9	5.58
P4.....	4.5	7.2	5.98	4.0	6.7	5.20
m1.....	4.0	10.5	6.58	2.0	16.5	4.45
m2.....	4.2	17.5	5.43	2.4	14.0	2.85
Lower:						
I2.....	.5	4.1	3.00	2.7	4.0	3.22
I3.....	1.0	6.7	4.64	3.0	4.8	4.06
C.....	22.0	27.0	25.00	9.0	17.3	13.94
pl.....	4.2	9.0	6.42	3.7	5.3	4.84
P2.....	5.0	7.8	6.42	4.5	6.1	5.43
P3.....	5.4	8.6	7.20	5.6	8.9	6.36
P4.....	4.9	9.0	7.02	4.9	6.7	6.04
m1.....	5.8	9.3	7.10	3.9	7.7	5.94

¹ Sample of four specimens only.

TABLE 12.—Estimated sequence of gingival eruption of permanent teeth in the male

Teeth	N ¹	Mean gingival height of tooth (mm)		Maturat- ion percent ⁴	Estimated sequence	
		In pups ²	In adults ³		A ⁵	B ⁶
Upper:						
I1.....	6	3.30	3.94	84	2	2
I2.....	6	3.43	5.18	66	4	4
I3.....	6	4.32	10.24	42	6	7
C.....	6	.58	30.60	2	16	16
pl.....	6	3.20	6.66	48	5	6
P2.....	6	1.33	6.72	20	9	9
P3.....	6	.78	5.66	14	11	12
P4.....	6	.45	5.98	7	14	14
m1.....	6	.67	6.58	10	12	13
m2.....	0	.00	5.43	0	18	18
Lower:						
I2.....	6	2.90	5.00	93	1	1
I3.....	6	3.82	4.64	82	3	3
C.....	2	.90	25.00	4	15	15
pl.....	6	2.65	6.42	41	7	5
P2.....	5	1.78	6.14	29	8	8
P3.....	5	1.82	7.20	18	10	10
P4.....	3	.58	7.02	8	13	11
m1.....	1	.03	7.10	1	17	17

¹ Number of specimens, out of six, in which the tooth has erupted.
² Mean gingival height of tooth in six pups (the first-listed in table 9).
³ Mean gingival height of five adults (table 11).
⁴ 100 (column 2/column 3).
⁵ Sequence estimated from percent height only (see page 304).
⁶ Sequence estimated from percent height and number of specimens in which the tooth has erupted.

It is clear that, within a tooth group, such as the upper incisors, eruption proceeds in an antero-posterior direction. It is not so clear, and is perhaps only a small-sample effect, that teeth in a mandibular group erupt earlier than those in the corresponding maxillary group. (It will be recalled that calcification is earlier in lower than in upper teeth.) The largest teeth, the canines, are 15th and 16th in order of eruption; only the

posterior molars erupt later, 17th and 18th. For about 6 weeks, while the permanent canines are erupting, the deciduous canines are functioning in their stead.

At birth, in each upper quadrant, from 2 to 7 of the 10 permanent teeth may have cut the gum (plate 4). Those which are consistently absent from the oral cavities of five newborn specimens are P4, m1, and m2. In each lower quadrant, from four to six of the eight permanent teeth may have cut the gum. Only m1 is consistently absent from the oral cavities of five newborn specimens. Upper C has erupted in one out of five specimens; lower C in two out of five. During a brief perinatal period, the pup may have no posterior teeth at all, when the three deciduous molars above and below have exfoliated and only p1 above and below have cut the gums. During this period, the posterior one-third of each gum line is dark pinkish gray, from congestion of blood at the sites of teeth about to erupt.

We conclude, from extrapolation of the evidence of tables 9 and 10, that the first permanent tooth (lower I3) to erupt from the fetal gum does so in the fetus of 4.0 kg. (80 percent MNW, about 29 weeks implanted age), in early June, about 5 weeks before birth. The last tooth (upper m2) to erupt does so 6 to 13 weeks after birth, in August to October. It is nearly erupted in a specimen of known-age 39 days; it is barely erupted in a specimen of 103 days. Permanent teeth in situ in the gums of a yearling are shown in plate 12.

There is some evidence that supernumerary teeth are late in eruption. In the right upper quadrant of a pup several weeks old, an extra premolar is just cutting the gum between p1 and P2. The normal premolars are already in place, their tips 3 mm. beyond the gum line.

An earlier statement by Scheffer (1950, p. 309) is inexact. "When the fur seal is born in mid-summer the canines, as well as most of the other permanent teeth, have erupted." In fact, while the canines may have erupted, the well-formed and functional teeth which are usually visible in each canine locus are the deciduous set. The permanent canines cut the gum before age 10 weeks (tables 9 and 10, plate 13, A).

In the skulls of five males, age 10 years or older, the tips of the teeth are highest above the gum in an adult, but not an old, individual, age 14

years (table 12). In the skulls of five females, ages 6 to 15 years, the teeth are highest in a 13-year-old (table 12).

Growth and Maturation of Permanent Teeth

Closure of the root.—As dentin is gradually deposited within the root canal of the permanent tooth, the diameter of the canal decreases. Eventually, the canal is filled and its blood vessels and nerves are pinched off (plate 13, B). The timing of root closure, by individual tooth and by sex, is shown in tables 13 and 14. Teeth such as lower

TABLE 13.—Root closure in the permanent teeth, male

Teeth	Age of specimen in months or years								
	9 mo.	14 mo.	14 mo.	2 yr.	2 yr.	3 yr.	3 yr.	4 yr.	4 yr.
	Stage of root closure ¹								
Upper:									
I1	—	o	—	x	x	x	x	x	x
I2	—	o	—	x	o	x	x	x	x
I3	—	—	—	—	—	—	—	—	—
C	closes in 7th to 10th year								
p1	—	—	—	—	—	—	—	o	—
P2	—	—	—	—	—	o	—	x	x
P3	—	—	—	—	—	x	—	x	x
P4	—	—	—	—	—	x	o	x	x
m1	—	—	—	x	o	x	x	x	x
m2	—	—	—	x	o	—	o	x	x
Lower:									
I2	—	x	x	x	x	x	x	x	x
I3	—	x	x	x	x	x	x	x	x
C	closes after 12th (?) year								
p1	—	—	—	x	o	x	o	x	x
P2	—	—	—	x	o	x	o	x	x
P3	—	—	—	o	—	x	o	x	x
P4	—	—	—	—	—	x	—	x	x
m1	—	—	—	o	—	x	o	x	x

¹ Symbols: Dash (—)=root canal open; o=root canal nearly closed; x=root canal closed.

TABLE 14.—Root closure in the permanent teeth, female

Teeth	Age of specimen in months or years					
	3 mo.	7 mo.	15 mo.	2 yr.	3 yr. ¹	3 yr. ²
	Stage of root closure ³					
Upper:						
I1	—	—	o	x	x	x
I2	—	—	o	x	x	x
I3	—	—	—	—	—	x
C	closes after 15th year					
p1	—	—	—	—	—	x
P2	—	—	—	—	—	x
P3	—	—	—	—	o	x
P4	—	—	—	—	x	x
m1	—	—	o	x	o	x
m2	—	—	—	—	o	x
Lower:						
I2	x	x	x	x	x	x
I3	o	o	x	x	x	x
C	closes in 7th or 8th year					
p1	—	—	—	o	o	x
P2	—	—	—	x	x	x
P3	—	—	—	—	o	x
P4	—	—	—	—	o	x
m1	—	—	—	—	o	x

¹ Slightly younger than 3 years on April 12.

² Slightly older than 3 years on September 11.

³ Symbols: Dash (—)=root canal open; o=root canal nearly closed; x=root canal closed.

TABLE 15.—Length of root of the permanent right upper canine with increasing age¹

Age	Males			Females		
	Length of root			Length of root		
	Number	Range	Mean	Number	Range	Mean
Years		<i>Mm.</i>	<i>Mm.</i>		<i>Mm.</i>	<i>Mm.</i>
0 ²	4	0.3-0.7	0.5			
1 ³	7	3.2-5.5	4.5			
1.....	2	9.1-9.2	9.1	2		8.9
2.....	25	9.5-13.0	11.6	8	10.0-13.6	12.1
3.....	8	12.3-15.5	13.6	20	11.9-17.2	13.7
4.....	17	13.8-17.7	16.2	20	12.2-17.0	14.7
5.....	2	17.0-17.1	17.1	20	13.7-18.0	14.9
6.....	1		21.8	20	13.7-20.6	16.7
7.....	2	22.3-24.1	23.2	20	16.5-20.2	18.5
8.....	1		33.1	18	15.6-20.9	18.3
9.....				5	15.7-19.8	18.3
10.....	3	28.4-33.2	30.3	21	17.6-23.9	19.8
11.....				13	18.9-23.4	20.3
12.....				2	17.0-23.0	19.6
Old ⁴				9	19.1-24.3	21.6

¹ Unless otherwise noted, data are from known-age (marked) seals recovered on the Pribilof Islands in summer.

² Full-term fetal, July 6, 1957.

³ "Yearlings" about 6 to 7 months old, found dead or dying on Oregon beaches after a storm, late January to early February 1950.

⁴ Nine canines with crown worn and root canal closed, or nearly closed, selected from 100 unmarked females killed on a breeding ground, October 3, 1950.

incisors, with slender roots, close earlier than teeth, such as canines, with larger roots.

Evidence on the maximum age of root closure in male teeth is poor (table 13). The oldest known-age skull in the collection is a 14-year-old. In three 10-year-olds, the diameter of the right upper canine root canal is 6, 8, and 8 mm., respectively—far from closed. In an 11-year-old, it is 8 mm., while the diameter of the lower canine canal is 0.3 mm. In the 14-year-old it is 7 mm., and the canals of the lower canines are closed. In a very old individual of undetermined age, with worn and polished teeth, the root of the left upper canine still has a canal 0.6 mm. in diameter, whereas the root of the left lower canine has long since closed. We tentatively conclude that upper canines in the male close after the 20th year (or in some individuals never?); lower canines after the 12th.

Evidence on the maximum age of root closure in female teeth is more conclusive (table 14). In the upper canines of 44 females (23 ten-year-olds, 15 eleven-year-olds, 4 twelve-year-olds, and 2 fifteen-year-olds), the diameter of the root canal varies from 0.1 to 1.5 mm., average about 0.5 mm. In the two 15-year-olds, the diameter of the canal is 0.2 mm. In a 21-year-old, the canal is closed. We conclude that the female upper canine closes after the 15th year.

Growth of the root.—Increase in size of the growing root has been studied for the right upper

canine. This tooth was selected in 1949 as the one which would be used, in future Pribilof seal studies, as an indication of age. Length of root by age and sex is given in table 15. Changes in the root are illustrated in plates 14 and 15. At birth, when the upper canine is largely hidden within the bony alveolus, the root is less than 1 mm. in length. On the evidence of its size and shape, the root grows rather uniformly during the 3- to 4-month period when the pup is nursing. At time of weaning, when the pup learns to feed for itself, growth of the root declines. The evidence is a faint "first-autumn depression" or valley circling the root. Some teeth show it plainly (plate 15), others do not. At completion of the first year of life, a "second-autumn depression" is formed around the root. Another depression is formed in the third autumn, and in each successive autumn until the seal approaches an age of 10 to 15 years. Then each depression tends to become shallow and narrow and to be hidden by a deposit of cementum (plate 16).

As long as the root canal remains open, dentin is deposited on the walls of the root cavity, the deposit being thicker and more opaque in winter, spring, and summer; thinner and more translucent in fall. As a result of this unequal deposition, each annual layer is visible on a longitudinally sectioned tooth as a discrete cone slightly smaller than, and nesting within, the cone of the previous year (plate 17). Meanwhile, a thin but fairly distinct layer of cementum is being laid down annually on the outside of the root. The source of the cementum is the connective tissue surrounding the root, not the pulp of the tooth. Cementum layers continue to be laid down after the root canal closes. Zander and Hürzeler (1958) measured cementum thickness on 233 single-rooted human teeth and found that it showed a straightline increase with age. Thickness tripled between ages 11 and 76 years. This was "surprising in view of the fact that growth processes usually decrease with advancing age" (p. 1043).

Kubota et al. (1961) described growth layers near the level of the cemento-enamel junction. These are, from outside inward: cementum, prenatal dentin (opaque), neonatal line (translucent), postnatal dentin consisting of (a) interglobular dentin mixed with the granular layer of Tomes and (b) a translucent layer which is formed in spring. When the root canal closes, dentin ceases to

form in regular conical layers. While stratified deposits of some tooth substance continue to form at the base of the root, they tend to be thin and irregular, and we do not know what to call them. We sliced longitudinally and polished all of the right teeth of a known-age 13-year-old female. The smallest tooth, the 1st lower incisor, whose root canal probably closed within the 1st year of life, shows no distinct layers in the dentin. The lower canine, where the root canal probably closed in the 7th or 8th year, shows seven conical layers of dentin. The upper canine, where the root canal is still open, shows 13 layers.

Annual growth lines in the teeth of the seal develop in both sexes, and in captive as well as wild individuals. Growth of the root is always slower in autumn. We suggest that the period of slow growth is related to the annual molt of the pelage which takes place in autumn in seals of all classes (Scheffer, 1962). A male seal was captured on the Pribilof Islands on October 17, 1948 and was delivered to the San Diego Zoo a few days later. It died on May 18, 1953, after almost 5 years in captivity. The root of its right upper canine is of normal size (length 22.6 mm.); the growth ridges are somewhat confused (plate 18). Nevertheless, two experienced biologists (C. E. Abegglen and A. Y. Roppel) estimated correctly and independently the age of the seal as 5 years. Mansfield and Fisher (1960) counted 18 to 20 layers on the tooth of a harbor seal *Phoca* that had been brought as a pup to the Seattle Zoo and died there at age 19½ years.

The relative importance of the various environmental factors which contribute to the formation of growth ridges cannot now be evaluated. It seems possible both that molt in autumn may cause a decrease in deposition of root substance and that heavy feeding in spring may cause an increase. There is ancillary evidence that most of the annual body weight increment is added in spring.

From the evidence of certain teeth (plate 19, B and C), the accretion of root substance may suddenly accelerate or decelerate. Ridges on the surface of the growing root, finer than annuli and spaced between them, are thought to originate in individual periods of intensive feeding. Plate 19, A reproduces a gelatin impression of the surface of a yearling male canine tooth. The seal was killed on September 13, at estimated age 14 months.

Around the root one can count about 25 fine ridges, more or less distinct, arranged in a near-rhythmic pattern.

Typical postcanine roots in situ in a middle-aged seal are illustrated in plate 8. Other roots, somewhat atypical as a result of bone resorption, are shown in plate 20, A.

Crown.—The crowns of the permanent teeth become streaked and stained dark brown soon after birth. In a specimen a few days old taken on June 26, (female, 4.4 kg., 92 percent MNW) the teeth are already moderately stained. The pigment is heaviest on the posterior series of teeth and on buccal, as opposed to lingual, surfaces. The chemistry of the pigment is not known.

Tooth crowns of the fur seal do not suffer wear to the same extent as do crowns of land carnivores like wolf and bear. Where the dentin of the seal tooth has been exposed, its surface becomes polished and shiny (plate 20, B).

For each canine showing crown-tip wear, we have estimated its height, had there been no wear (tables 7 and 8). Tip wear is insignificant in 1-, 2-, and 3-year-olds. On the upper canines of 6- and 7-year-olds, it may reach 1 mm. in males and 0.7 in females; on the lower canines, a little less.

GROWTH CHANGES IN SKULL AND JAWS

In both sexes, the halves of the mandible remain separate through life, as in the dog but not in man. They are united by tough connective tissue and cannot easily be pulled apart. Right and left molariform tooth rows are nearly parallel. They may diverge posteriorly up to 5 degrees. Each approaches a straight line, though it may be slightly convex or, rarely, concave. The shape of the tooth row does not vary appreciably with age or sex (plates 21 and 22).

A useful indication of physiological age or maturity of the individual is the size of the skull. We have measured condylobasal length and cranial width for 76 skulls (34 males and 42 females), and have compared them with measurements of the upper and lower postcanine series (tables 16 and 17 and figures 3 and 4). The results are summarized on page 310.

Male

Condylobasal lengths in two newborn males are 121 and 122 mm.; in three old adults they are

TABLE 16.—Skull size and length of the permanent postcanine series, by age, male

Age	Specimens	Condylobasal length	Cranial width	Length of postcanine series	
				Upper	Lower
Percent MNW ¹	Number	Mm.	Mm.	Mm.	Mm.
25.....	1	72	55	19	21
33.....	1	81	58	20	18
38.....	1	85	61	20	20
42.....	1	90	67	22	21
Newborn.....	3	121	85	33	29
Weeks, 1-2.....	1	129	86	33	32
Ca. 9 months.....	1	143	91	35	30
Ca. 14 months.....	2	165	95	39	35
Years:					
2.....	2	173	93	40	33
3.....	3	180	98	43	36
4.....	2	191	95	44	36
5.....	3	200	102	47	38
6.....	2	213	107	49	40
7.....	2	215	106	45	38
8.....	4	241	133	53	43
9.....	1	232	128	52	43
10.....	3	230	122	50	41
10+.....	3	241	132	54	43
Total.....	34				

- ¹ Fetus, 25 percent of mean newborn weight.
- ² One skull has an extra pair of upper premolars.
- ³ One skull lacks a pair of upper premolars.
- ⁴ For one broken skull, measurements of skull size are lacking.

TABLE 17.—Skull size and length of the permanent postcanine series, by age, female

Age	Specimens	Condylobasal length	Cranial width	Length of postcanine series	
				Upper	Lower
Percent MNW ¹	Number	Mm.	Mm.	Mm.	Mm.
28.....	1	79	59	21	19
33.....	1	84	64	21	20
38.....	1	85	63	21	22
56.....	1	99	76	24	22
Newborn.....	3	122	84	33	27
Ca. 3 months.....	1			33	29
Ca. 7 months.....	1	140	88	33	28
Ca. 8 months.....	1	145	89	35	31
Ca. 15 months.....	2	159	95	38	35
Years:					
2.....	3	163	93	40	32
3.....	2	173	94	39	32
4.....	4	172	93	42	33
5.....	7	174	91	41	34
6.....	2	185	93	48	37
7.....	2	183	98	44	37
8.....	2	180	92	43	33
9.....	3	183	95	44	35
10.....	1	180	91	42	33
10+.....	5	190	96	46	36
Total.....	42				

¹ Fetus, 28 percent of mean newborn weight.

237, 242, and 243 mm. The difference represents a mean increase through life of 98 percent over newborn size. Cranial widths in two newborn males are 85 and 86 mm.; in three old adults they are 131, 131, and 135 mm. The difference represents a mean increase through life of 55 percent. The skull of a male at age 8 or 9 is about as large as it ever will be, though length and width increase slightly after age 9 as a result of bony growth of the premaxillary and mastoid processes.

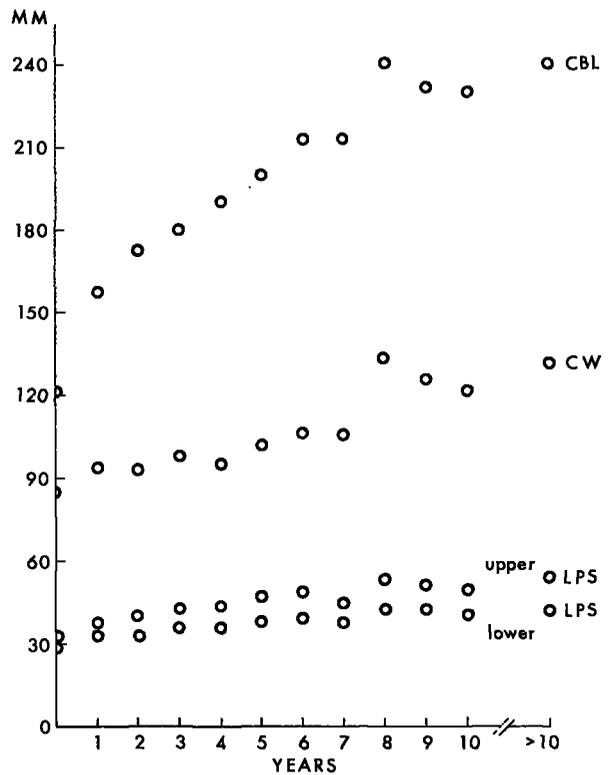


FIGURE 3.—Condyllobasal length, cranial width, and length of permanent postcanine series, by age, male. (From table 16, based on 30 specimens.)

In estimating the age at which skull growth reaches a plateau, we have also referred to published data on condyllobasal length and mastoid width of 108 fur seal skulls (Scheffer and Wilke, 1953).

Lengths of upper postcanine series in two newborn males are 32 and 33 mm.; in three old adults, 53, 55, and 55 mm. The difference represents a mean increase of 67 percent. The upper jaw does not increase in length after age 8 or 9.

Lengths of lower postcanine series in two newborn males are 29 and 29 mm.; in two old adults, 43 and 43 mm. The difference represents a mean increase of 48 percent. The lower jaw does not increase in length after age 8 or 9. Growth changes in the lower jaw of the male are illustrated in plate 23. In the sample illustrated, the length of the jaw increased by 54 percent in the period from birth to age 3 (the age of sexual maturity in some males). It increased 53 percent between age 3 and adulthood. This growth spurt in postpubertal life, observed in the male

only, is related to the fact that the fur seal is polygynous. To the adult male attempting to hold his place in a fiercely competitive social order, strong jaws and teeth have survival value. In the same sample, the ratio of length of jaw to length of postcanine series is 2.4:1 for the full-term fetus and 3.9:1 for the old adult. The postcanine tooth-row grows slower than the mandibular corpus posterior to it. The postcanine tooth-row itself increased 45 percent (29 to 42 mm.). As the tooth row lengthens, the diameter of each socket increases; the spatial arrangement of the tooth row remains fairly constant.

Female

Condylbasal lengths in two newborn females are 121 and 123 mm.; in five old adults they are 185, 189, 191, 191, and 196 mm. The difference represents a mean increase through life of 56 percent. Cranial widths in two newborn females are 82 and 96 mm.; in five old adults they are 95, 96, 96, 96, and 99 mm. The difference represents a mean increase through life of 15 percent. The skull of the female does not appear to grow in length or width after age 5 or 6. With respect to skull size, the female reaches maturity about 3 years before the male.

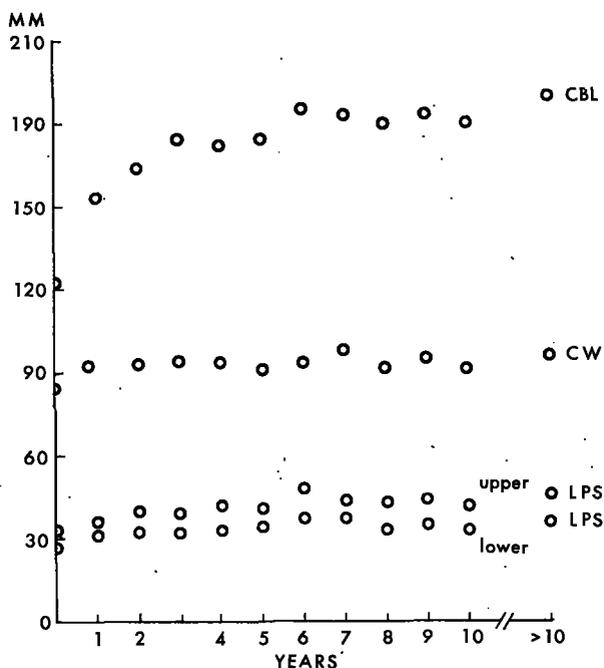


FIGURE 4.—Condylbasal length, cranial width, and length of permanent postcanine series, by age, female. (From table 17, based on 38 specimens.)

Length of upper postcanine series in two newborn females are 32 and 33 mm.; in five old adults 45, 45, 46, 46, and 49 mm. The difference represents a mean increase of 42 percent. The upper jaw continues to grow in length until age 5 or 6.

Lengths of lower postcanine series in two newborn females are 26 and 28 mm.; in five old adults 34, 35, 36, 37, and 37 mm. The difference represents a mean increase of 33 percent. The lower jaw continues to increase in length until age 5 or 6.

ANOMALIES

Prenatal

In a sample of 123 skulls of both sexes, 14 (or 11 percent) show anomalies of the dentition. Four have extra teeth. Ten lack one or two teeth, and apparently did not have them at time of birth.

Of the four skulls with extra teeth, three have extra premolars in the upper middle series and one has extra premolars in the lower middle series (plate 24). The skull with extra lower premolars is remarkable for having 45 teeth—9 extra! It has three extra upper incisors lingual to, and similar to, I1 and 2; four extra lower incisors lingual to I2 and 3; and a pair of extra lower premolars between P2 and 3.

In the dog, when supernumerary teeth are present, they are incisors or premolars, usually unilateral and in the upper jaw (Miller, 1952). In the fur seal (as noted in three out of four cases), extra premolars in the upper jaw are more common than in the lower.

Of the 10 skulls with teeth prenatally lost, 4 lack one and 6 lack both upper m2. This posterior tooth, which is unopposed, is small and weak. It quite certainly has the least function of any of the teeth. Where there is unilateral absence, the remaining one may be unusually small, or be broken off at the alveolar rim. We suspect that m2 can be lost in early postnatal life when the maxillary bone is still growing actively and is able to fill in the bony alveolus without trace. Thus, one cannot always distinguish, in an adult skull, between prenatal and postnatal loss of m2. According to Simpson (1961, p. 100) "a tooth . . . that no longer occludes or that is in the process of reduction and loss of essential function (like the human wisdom teeth) is demonstrably exceptionally variable in both structure and size."

In addition to the random sample of 123 skulls utilized in this report, 4 selected "freaks" were

TABLE 18.—Beginning events in the dental development to age 12 weeks¹

Body weight	Approximate percent mean newborn weight	Approximate month	Deciduous teeth				Permanent teeth		
Kg									
0.05	1	December							
10	2	January	CC						
15	3	January	CC				CC		
20	4	January		AE			CC		
25	5	January		AE			CC		
30	6	February		AE			CC		
35	7	February		AE			CC		
40	8	February		AE			CC		
45	9	February					CC		
5	10	February					CC		
1.0	20	March			RC		CC		
1.5	30	March		GE	RC		CC		
2.0	40	April		GE	RC		CC		
2.5	50	April		GE	RC	EX	CC	AE	
3.0	60	May		GE	RC	EX	CC	AE	
3.5	70	May			RC	EX	CC	AE	
4.0	80	June			RC	EX		AE	GE
4.5	90	June			RC	EX		AE	GE
5.0	100	July (birth)			RC	EX		AE	GE
8.0	180	August (age 6 weeks)				EX			GE
13.0	260	October (age 12 weeks)							RC

¹ These events are beginning in one or more teeth: CC=crown calcification, AE=alveolar eruption, GE=gingival eruption, RC=root closure, and EX=exfoliation.

observed: (1) a skull with an extra pair of upper premolars between P2 and 3, (2) a skull with supernumerary upper canines, (3) a skull with seven extra teeth in the upper and lower series of incisors and anterior premolars, and (4) a skull with an extra pair of lower molars. The last was figured by Scheffer (1958). It is remarkable in that it represents the only known specimen having an extra tooth at the posterior end of a tooth row.

Postnatal

Damage represented by empty sockets, or teeth broken off, is apparent in both sexes and in both upper and lower jaws. In the lower jaw of a 7-year-old female, P3 is deformed and blackened (plate 25, A). Evidently the crown was accidentally broken; then an abscess formed around the root and the bone of the socket eroded. In a young male, about 6 years old, that died in the Seattle Zoo, right upper C is greatly deformed (plate 25, B). Here also a root abscess is the cause. From the left mandible of an old female, the four premolars have been lost and the bone itself has undergone extensive change (plate 26, A). The bony alveoli of a male raised in captivity have a spongy, eroded appearance (plate 26, B).

We have seen no evidence of caries in seal teeth. Hall (1940) examined the skulls of 3,761 land carnivores and found caries in 2 percent of 360 bears (*Ursus* and *Euarctos*), but in no other carnivores.

SUMMARY AND CONCLUSIONS

The dentitions of 167 specimens of *Callorhinus ursinus* ranging from early fetal life to adulthood have been studied. Crown and root morphology of deciduous and permanent teeth are described. A terminology is presented for the kinds of teeth, their topographic relationships, their developmental stages, and their measurements. The time sequence is shown for calcification, alveolar eruption, gingival eruption, root closure, and exfoliation (table 18). Formulas are presented for deciduous, mixed, and permanent dentitions (fig. 5). Increase with age is shown for skull length and width, and for length of upper and lower postcanine series. Certain prenatal and postnatal anomalies, especially supernumerary and absent teeth, are described. The following observations and conclusions are believed to be new or worthy of emphasis:

1. Calcification is initiated in all deciduous teeth between implanted ages 7 and 9 weeks, when the fetus has attained 2 or 3 percent of its estimated newborn weight. Initial calcification in the permanent teeth overlaps that in the deciduous teeth, though it is still in progress up to about implanted age 27 weeks and 70 percent estimated newborn weight. The very early development of the permanent teeth enables the young seal, at age 3 or 4 months, to convert abruptly from a diet of milk to one of fish and squid.

Body weight in kg	Approximate percent mean newborn weight	Gingivally erupted dentition	Dental formulas *												Number of teeth							
			Incisors						Canines		Premolars						Molars					
			p	S	p	S	p	S	p	-	p	S	p	S	p	-	p	-				
1.5	30	DECIDUOUS																				
2.0	40																					
2.5	50																					
3.0	60																				7	7
3.5	70																				6	6
4.0	80	MIXED																				
4.5	90																					
5.0	100 (newborn)																				10	10 **
5.0	100 (newborn)	PERMANENT																			9	9
8.0	160 (6 weeks)																				10	10
278.0	(mature male)																				8	8
63.0	(mature female)																					

FIGURE 5.—Dental formulas at three stages of development.

*Primary teeth are in small letters; secondary teeth in large. Maxillary teeth are shown above the bar, mandibular teeth below.

**The mixed (successional) dentition is highly variable. Shown here are teeth which have usually erupted in the perinatal period.

2. With the exception of the canines, the deciduous teeth are nonfunctional. The smaller ones (incisors) exfoliate during fetal life; the premolars exfoliate during perinatal life; one or another of the canines may persist for 13 weeks after birth. With the exception of the canines, which cut the gums early, the sequence of gingival eruption is random, or nondirectional, in the tooth rows.

3. At birth, the crown tips of all of the permanent teeth are at, or above, the bony alveolar rims. From two to seven teeth in each upper quadrant, and from four to six in each lower quadrant, may have cut the gums. Variability in the neonatal (mixed) dentition has apparently little significance for survival. The last permanent tooth (upper m2) erupts at age 6 to 13 weeks. Directionally, the sequence of gingival eruption is anterior to posterior, except in the canines.

4. If a "lower 1st incisor" was present in ancestral seals, it has left no embryological trace. In each upper quadrant the 1st premolar (1st post-canine) and the 1st and 2d molars (5th and 6th postcanines) are, on embryological evidence, primary permanent teeth. Similarly, in each lower quadrant the 1st premolar and the 1st molar are primary permanent teeth.

5. The lower medial incisors (I2) and the upper and lower premolars (P2, P3, and P4) usually have

anterior and posterior cusplets, suggesting an origin in distinctly tricuspid, perhaps triconodont, teeth. Upper m2 is nearly always double-rooted; certain other posterior teeth are occasionally so. The percentage of consistently double-rooted teeth in the deciduous dentition is 23.1; in the permanent dentition 5.5, suggesting that there has been an evolutionary trend toward a single root.

6. The roots of the permanent teeth continue to grow through life, more slowly after the root canal closes. It closes at age 3 months in small teeth, and at some time after 20 years in large teeth. Annual discontinuities (ridges and layers) occur outside and inside the root; up to 27 have been counted.

7. Skull size and length of postcanine series increase very little after age 8 or 9 years in the male and age 5 or 6 years in the female.

8. In a sample of 123 skulls, the dentitions of 14 (or 11 percent) are anomalous. Four have supernumerary teeth and ten have prenatally absent teeth. Supernumerary teeth have been found in the molar series only once: in lower m1 locus. Upper m2 has no antagonist and, when present, is quite variable in size.

9. Among the problems remaining unsolved are the sequence of calcification of the upper deciduous teeth and the mechanism of gingival eruption of

the deciduous teeth. The frequency distribution of deciduous and permanent teeth in the neonatal (mixed) dentition is known to be highly variable. A more precise understanding of the variability could be obtained by collecting more specimens of newborn pups.

LITERATURE CITED

- ALLEN, GLOVER M.
1880. History of North American pinnipeds, a monograph of the walruses, sea-lions, sea-bears, and seals of North America. United States Geological and Geographical Survey of the Territories, Miscellaneous Publications 12, 16+785 pp.
- ALLEN, JOEL ASAPH, and CHARLES BRYANT.
1870. On the eared seals (Otariadae), with detailed descriptions of the North Pacific species . . . Bulletin of the Museum of Comparative Zoology, Harvard, vol. 2, pp. 1-108, 3 pls.
- BARTHOLOMEW, GEORGE A., JR., and PAUL G. HOEL.
1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. Journal of Mammalogy, vol. 34, No. 4, pp. 417-436.
- BOKSTROM, PETER.
1961. A study of the maxillary permanent dentition of the Alaskan fur seal during fetal life. Seattle, University of Washington, Thesis, Master of Science in Dentistry, 55 typewritten pages.
- CHIASSON, ROBERT B.
1955. Dental abnormalities of the Alaskan fur seal. Journal of Mammalogy, vol. 36, pp. 562-564.
1957. The dentition of the Alaskan fur seal. Journal of Mammalogy, vol. 38, pp. 310-319.
- FRECHKOP, SERGE.
1955. [Teeth of pinnipeds, Tome 17, Fascicle 1, p. 299-300.] In *Traité de zoologie* . . . publié sur la direction de Pierre -P. Grassé. Masson, Paris, 18 vols.
- GRASSÉ, PIERRE -P.
1955. [Teeth of carnivores, Tome 17, Fascicle 1, p. 205-207.] In *Traité de zoologie* . . . publié sur la direction de Pierre -P. Grassé. Masson, Paris, 18 vols.
- GREGORY, WILLIAM KING.
1951. Evolution emerging. Macmillan, New York, 2 vols.
- HALL, E. RAYMOND.
1940. Supernumerary and missing teeth in wild mammals of the orders Insectivora and Carnivora, with some notes on disease. Journal of Dental Research, vol. 19, pp. 103-143 (including 12 pls.).
- HOWELL, A. BRAZIER.
1929. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). Proceedings of the U.S. National Museum, vol. 73, pp. 1-142, 1 pl.
- KELLOGG, REMINGTON.
1922. Pinnipeds from Miocene and Pleistocene deposits of California . . . and a résumé of current theories regarding origin of Pinnipedia. Bulletin of the Department of Geology, University of California, vol. 13, pp. 23-132.
- KRAUS, BERTRAM S.
1959. Calcification of the human deciduous teeth. Journal of American Dental Association, vol. 59, pp. 1128-1136.
- KUBOTA, KINZIRO, HIROSHI KOMURO, FUKUZO NAGASAKI, MORIO TSUBOI, and KOJI MATSUMOTO.
1961a. The eruption and shedding of teeth in the fur seal. *Okajimas Folia Anatomica Japonica*, Band 37, Heft 4-5, pp. 331-337. (English)
1961b. The calcification of teeth of the fur seals (roentgenographic examination). *Okajimas Folia Anatomica Japonica*, Band 37, Heft 6, pp. 339-419. (English)
- KUBOTA, KINZIRO, FUKUZO NAGASAKI, KOJI MATSUMOTO, and MORIO TSUBOI.
1961. Histological studies on the growth layers in the maxillary canines of fur seals as an indicator of age. Part 1. The teeth at the age of one to nine year. Bulletin, Tokyo Medical and Dental University, vol. 8, No. 3, pp. 261-285. (English)
- KÜKENTHAL, WILLY.
1894. Entwicklungsgeschichtliche Untersuchungen am Pinnipediergebnisse. *Jenaische Zeitschrift f. Naturwissenschaft*, Band 28 (Neue Folge, Band 21), pp. 76-118, 2 pls.
- LAMB, MARDON C.
1962. Observations on the embryonic development of the mandibular dentition in the Alaska fur seal. Thesis, Master of Science in Dentistry, University of Washington, Seattle, 4+57 pp. processed.
- LAWS, R. M.
1962. Age determination of pinnipeds with special reference to growth layers in teeth. *Zeitschrift für Säugetierkunde*, Band 27, Heft 3, pp. 129-146.
- LUCAS, FREDERIC A.
1899. The dentition of the fur seal [part 3, pp. 9-11, pls. 1-2]. In *The fur seals and fur-seal islands of the north Pacific Ocean* . . . by Jordan *et al.* U.S. Treasury Department, Document 2017, 4 parts.
- MANSFIELD, A. W., and H. D. FISHER.
1960. Age determination in the harbour seal, *Phoca vitulina* L. *Nature*, vol. 186, pp. 92-93.
- MILLER, MALCOLM E.
1952. Teeth [pp. 32-35]. In *Guide to the dissection of the dog*. 3d edition, reprinted. Published by author; Ithaca, New York, 427 pp.
- OSBORN, HENRY FAIRFIELD.
1907. Pinnipedia [pp. 143-144]. In *Evolution of mammalian molar teeth*. . . Edited by W. K. Gregory. Macmillan, New York, 10+250 pp.

- PEARSON, ANITA K., and ROBERT K. ENDERS.
1951. Further observations on the reproduction of the Alaskan fur seal. *Anatomical Record*, vol. 111, No. 4, pp. 695-711.
- RAND, ROBERT W.
1950. On the milk dentition of the Cape fur seal. *Journal of the Dental Association of South Africa*, vol. 5, pp. 462-471.
- SCHEFFER, VICTOR B.
1950. Growth layers on the teeth of Pinnipedia as an indication of age. *Science*, vol. 112, pp. 309-311.
1958. Seals, sea lions, and walruses; a review of the Pinnipedia. Stanford University Press, 10+179 pp., 32 pls.
1960. Early embryos of the northern fur seal. *Mammalia*, Tome 24, No. 3, pp. 482-483, 1 pl.
1962. Pelage and surface topography of the northern fur seal. U.S. Fish and Wildlife Service, North American Fauna 64, 6+206 pp.
- SCHEFFER, VICTOR B., and FORD WILKE.
1953. Relative growth in the northern fur seal. *Growth*, vol. 17, pp. 129-145.
- SERGEANT, D. E.
1959. Age determination in odontocete whales from dentinal growth layers. *Norsk Hvalfangst-Tidende (Norwegian Whaling Gazette)*, vol. 48, pp. 273-288, illus., June.
- SIMPSON, GEORGE GAYLORD.
1945. The principles of classification and a classification of mammals. *American Museum Natural History, Bulletin* 85, 16+350 pp.
1961. Principles of animal taxonomy. Columbia University Press, New York, 14+247 pp.
- SWINDLER, D. R., and J. A. GAVAN.
1962. Calcification of the mandibular molars in rhesus monkeys. *Archives of Oral Biology*, vol. 7, pp. 727-734.
- TAKANO, JAMES H.
1961. A study of the mandibular dentition of the Alaska fur seal fetus. Seattle, University of Washington, Thesis, Master of Science in Dentistry, 56 typewritten pp.
- TODD, T. WINGATE.
1918. Pinnipedia [p. 185-187]. *In* An introduction to the mammalian dentition. Henry Kimpton, London, 290 pp.
- WEBER, MAX.
1928. Carnivora Pinnipedia [Band 2, pp. 342-354]. *In* Die Säugetiere . . . with collaboration of Othenio Abel. Gustav Fischer, Jena, 1927-28, 2 vols.
- ZANDER, H. A., and BEAT HÜRZELER.
1958. Continuous cementum apposition. *Journal of Dental Research*, vol. 37, pp. 1035-1044.

PLATES

The numbers in parentheses following a caption are photo-catalog numbers in the VBS series, the Marine Mammal Biological Laboratory.

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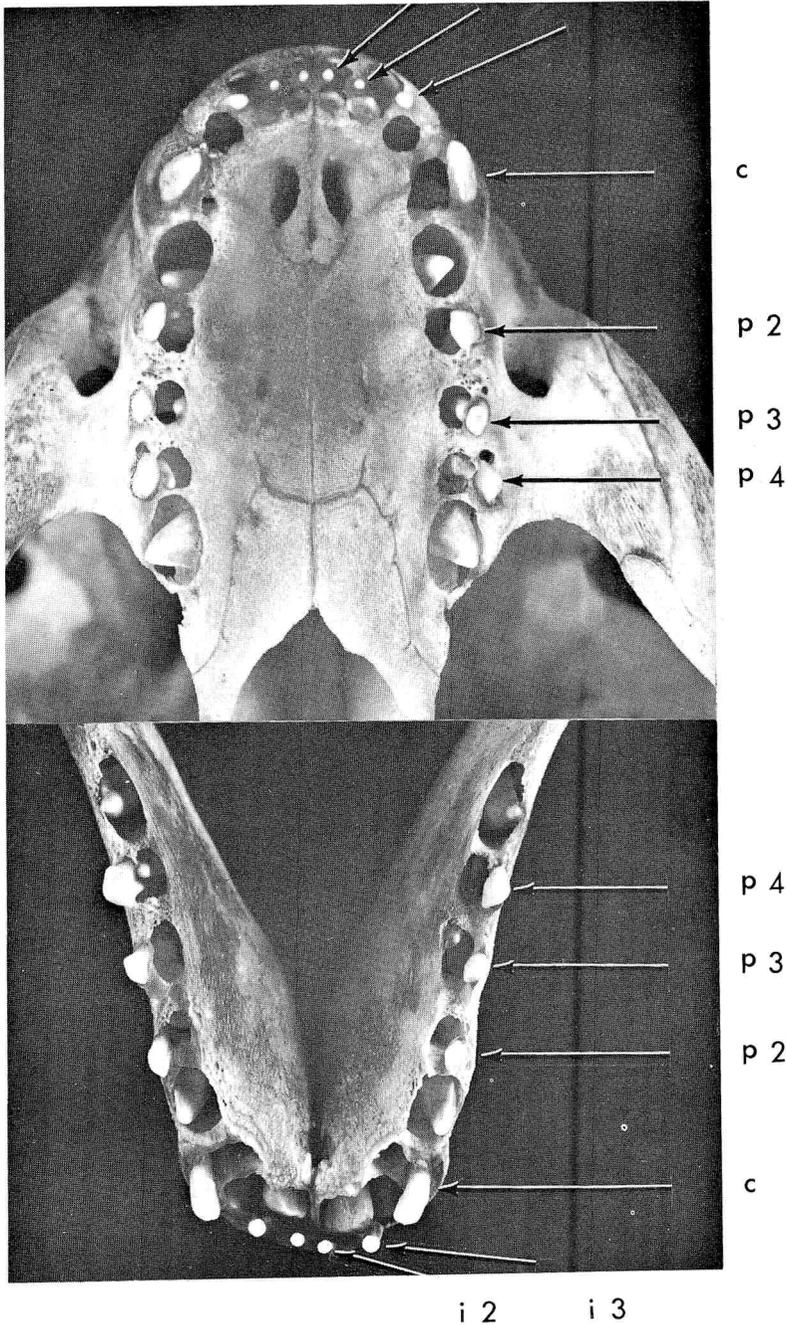


PLATE 1.—Complete deciduous dentition of a fetal female of 1.59 kg., 33 percent MNW. (For terminology of teeth see p. 296.) (4348, 4349)

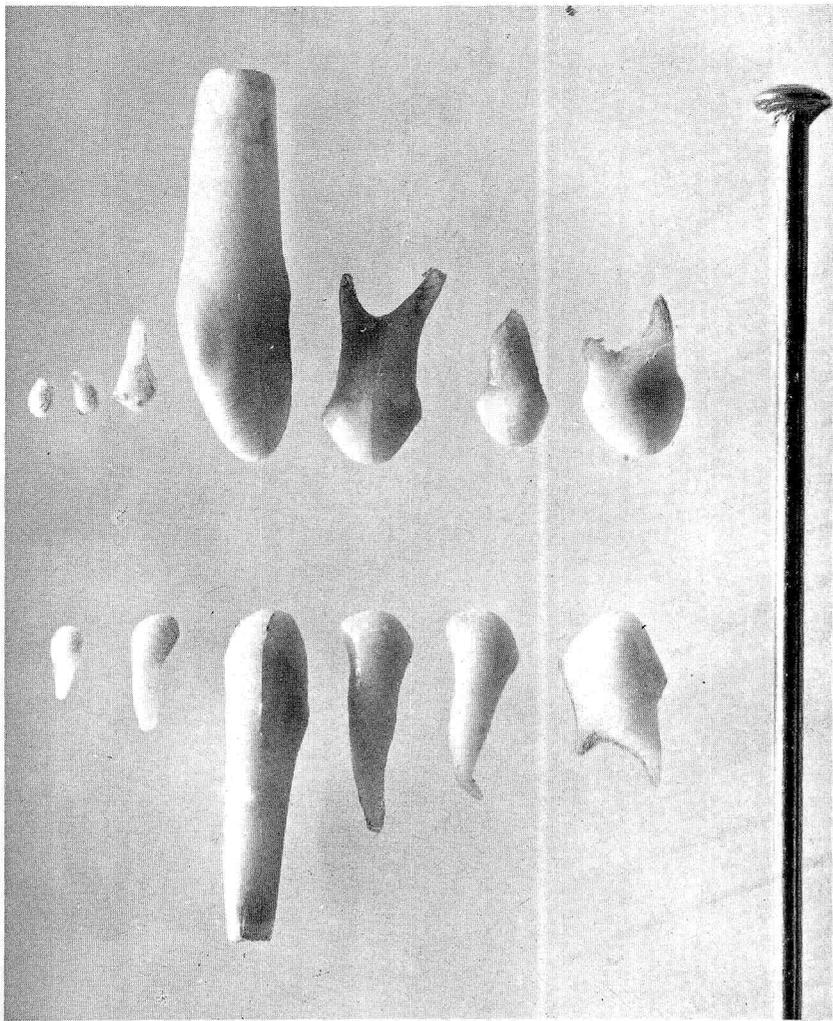


PLATE 2.—Deciduous teeth of the fetal female illustrated in plate 1; left teeth, labial or buccal surfaces; common pin at right. (4385)

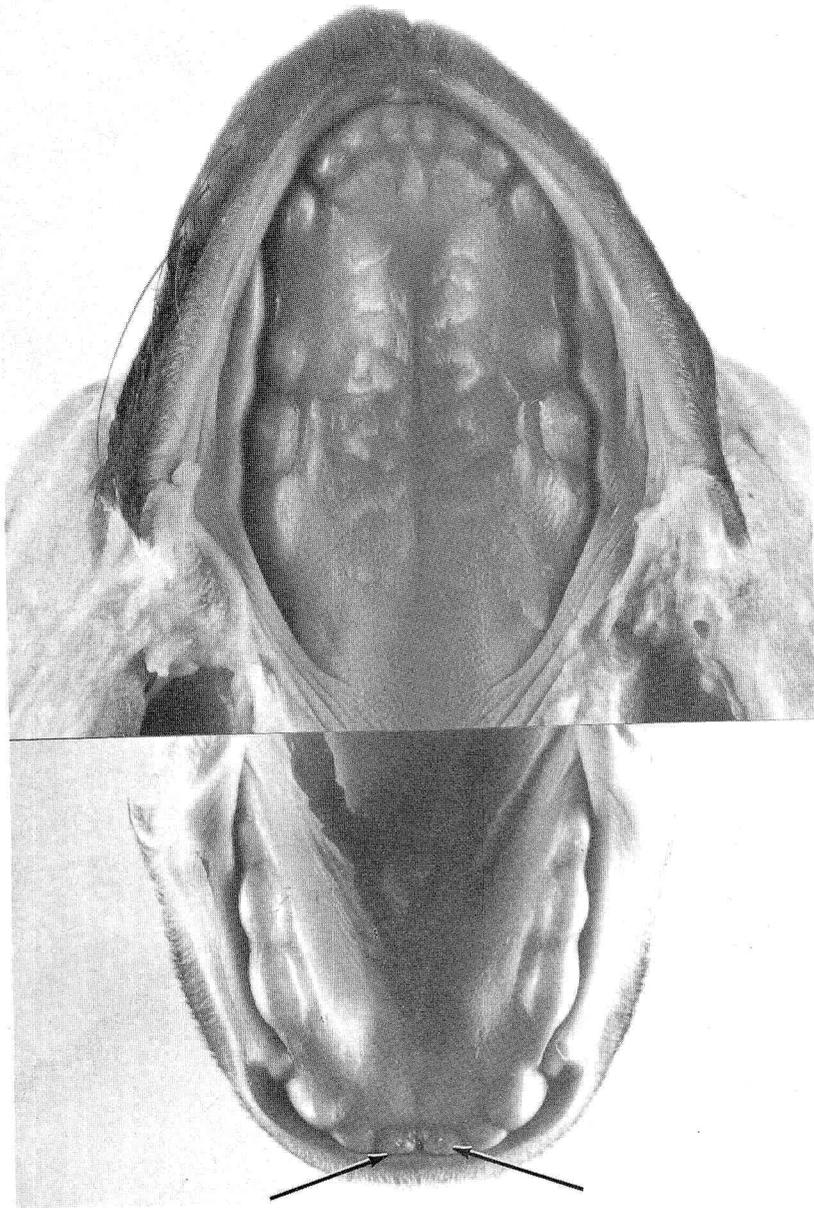


PLATE 3.—Deciduous dentition of a fetal female of 1.70 kg., 34 percent MNW, at onset of gingival eruption. Only lower right and left i2 (arrows) have started to erupt. (4388, 4389)

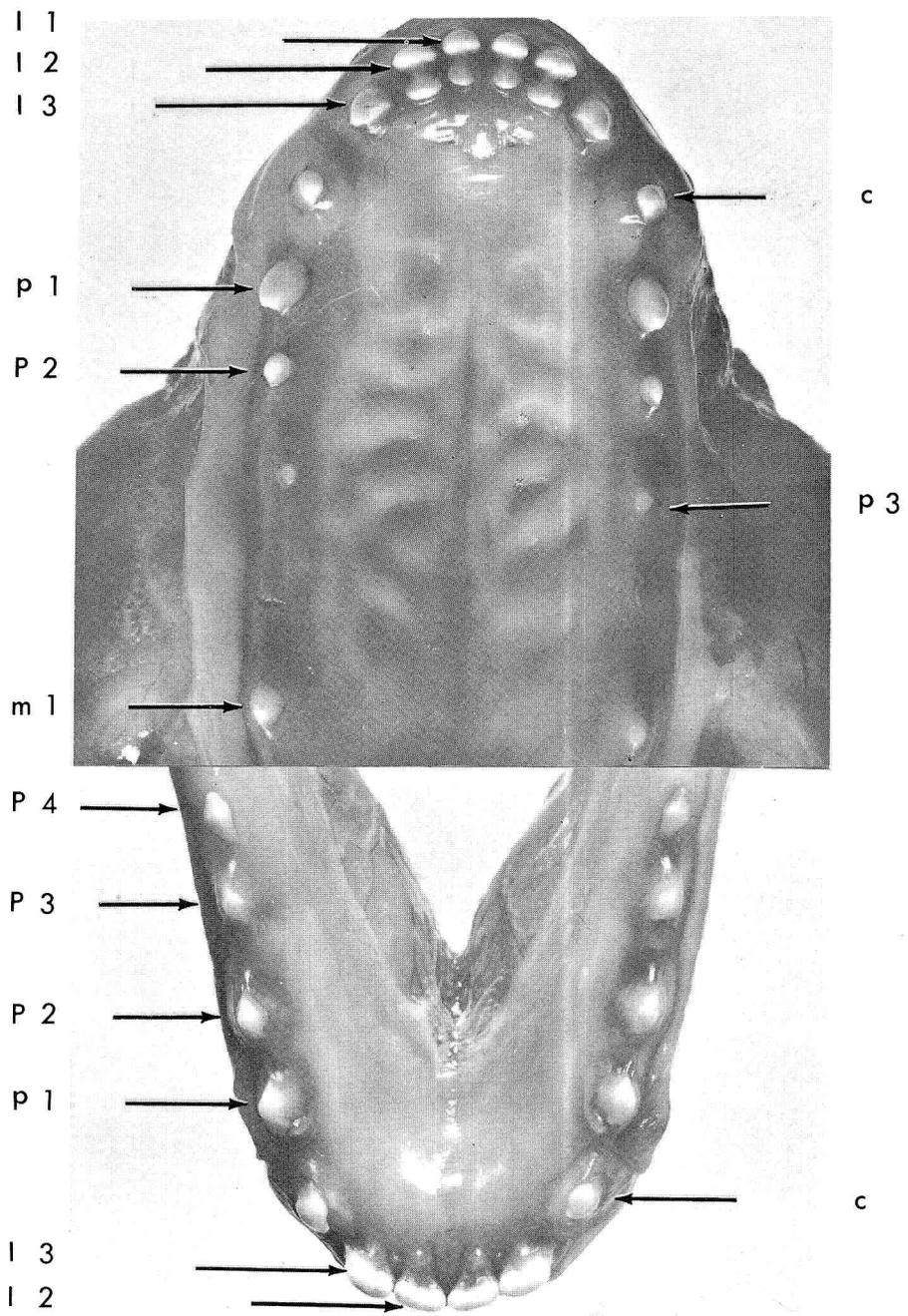


PLATE 4.—Deciduous dentition (arrows at right) and permanent dentition (arrows at left) of a full-term fetal male of 4.3 kg., 89 percent MNW. (2078, 2079)

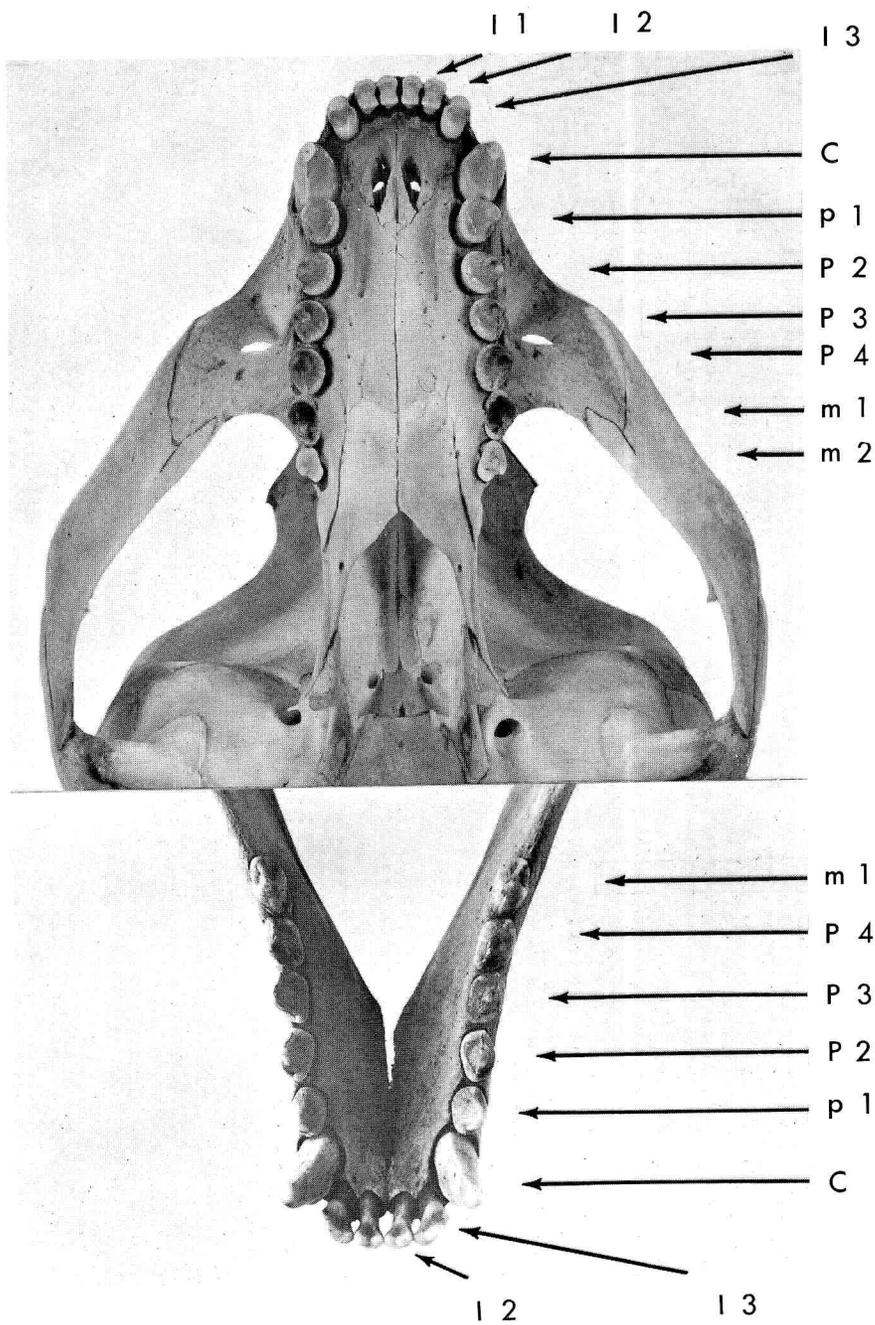


PLATE 5.—Complete dentition of a female about 7 months old, occlusal aspect.
(3041, 4311)

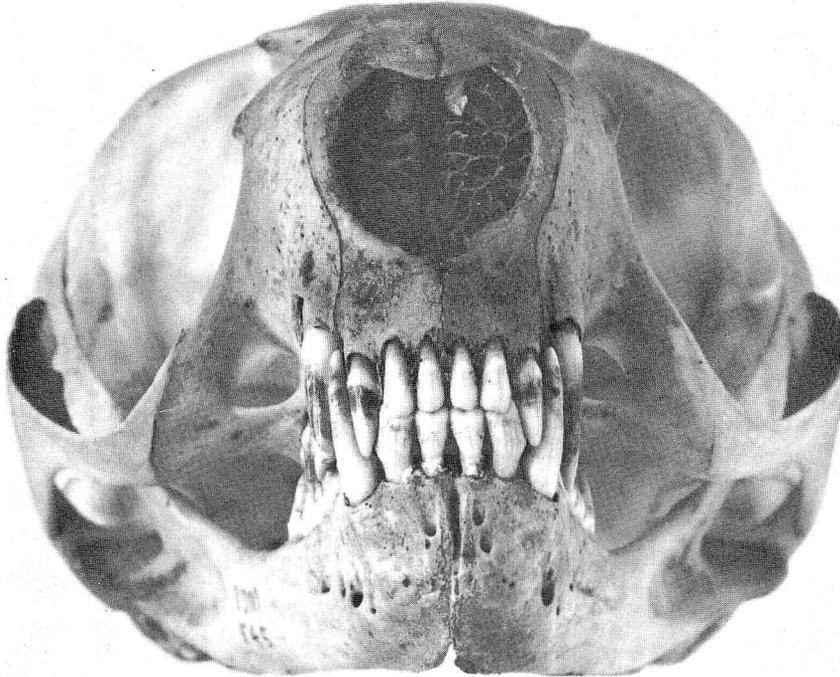


PLATE 6.—Complete permanent dentition of a female about 7 months old, lateral and anterior aspects. (Same skull as shown in plate 5.) (4310, 4309)

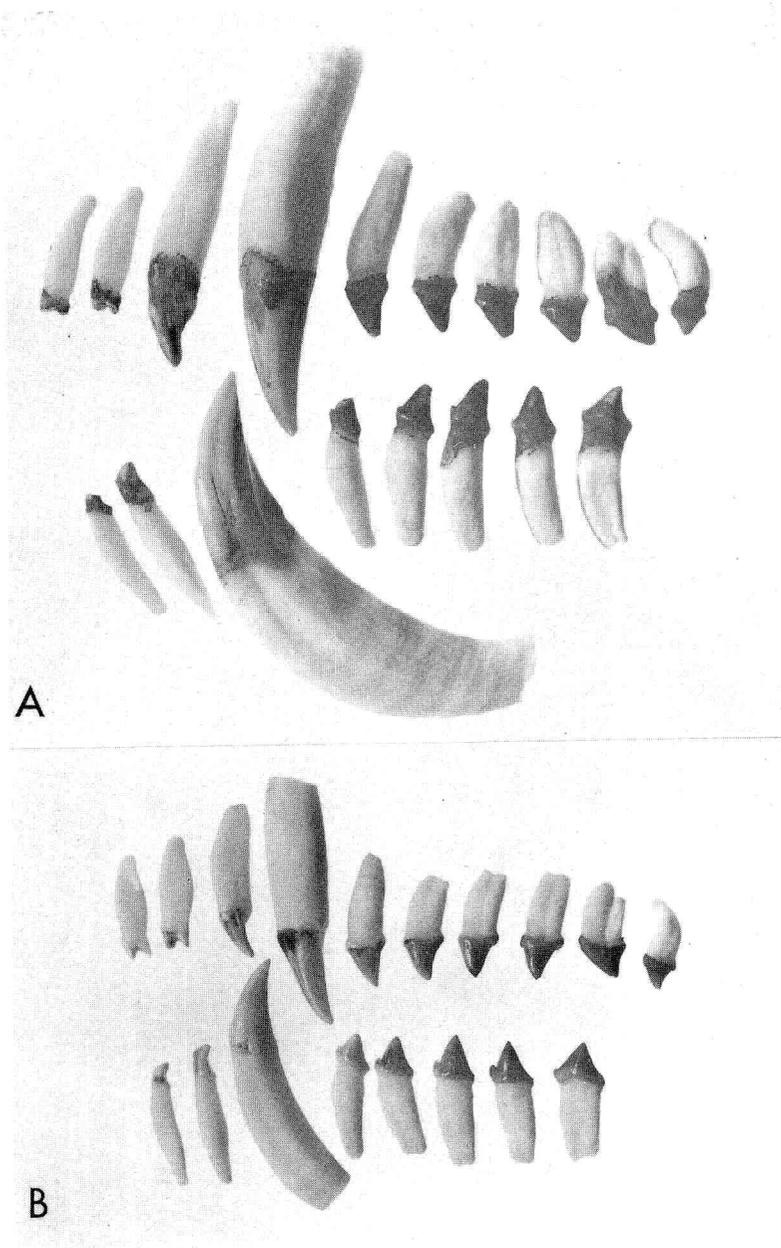


PLATE 7.—Permanent teeth of adults. Left teeth; distal surface of incisors, buccal surface of canines and postcanines; natural size. (A) Male, 10 or 11 years. (B) Female about 6 years. (2430, 2429)

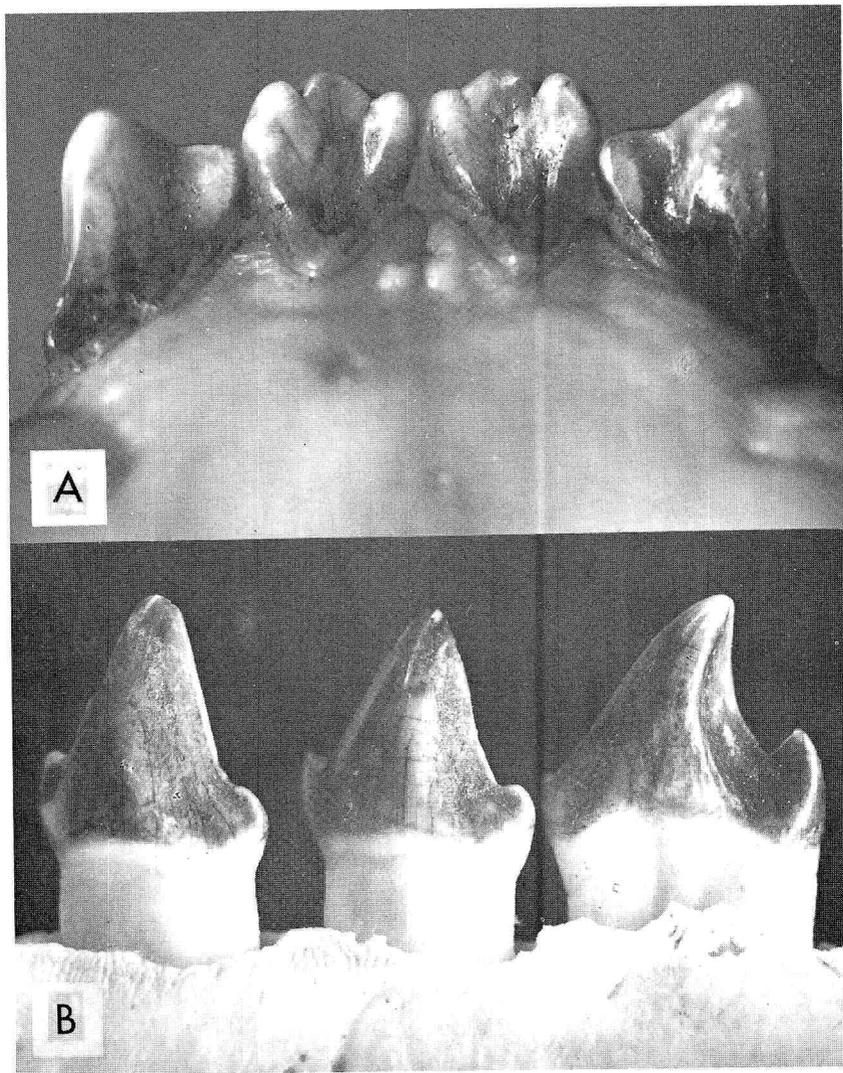


PLATE 8.—Shape of cusps of permanent teeth. (A) Lower incisors of 1-month female; lingual surface. (B) Three lower molariform teeth—left P3, P4, and m1—of 7-year female; buccal surface. (4428, 4375)

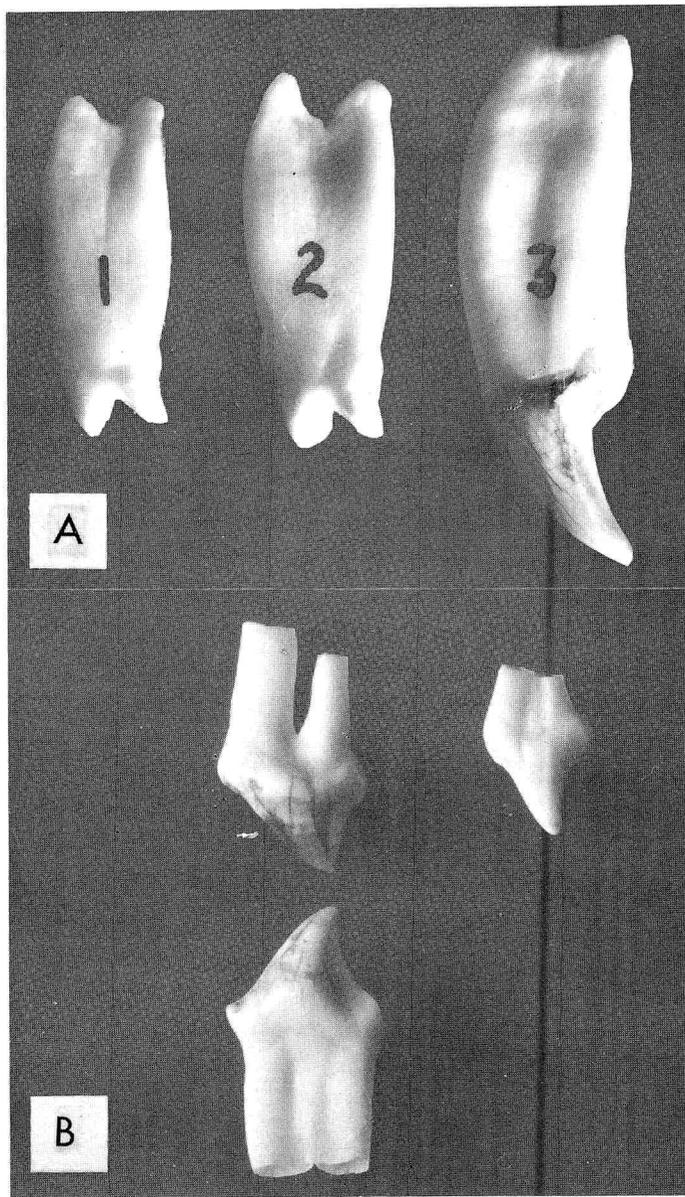


PLATE 9.—Shape of roots of permanent teeth. (A) Left upper incisors of 7-year female; distal surface. (B) Roots of left upper m1 and m2, and lower m1, of 3-month female; buccal surface. (4406, 4396)

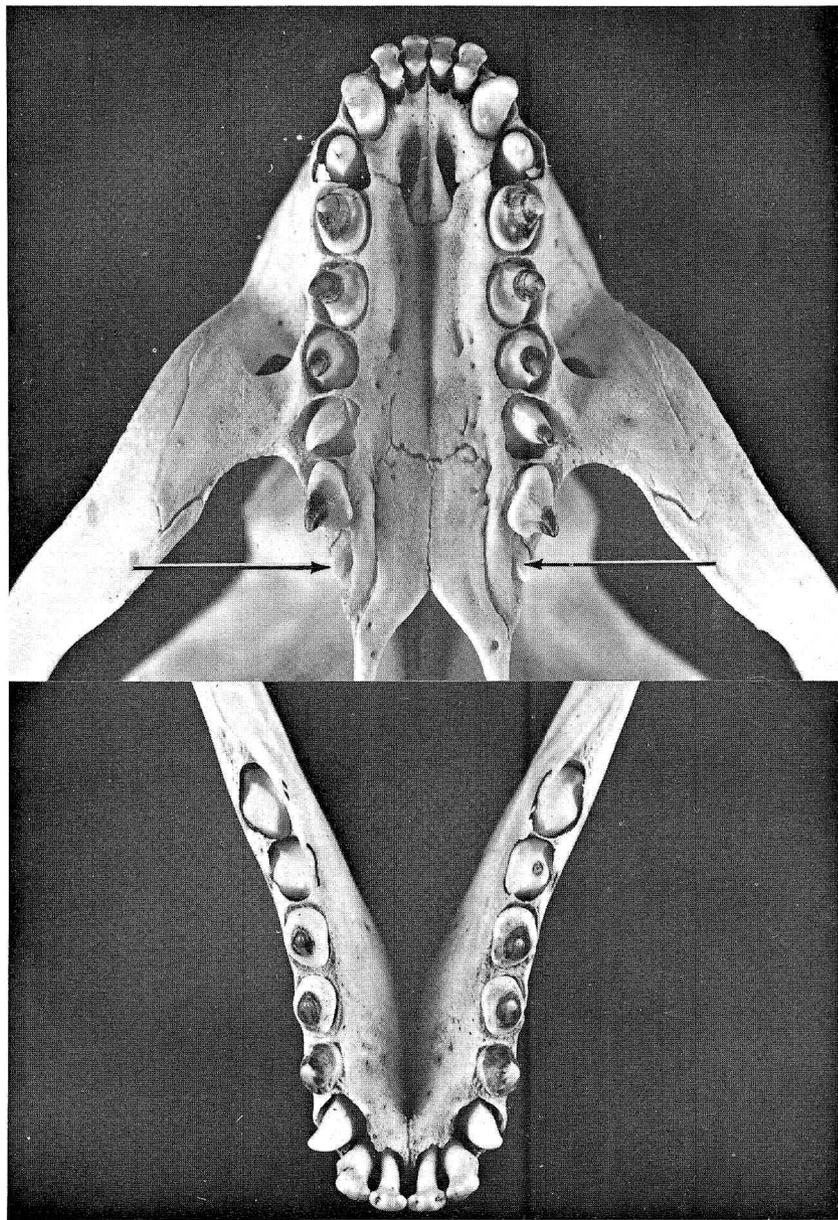


PLATE 10.—Permanent dentition, after alveolar eruption, of a female several days old; upper m2 on each side (arrow) has barely erupted; all deciduous teeth have exfoliated. (4339, 4340)

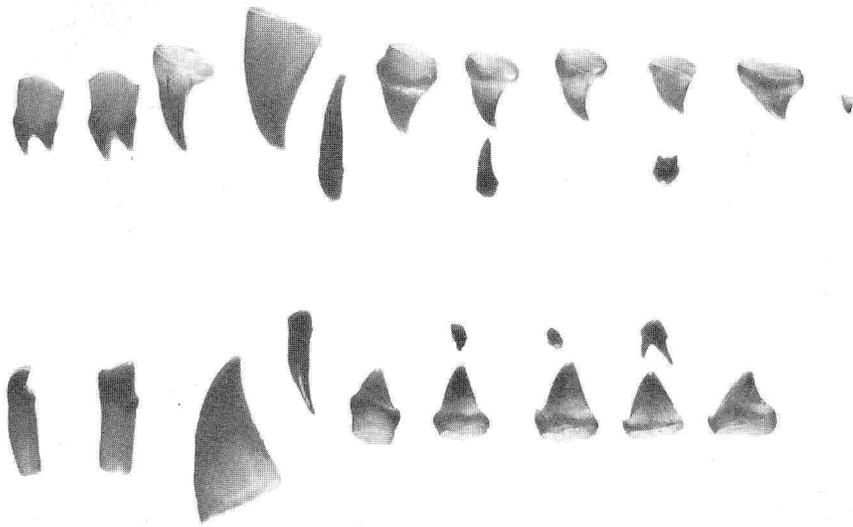


PLATE 11.—Permanent teeth and persistent deciduous teeth of a newborn male.
Left teeth; distal surface of incisors, buccal surface of canines and postcanines.
Seven deciduous teeth persist; upper p3 and all incisors have disappeared.
(Lower i3 was present in the right mandible.) (2814A)

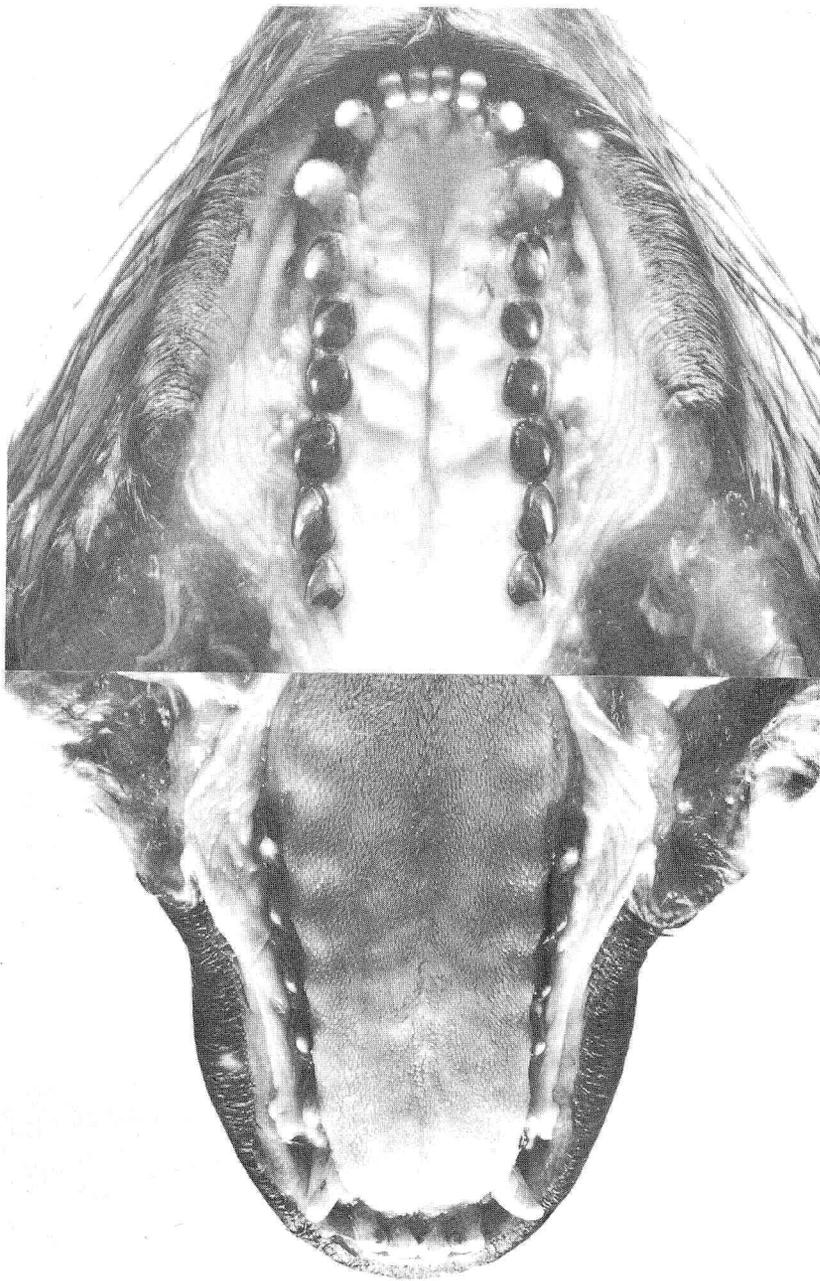


PLATE 12.—Permanent dentition, after gingival eruption, of an 8-month female, March 10, 1960. (4364, 4365)



PLATE 13.—(A) Upper canines in a mixed dentition stage; arrow indicates left permanent canine erupting along mesiolingual side of deciduous canine, in 1-month female. (B) Closure of root canal in an upper canine of a 12-year female. (4429, 4405)

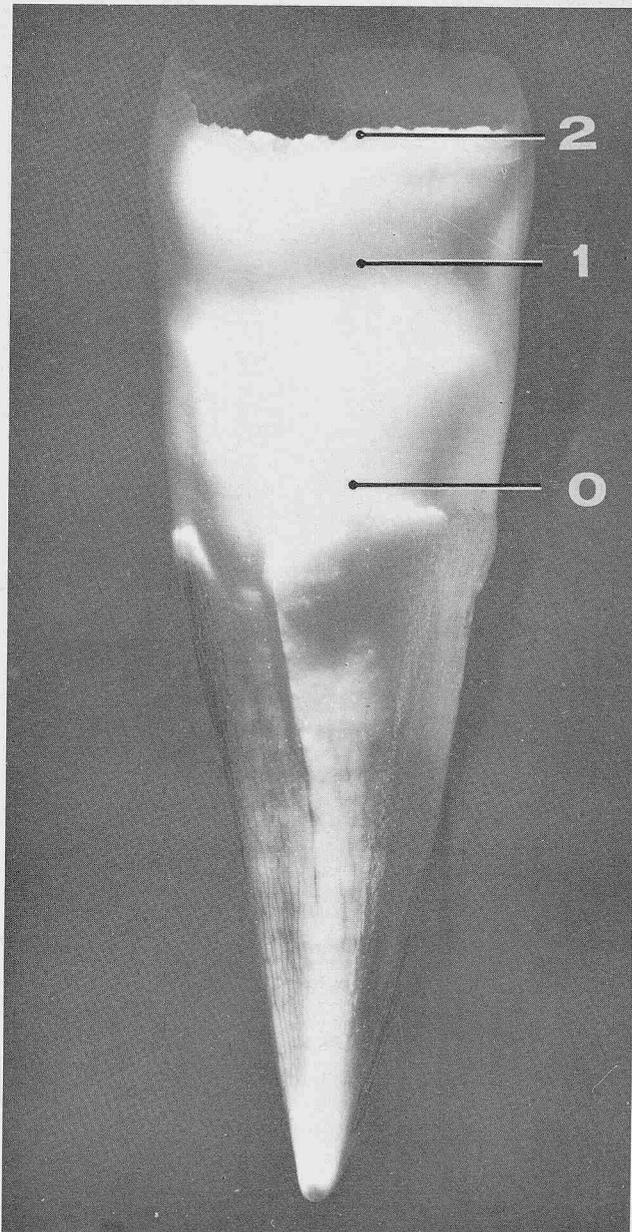


PLATE 14.—Annuli on right upper canine of a 2-year male, July 17, 1949; distal surface; $\times 5$. Numbers show approximate position of root base at ages 0 (birth), 1 and 2 years. (2697)

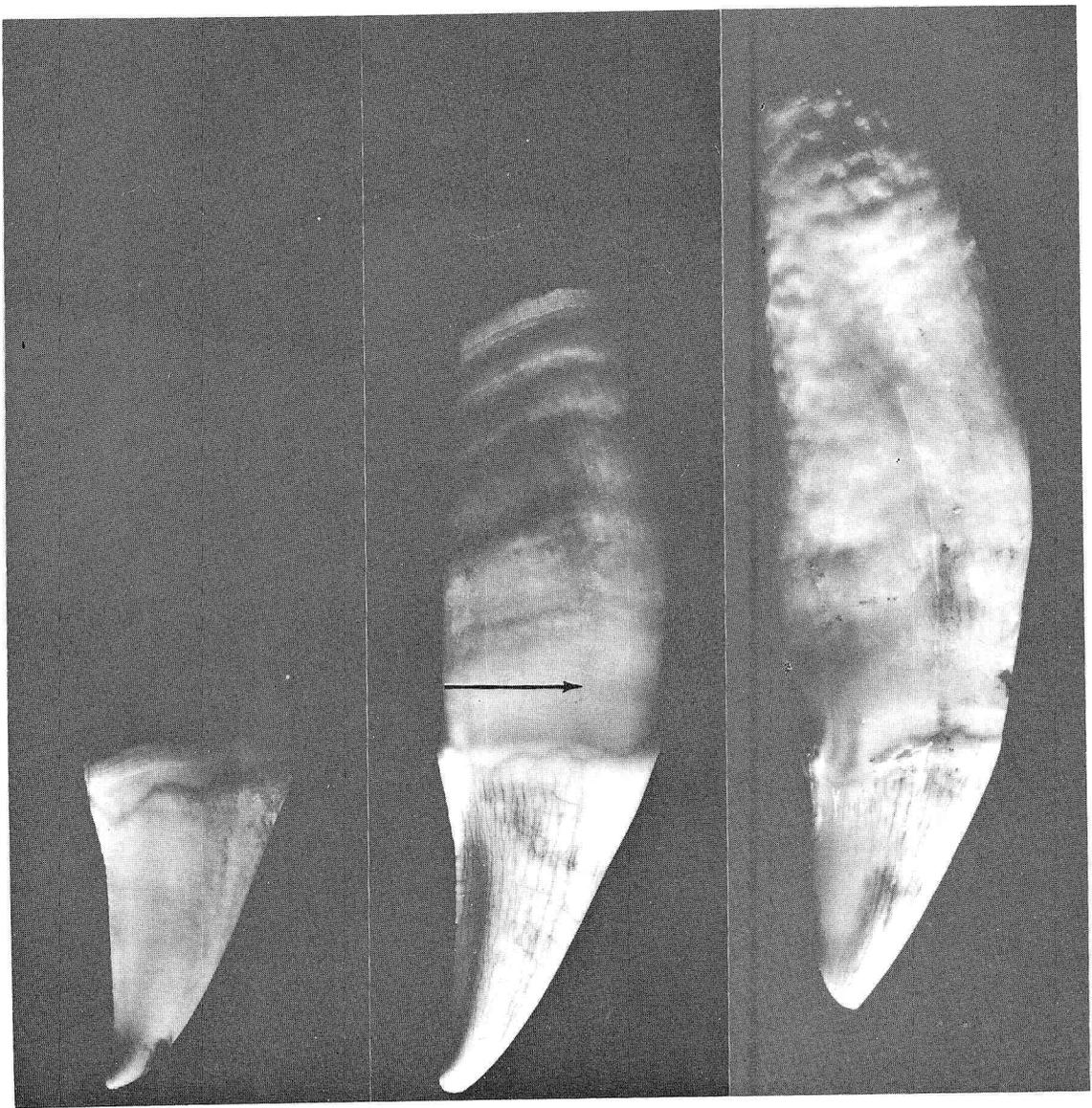


PLATE 15.—Annuli on right upper canines of males of three ages; buccal surface. (Left to right) pup several weeks old, killed on 8 August; 6-year-old (tagged), killed on June 17, (arrow points to first-autumn depression); 14-year-old (tagged), killed on July 16. (2701, 2703, 5295)

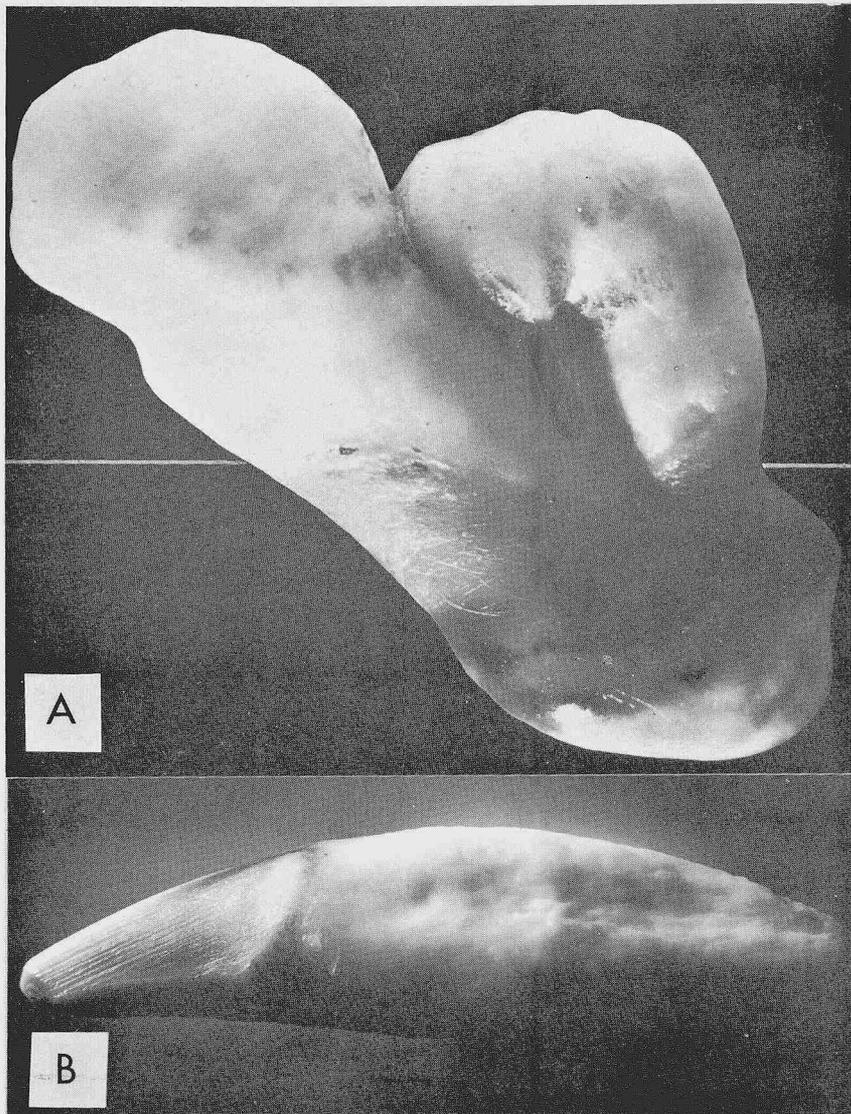


PLATE 16.—Cementum on teeth of old adults. (A) Left upper 1st molar of male; buccal surface; white line indicates gum level. (B) Right upper canine of 19-year (tagged) female; lingual surface; crown at left. (4423, 4488)

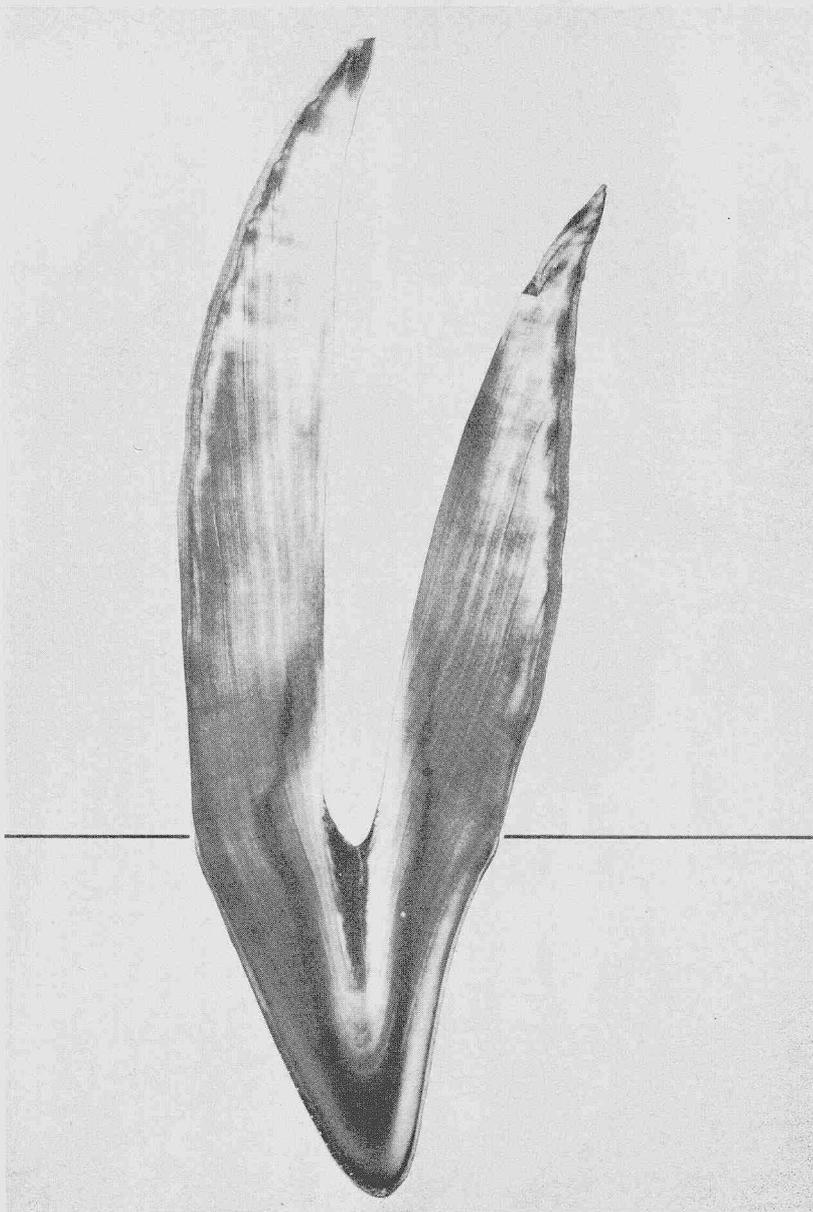


PLATE 17.—Internal structure of right upper canine, showing annuli; median section; 9-year (tagged) male; photographed by UV-excited fluorescence; lingual aspect; line indicates cemento-enamel junction. (US 58-737, Mrs. Marion P. Kumpula.)

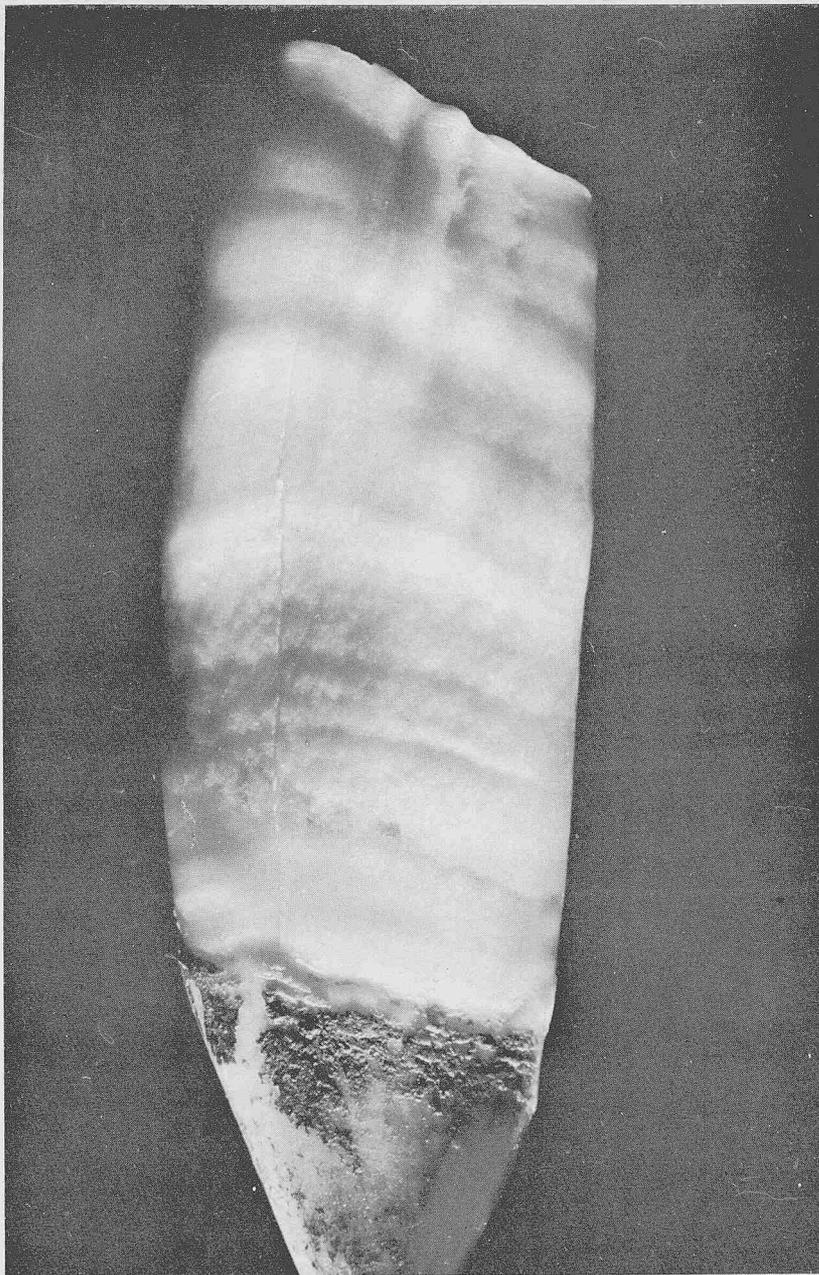


PLATE 18.—Annuli on right upper canine of a seal raised in captivity; known age 5-year male; lingual surface. (4487)

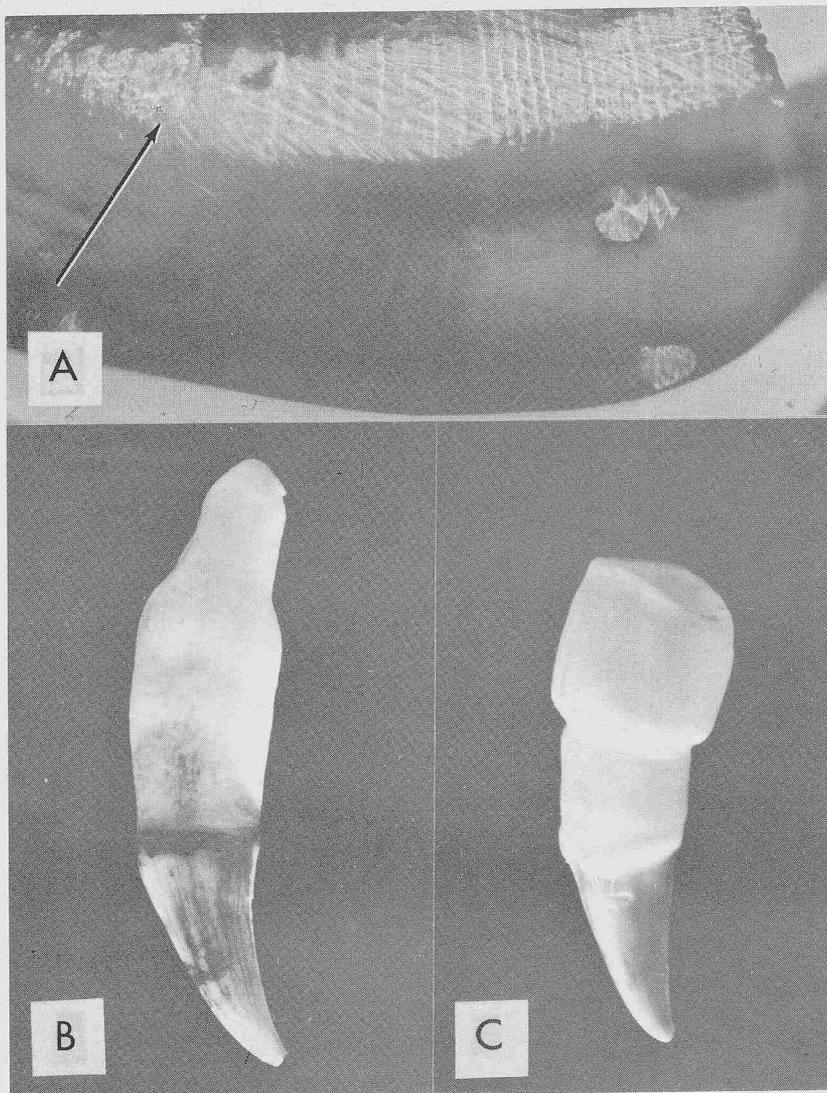


PLATE 19.—Differential growth of the root. (A) Gelatin impression of fine ridges on left lower canine of yearling male; labial surface; cemento-enamel junction at arrow; root at right. (B) Left upper canine of female over 10 years old; labial surface. (C) Right upper canine of female, estimated age 4 years; lingual surface. (4409A, 4402, 4403)

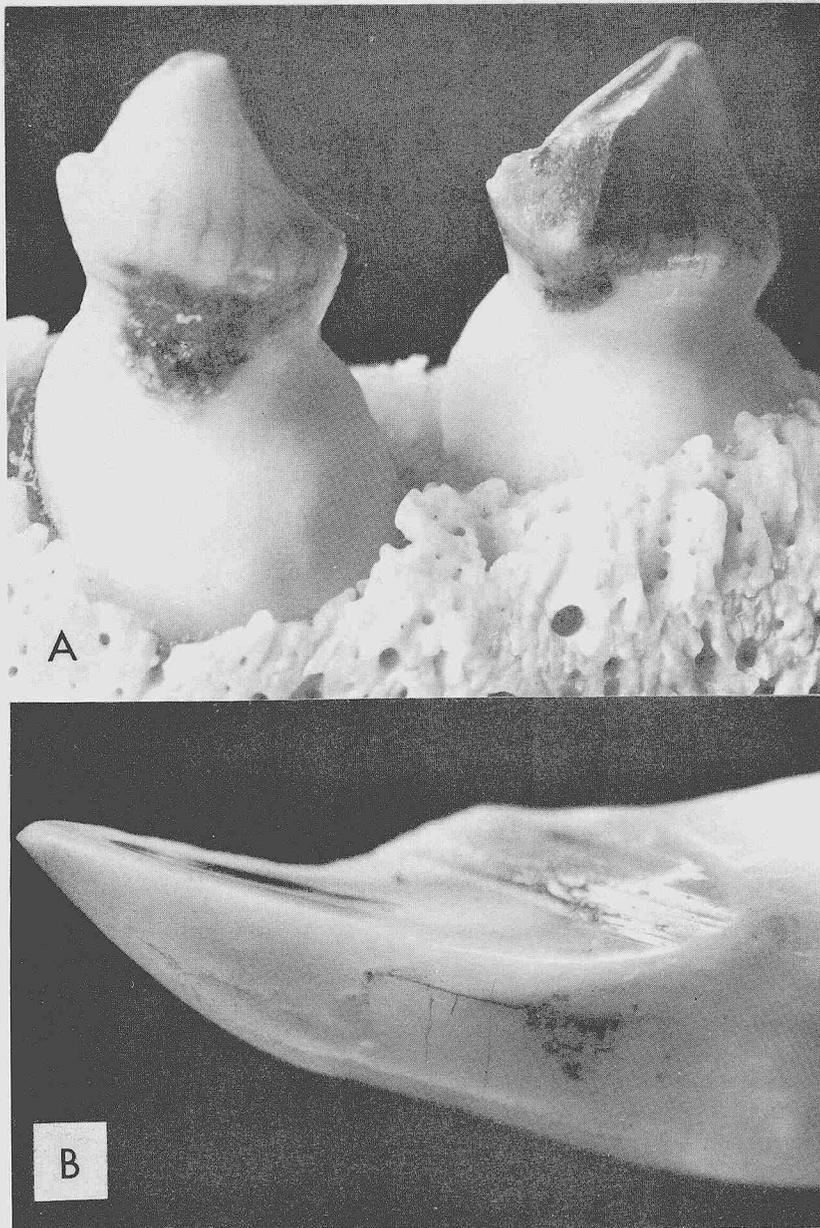


PLATE 20.—(A) Appearance in situ of premolars of an 8-year (tagged) male; lower left 1st and 2d; buccal surface. (B) Wear on the crown of the left lower canine of a female over 10 years old; labial surface. (4380, 4404)

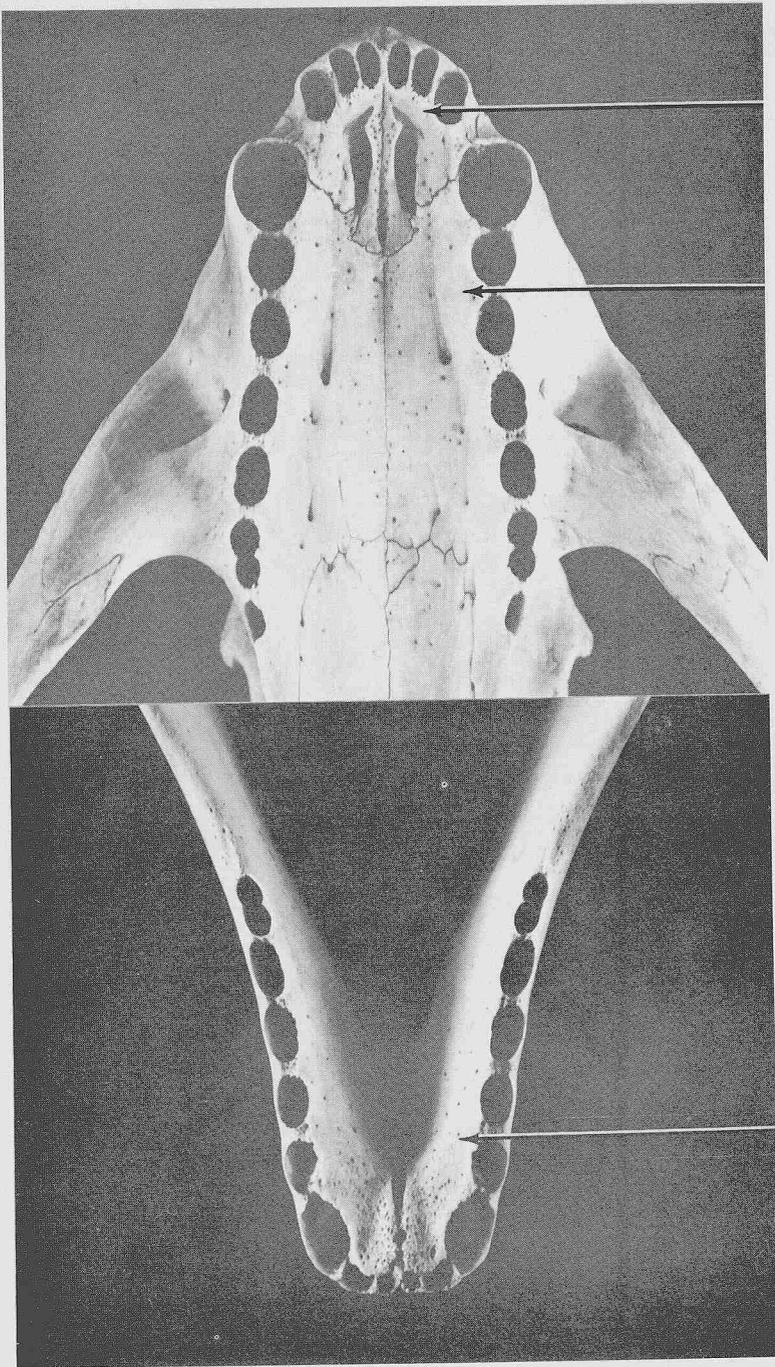


PLATE 21.—Jaw bones of a female, estimated age 5 years. Arrows show (top to bottom) premaxilla, maxilla, and mandible. (4410, 4411)

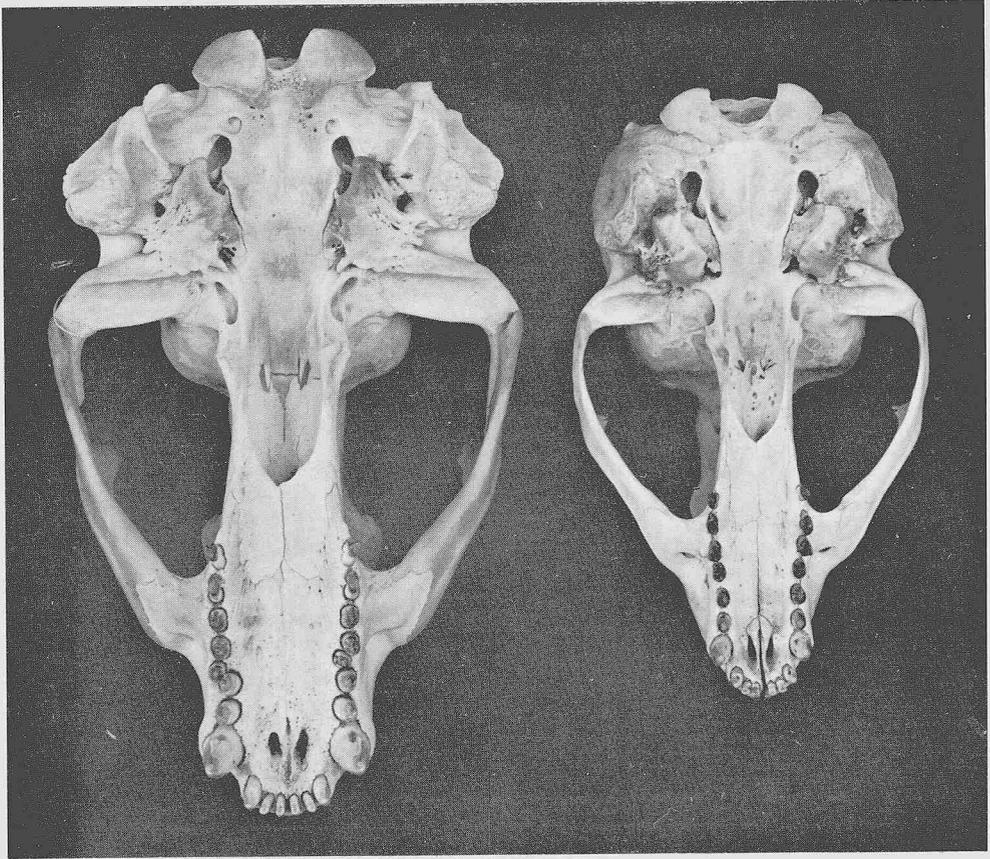


PLATE 22.—Skulls of 8-year male and female (both tagged); male (left) condylobasal length 235 mm., female 184 mm. (4494)

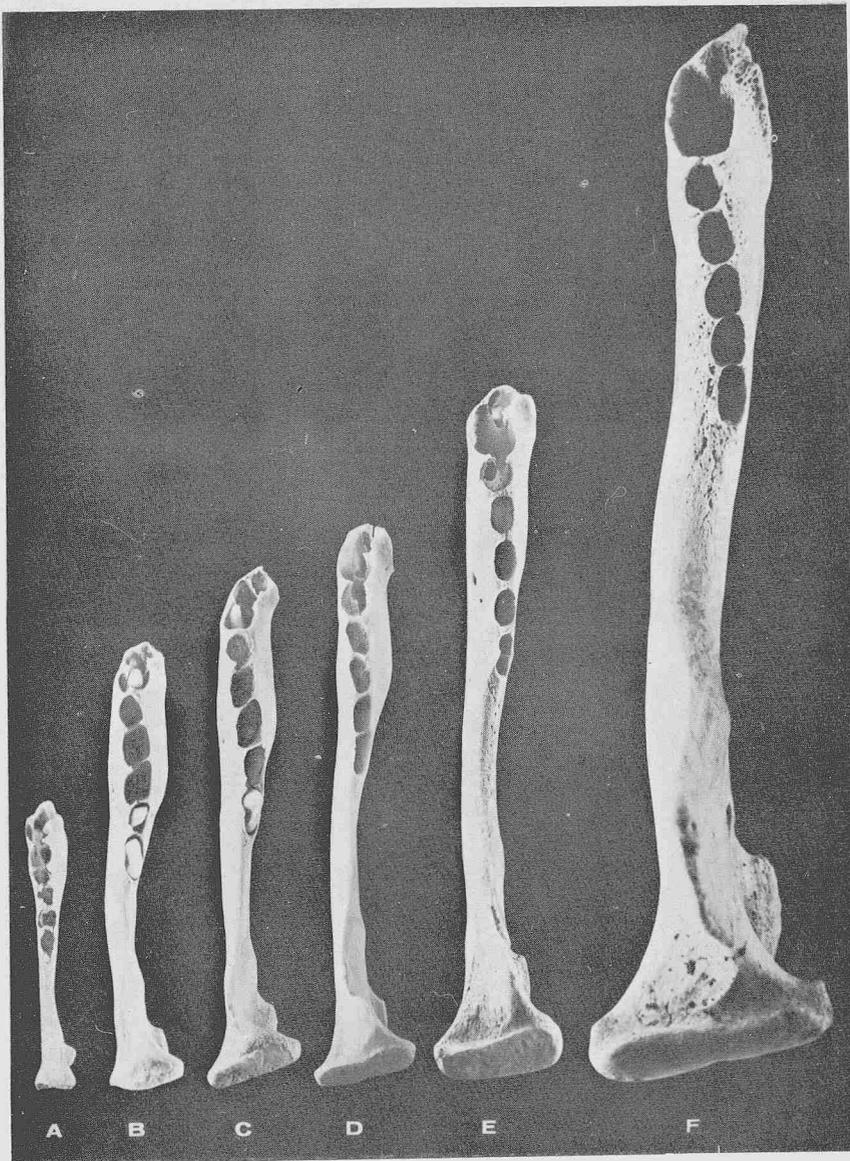


PLATE 23.—Left mandibles of six males, illustrating growth changes with age, natural size. (A) Fetus of 1.36 kg., 25 percent MNW. (B) Fetus of 6.0 kg., 111 percent MNW. (C) Pup 1-2 weeks old. (D) Yearling about 9 months old. (E) Three-year-old (tagged). (F) Old adult. (4426)

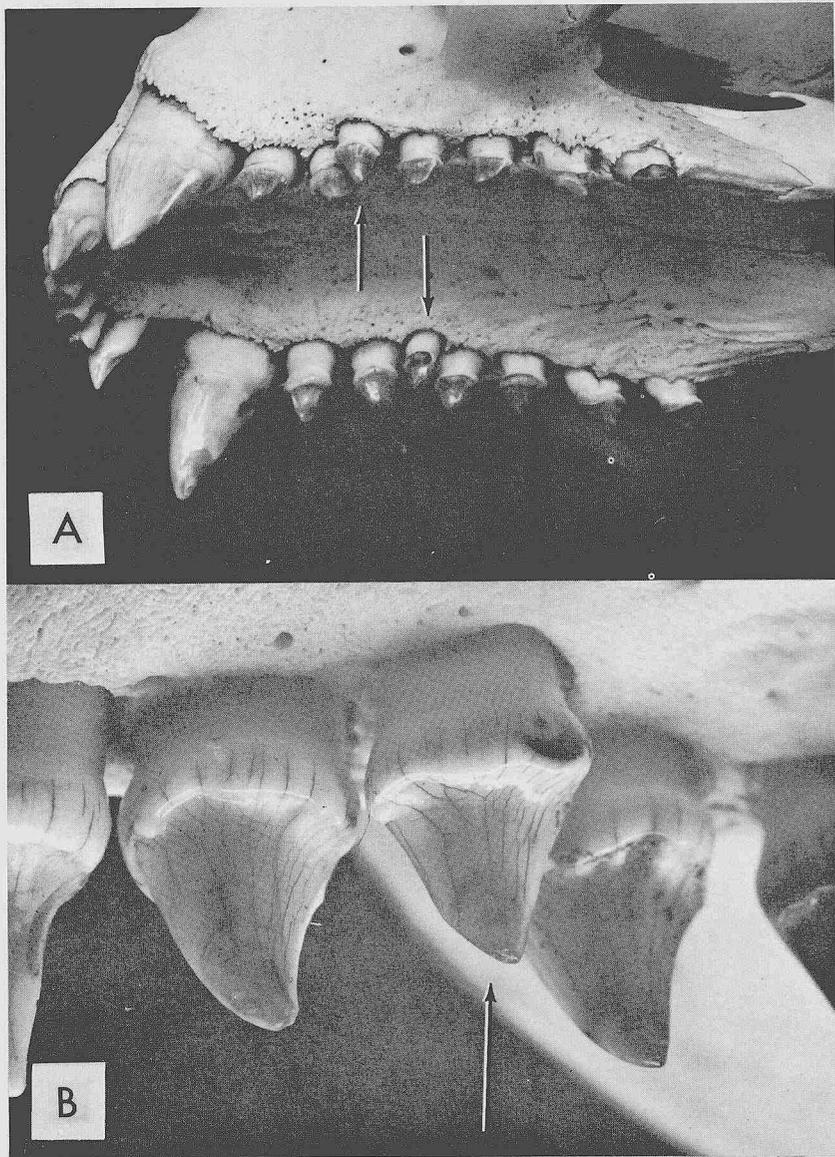


PLATE 24.—Extra premolars in two males. (A) Pair between upper P2 and 3 in an 8-year-old (tagged). (B) One of a pair between upper P2 and 3 in a yearling; right jaw; lingual surface. (4374, 4377)

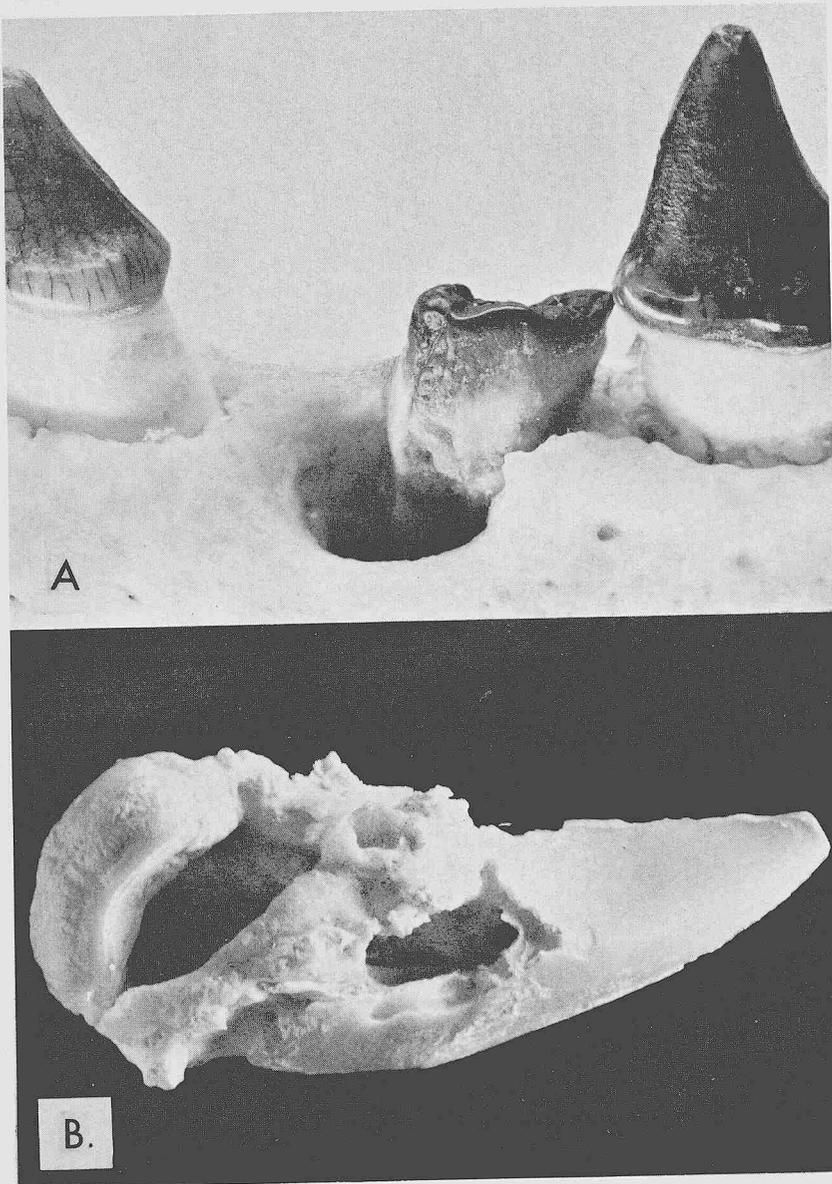


PLATE 25.—Effect of root abscesses on tooth and jaw. (A) Lower right P3 of a 7-year (tagged) female; lingual surface. (B) Upper right canine of a known-age 6-year male raised in captivity; lingual surface. (4378, 4401)

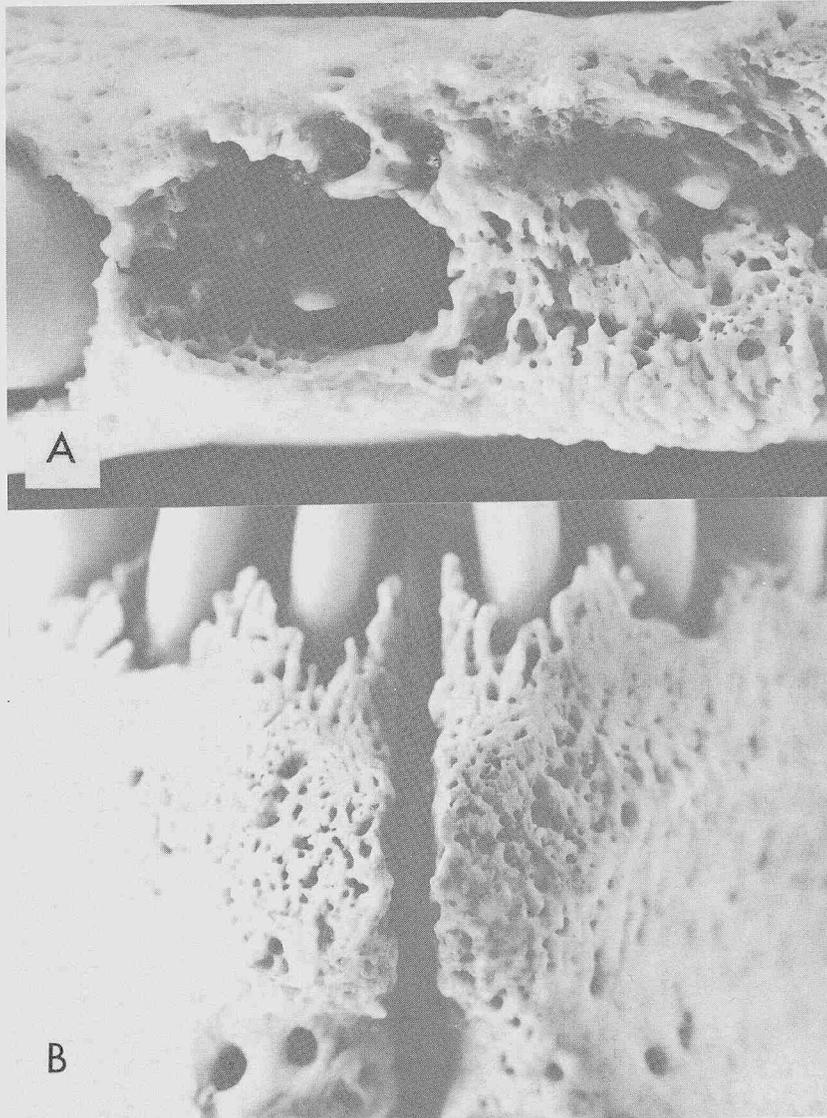


PLATE 26.—Spongy bone of the jaw. (A) Left mandible of female over 10 years old; canine at left; all premolars missing; occlusal surface. (B) Mesial end of mandible of 5-year male raised in captivity. (4373, 4376)

A BENTHIC COMMUNITY IN THE SHEEPSCOT RIVER ESTUARY, MAINE¹

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BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

The benthos in two selected areas of the Sheepscot River estuary, Maine, was surveyed quantitatively as part of a research program of the Bureau of Commercial Fisheries. A Petersen-type grab obtained 78 one-tenth square meter samples from the soft mud sediments. Samples were screened through openings of 1.5 mm., to separate the macrofauna from microfauna and sediments.

The 108 species collected conformed to the descrip-

tion of a *Nephtys incisa-Nucula proxima* community. Fifteen species accounted for 80 percent of the total number of organisms. Variations within the community are described, and some factors that may control size composition in the community are discussed. The Sheepscot infaunal community is compared with the faunal composition of two previously described *Nephtys-Nucula* communities.

In the summer of 1954, Gunnar Thorson of the University of Copenhagen invited the Fish and Wildlife Service to cooperate in quantitative surveys of the level sea bottom² fauna. Interest in the benthos has increased considerably in recent years, and studies of the level-bottom fauna are widely established. A benthic survey of the Atlantic coast of the United States and Canada could contribute valuable information on coastal ecology, particularly if the survey methods were comparable with European studies. Knowledge of benthic populations also contributes to a better understanding of the ecological factors affecting commercial species of fish and shellfish. It was agreed to undertake an initial program at the Bureau of Commercial Fisheries Biological Laboratory in Boothbay Harbor. The primary objective was to quantitatively survey the benthic fauna in limited areas. Sampling methods were to be established for future shallow-water benthic studies by the Bureau.

Benthic marine animals are divided into two ecologically different groups described by Petersen (1913) and further defined by Thorson (1951, 1956,

1957). The epifauna are those animals living above or on the bottom surface, sometimes attached to rocks, algae, logs, and other solid objects. These organisms are most abundant in the shallow coastal waters, especially in the intertidal zones, and are subject to great variations in environmental conditions. They are usually found in local groups and depend upon the occurrence of suitable substrata for their establishment. The diverse habitat available supports many species within the epifauna. The infauna are those animals that live in the substratum of the gradually sloping (level bottom) portions of the ocean floor. They occupy ". . . more than half the surface of the globe . . ." (Thorson, 1957) and reach their fullest development below the intertidal zone. The infaunal environment is more stable than the epifaunal environment. Characteristically, the

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¹ This paper is based on a thesis submitted to the University of New Hampshire in partial fulfillment of the requirements for the degree of Master of Science.

² The "level sea bottom" is the vast uniform area of the continental shelf characterized by a regular slope without abrupt changes in the bottom contour (see Thorson 1957, p. 466).

infauna comprises few genera having an extremely uniform distribution over broad geographical areas, and these animals have become widely used as index organisms in descriptive marine ecology.

The literature relating to benthic fauna has been extensively reviewed by various authors. Jones (1950) has an excellent review of the European literature. Kirsop (1922), Shelford, et al. (1935), and Hartman (1955), among others, have investigated the Pacific fauna. Parker (1956, 1959, 1960) made a detailed series of studies on both the recent and ancient faunal assemblages in the Gulf of Mexico. Atlantic faunistic studies date back to the qualitative surveys of Verrill (1873), followed by those of Kingsley (1901), Sumner, Osborn, and Cole (1913), Cowles (1930), and Allee (1934). Considering that the first truly quantitative benthic survey of any area of the Atlantic coast was not published until 1944 (Lee), advances in recent years are impressive. The New England region is represented in studies by Dexter (1944, 1947), Sanders (1956, 1958, 1960), Wigley (1956), Stickney and Stringer (1957), and Stickney (1959). Sanders' works, together with those of his associates (Wieser, 1960), in Buzzards Bay, Mass., have produced one of the most complete studies on the eastern coast to date. The present paper and that of Stickney (1959) provide a description of the fauna of the Sheepscot River estuary and part of Sheepscot Bay.

PHYSICAL FEATURES OF THE SHEEPSCOT ESTUARY

The Sheepscot River estuary cuts deeply into the Maine coast between Georgetown and Southport Islands (fig. 1). Its mouth, forming Sheepscot Bay, is located at approximately lat. $43^{\circ}47'$ N. and long. $69^{\circ}42'$ W. The lower portion of the estuary extends southward 13.6 miles from the town of Wiscasset to the open sea and varies in width from 2.9 miles to less than 0.1 of a mile. The banks are precipitous in parts of the upper portions of the estuary, and depths of the main river channel vary from about 60 feet at Wiscasset to 166 feet at the mouth. The shores of the lower estuary are exposed bedrock interspersed with mud flats. There are few sandy areas, and the bottom sediments, notably lacking in sand, are composed of a thick, soft, black mud. In places

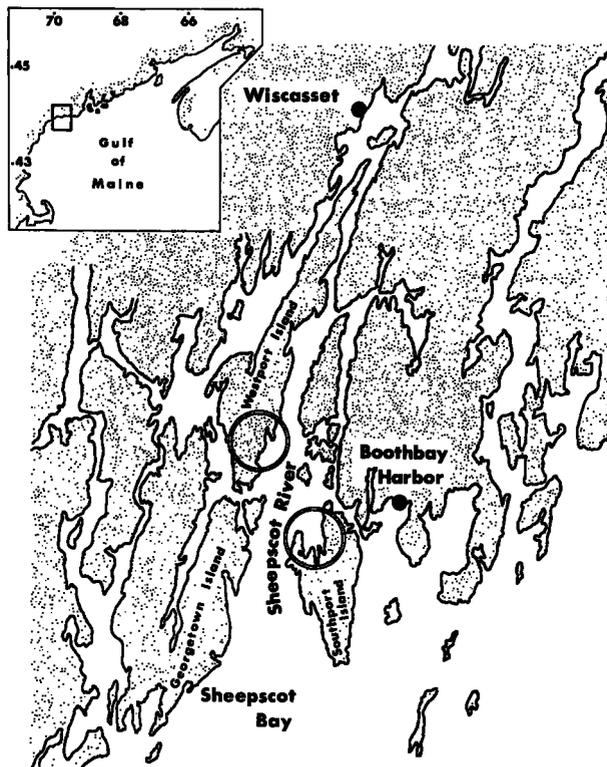


FIGURE 1.—The Sheepscot River and selected study areas. The upper circle encloses Jewett Cove; the lower circle encloses Ebenecook Harbor. (The small square in the upper left inset is not drawn to scale.)

the strong currents have washed away sediments exposing a rocky bottom.

DESCRIPTION OF EBENECOOK HARBOR

Ebenecook Harbor (fig. 2) is located on the northern end of Southport Island at lat. $43^{\circ}50'$ N. and long. $69^{\circ}40'$ W. There are three parallel coves—Love, Pierce, and Maddock—opening on a narrow, outer channel which forms a convenient northern boundary for the survey area. This channel conducts relatively swift currents into the estuary proper (see fig. 1), and the abrupt channel banks drop to depths of over 100 feet.

Love Cove, easternmost of the three-cove complex, is about 1,050 yards long and 150 yards wide with depths from 4 to 17 feet. Soft mud bottom material is typical with an occasional rocky outcrop. Mud flats cover the head of the cove but most of the shore is exposed bedrock. Pierce Cove is the longest (1,375 yards) of the three coves and has a uniform width of about 100 yards. The shore is rocky with remnants of old, stone wharfs

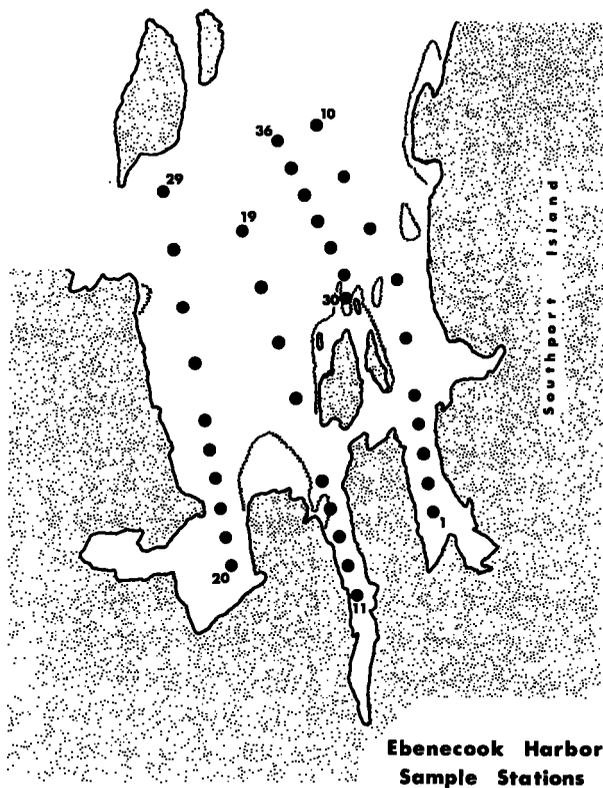


FIGURE 2.—Location of sample stations in Ebenecook Harbor.

in two places on the western side. This is a shallow cove, ranging in depth from 3 to 9 feet at mean low water. Past mussel (*Mytilus*) beds are indicated by an accumulation of shells on the soft bottom sediments. Maddock Cove is wider, about 250 yards, and deeper than the other coves with similar bottom sediments and shoreline.

The principal source of fresh water comes from the Sheepscot River, with headwaters located north of Wiscasset between the Penobscot and Kennebec valleys. Near Wiscasset salinities range from 22 ‰ to 30 ‰ at the surface, while bottom salinities are more constant ranging from 29 ‰ to 30 ‰. The basis for division of the estuary, upper and lower, and a more detailed description of the entire area including tidal exchange, salinity and temperature variations, currents, and biota were discussed by Stickney (1959). Bryant (1956) described the river proper. The two study areas, Ebenecook Harbor and Jewett Cove, are representative of the general environmental characteristics of the estuary. Salinities were in the range of bottom salinities cited, and

bottom temperatures varied from 10.1° C. to 12.8° C. in Ebenecook Harbor, and from 10.6° C. to 14.7° C. in Jewett Cove.

DESCRIPTION OF JEWETT COVE

Jewett Cove, on the southeastern shore of Westport Island (fig. 3), is about 725 yards from north to south and about 350 yards from east to west. The shoreline in some sections is rocky and drops off sharply into deeper water, while in others it is composed of muddy flats gently sloping into the sea. Midway along the shore there are pilings of a fish weir built out for some distance into the cove. Sampling stations were not located in this area to avoid damage to the weir and possible loss of gear through fouling of lines on the weir stakes. The bottom slopes gradually into depths of 50 feet, beyond which it drops off sharply into the main channel where depths reach 147 feet.

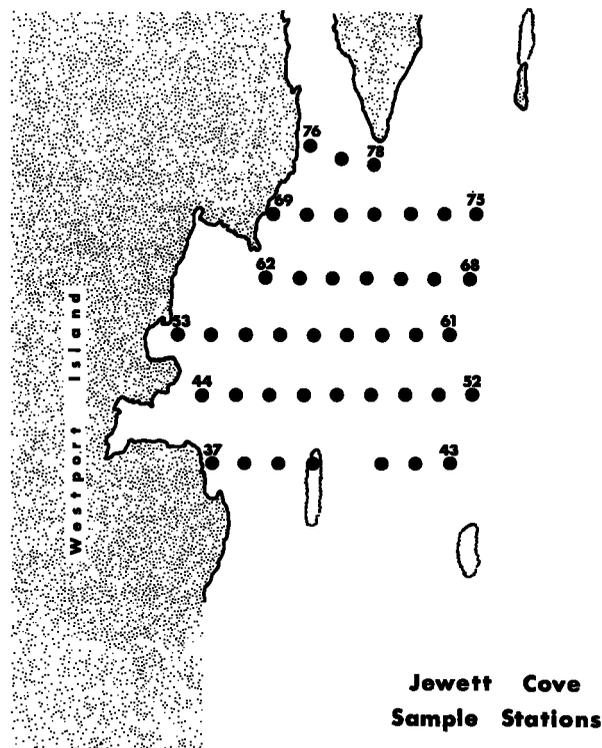


FIGURE 3.—Location of sample stations in Jewett Cove.

APPARATUS AND METHODS

FIELD PROCEDURE

Samples were collected throughout the period of late July to early November in 1955. Both areas were sampled essentially on a grid basis

(figs. 2 and 3). Stations were spaced 300 feet apart in shallow water and 600 feet apart in the deeper portions with about 600-foot intervals between adjacent course lines. The stations were located by running the boat on compass courses at a predetermined speed and dropping marker buoys at selected time intervals. Ten different stations were occupied each week with one sample from each of the total 78 stations (table 1). A 28-foot cruiser, with a draft of 3 feet, and a speed of 15 knots, was equipped with winch and pump and used as a sampling platform. The small size was advantageous for shallow-water work, but limited working space and restricted operations to fair weather.

TABLE 1.—Station data for Ebenecook Harbor and Jewett Cove, Maine, July to November 1955

Station	Date	Depth, feet	Station	Date	Depth, feet
Ebenecook Harbor:			Jewett Cove—Con.		
1	July 29	3	40	Sept. 15	20
2	do	4	41	do	31
3	do	5	42	do	32
4	do	10	43	do	44
5	do	15	44	Sept. 22	13
6	do	15	45	do	13
7	do	20	46	do	15
8	do	23	47	do	19
9	do	23	48	do	18
10	do	29	49	do	25
11	Aug. 2	4	50	do	30
12	do	7	51	do	41
13	do	10	52	do	14
14	do	10	53	Sept. 29	14
15	do	9	54	do	15
16	do	15	55	do	16
17	do	22	56	do	20
18	do	24	57	do	21
19	do	26	58	do	23
20	Aug. 8	12	59	do	34
21	do	16	60	Oct. 6	20
22	do	20	61	do	24
23	do	22	62	Oct. 20	24
24	do	27	63	Oct. 6	24
25	Aug. 10	32	64	do	22
26	do	35	65	do	26
27	Aug. 8	35	66	Oct. 20	26
28	do	45	67	do	30
29	Aug. 10	100	68	do	20
30	Aug. 17	14	69	do	26
31	do	23	70	do	25
32	do	27	71	do	39
33	do	27	72	Nov. 8	26
34	do	27	73	do	21
35	do	31	74	do	36
36	do	44	75	do	13
Jewett Cove:			76	do	18
37	Sept. 15	14	77	do	26
38	do	26	78	do	
39	do	25			

A modified Petersen-type grab (Petersen and Boysen-Jensen, 1911) was used to obtain intact segments of the bottom sediments 0.1 meter square and about 20 cm. in depth (fig. 4). No sample was retained if the dredge was less than two-thirds full. The sample was placed in a screen box (fig. 5), which hung over the side of the vessel, and was washed with water from a pump. The

box contained three trays with bottoms of plastic screen; the top screen of 8- by 8-mesh per inch, the next of 14- by 16-mesh, and the bottom tray of 20- by 20-mesh with openings of about 1.5 mm. Organisms were thus separated from sediments by a screen with 1.5 mm. openings; providing an arbitrary division between the macrofauna and microfauna. Each screen retained a portion of the material collected, and this reduced clogging. Clay, silt, and sand were washed through the screens with water, but quantities of broken shell, *Spartina* fragments, gravel, etc., were retained. Organisms collected in the top tray were large enough to remove and classify aboard the boat. The contents of the other two trays were emptied on a collecting board, washed into quart jars, and returned to the laboratory for identification.

Although routine sediment analyses were not made, several random samples were processed through a series of sieves. The finest screen used in this series was 250-mesh per inch (openings of 0.062 mm.). Silt is defined as being composed of particles from 0.05 to 0.002 mm. in diameter (Soil Survey Staff, 1951). Since all of the material in the samples passed through this finer screen, except shell fragments (less than 1 percent), the sediments in the survey areas were considered to be at least 90 percent silt and clay.

Measurements directly related to the sampler, screen size, and sample dimensions are given in the metric system because metric measurements were essential to the experimental design in relating it to other studies.

LABORATORY PROCEDURE

The contents of a quart jar from the field collections were placed in a large, white photographic tray and the organisms picked out by visual inspection. The animals were sorted into five major groups: mollusks, annelids, nemertean, echinoderms, and miscellaneous. No dead organisms were counted with the single exception of *Volsella modiolus* shells, which were present in large numbers and were uniformly distributed. Epifaunal species were retained for study, but not considered as part of the infaunal association. The organisms were preserved in 10 percent neutralized formalin and later transferred to 70 percent alcohol to prevent deterioration of the calcified parts. Usually no narcotization was used, but when time permitted, or in the case of

unusual or rare specimens, particularly polychaetes, coelenterates, and nemerteans, an 8-percent solution of magnesium chloride (isotonic with sea water) was used to relax and extend the animals before fixing. The material gathered each week was stored until the end of the collecting period, when all the organisms from each group were re-examined and identified to species, or to the lowest taxonomic category feasible.

Abundance (number of organisms) has been used as the basis of faunal evaluation for this study. Other factors, such as biomass or dry weight measurements, are recognized as being equally valuable, but were not within the scope of this work. A review of the literature on marine communities will show that the numerical basis of evaluation is not without precedent and one

investigator (Sanders, 1960) has supported animal numbers as the most valid measurement.

RESULTS

DISTRIBUTION AND ABUNDANCE

Ebenecook Harbor and Jewett Cove faunas can be considered as one community (table 2) since they differ only in minor aspects. Two species were selected as dominants: the protobranchiate pelecypod *Nucula proxima* Say, the most abundant animal; and the polychaetous annelid *Nephtys incisa* Malmgren, the most uniformly distributed animal. Associated with these dominants are other species that were also evenly distributed in large numbers.

Cumaceans were second in abundance and were

TABLE 2.—Species in the *Nephtys-Nucula* community found at 10 or more stations in Ebenecook Harbor and Jewett Cove, Maine, and listed in order of abundance

Rank by number	Species	Number	Number stations	Percent by number	Cumulative percent by number	Percent stations	Average number per square meter	Area ¹	Depth range in survey
1.	<i>Nucula proxima</i>	2,358	59	18.3	18.3	75.6	399.6	E&J	Meters 4-30
2.	Cumacea sp. (4+species)	1,973	55	15.3	33.6	70.5	358.7	E&J	4-14
3.	<i>Stereobalanus canadensis</i>	768	34	6.0	39.6	43.6	225.8	E&J	3-31
4.	<i>Thyasira gouldi</i>	717	46	5.6	45.2	56.0	155.8	E&J	4-31
5.	<i>Phorocephalus holboellii</i>	623	39	4.3	50.0	50.0	159.7	E&J	1-9
6.	<i>Volseella modiolus</i>	573	68	4.4	54.4	87.2	84.2	E&J	1-31
7.	<i>Corophium</i> sp.	557	22	4.3	58.7	28.2	253.1	E, mostly J	0-8
8.	<i>Nucula tenuis</i>	515	46	4.0	62.7	59.0	111.9	E&J	4-31
9.	<i>Dulichia</i> sp.	407	39	3.2	65.9	50.0	104.3	E&J	5-14
10.	<i>Scaloptos armiger</i>	402	47	3.1	69.0	60.3	85.5	E&J	4-14
11.	<i>Aricidea</i> sp.	395	43	3.1	72.1	55.1	91.8	E&J	1-14
12.	<i>Nephtys incisa</i>	332	70	2.6	74.7	89.7	47.4	E&J	1-31
13.	<i>Orchomenella pinguis</i>	292	28	2.3	79.3	35.9	104.2	E&J	4-14
14.	<i>Ampelisca spinipes</i>	291	28	2.3	77.0	35.9	103.9	E&J	1-14
15.	<i>Diplocirrus hirsutus</i>	253	19	2.0	81.3	24.4	133.1	E&J	6-13
16.	<i>Retusa obtusa</i>	206	48	1.6	82.9	61.5	42.9	E&J	2-31
17.	<i>Sternaspis scutata</i>	198	31	1.5	84.4	39.7	63.8	E&J	5-31
18.	<i>Hartmania moorei</i>	155	39	1.2	85.6	50.0	39.7	E&J	5-31
19.	<i>Ampharete aculifrons</i>	135	42	1.0	86.6	53.8	32.1	E&J	4-31
20.	Nemertea sp.	134	49	1.0	87.6	62.8	27.3	E&J	4-31
21.	<i>Casco bigelovi</i>	134	16	1.0	88.6	20.5	83.7	E&J	5-8
22.	<i>Nucula delphinodonta</i>	119	11	.9	89.5	14.1	108.1	E	3-8
23.	<i>Pholoe minuta</i>	100	40	.8	90.3	51.3	25.0	E&J	4-13
24.	<i>Cingula aculeus</i>	94	18	.7	91.0	23.1	52.2	E&J	4-14
25.	<i>Crenella decussata</i>	76	24	.6	91.6	30.8	31.6	E&J	4-31
26.	<i>Lacuna vineta</i>	75	31	.6	92.2	39.7	24.1	E&J	4-31
27.	<i>Lumbrineris fragilis</i>	74	40	.6	92.8	51.3	18.5	E&J	4-31
28.	<i>Pherusa plumosa</i>	66	23	.5	93.3	35.9	23.5	E&J	4-13
29.	<i>Yoldia sapotilla</i>	66	20	.5	93.8	25.6	33.0	E&J	3-31
30.	<i>Aeginina longicornis</i>	64	20	.5	94.3	25.6	32.0	E&J	6-14
31.	<i>Ninoc nigripes</i>	48	27	.4	94.7	34.6	17.7	E&J	4-31
32.	<i>Ammotrypane autogaster</i>	34	12	.3	95.0	15.4	28.3	E&J	1-31
33.	<i>Aricidea quadrilobata</i>	33	14	.3	95.3	17.9	23.5	E&J	1-14
34.	<i>Cerastoderma pinnulatum</i>	32	17	.2	95.5	21.8	18.8	E&J	3-31
35.	<i>Tellina agilis</i>	32	19	.2	95.7	24.4	16.8	E&J	1-31
36.	<i>Lora scalaris</i>	31	20	.2	95.9	25.6	15.5	E&J	4-14
37.	<i>Leptocheirus pinguis</i>	27	15	.2	96.1	19.2	18.0	J	4-13
38.	<i>Trichobranchus roseus</i>	27	14	.2	96.3	17.9	19.2	E&J	3-31
39.	<i>Rhodine loeni</i>	25	16	.2	96.5	20.5	15.6	E&J	4-13
40.	<i>Yoldia limatula</i>	25	15	.2	96.7	19.2	16.6	E&J	5-10
41.	<i>Nassarius trivittatus</i>	20	16	.2	96.9	20.5	12.5	E&J	5-31
42.	<i>Phyllodoce groenlandica</i>	18	12	.1	97.0	15.4	15.0	J	4-13
43.	<i>Terebellides stroemi</i>	17	14	.1	97.1	17.9	12.1	E&J	5-14
44.	<i>Pitar morrhuaana</i>	16	11	.1	97.2	14.1	14.5	E&J	5-31
45.	<i>Astarte undata</i>	15	11	.1	97.3	14.1	13.6	E&J	4-31
46.	<i>Priapulius caudatus</i>	15	11	.1	97.4	14.1	13.6	E&J	6-14
47.	<i>Edotea triloba</i>	14	11	.1	97.5	14.1	12.7	mostly J	1-13
48.	<i>Sarsiella americana</i>	11	10	.1	97.6	12.8	11.0	mostly J	1-13
49.	Miscellaneous			2.4	100.0				

¹ E=Ebenecook Harbor. J=Jewett Cove.

represented by several species tentatively identified as belonging to the genera *Eudorella* and *Diastylis*. Next in order was the hemichordate *Stereobalanus canadensis*; a selective deposit feeder living in fragile mucus-lined tubes that undoubtedly alter the texture of the sediments considerably. These tubes may also offer habitat for such potentially commensal animals as the amphipod *Corophium* sp. and the polychaete *Hartmania moorei*. *Thyasira gouldii*, a small bivalve, and *Phoxocephalus holbolli*, an amphipod, were fourth and fifth in abundance.

Sixth, in order of abundance, was the bivalve *Volsella modiolus* L., contributing 4.4 percent of all animals and uniformly distributed, occurring at 87.2 percent of the stations. This is a known epifaunal species and cannot be regarded as a member of the Sheepscoot infaunal community. The fact that nearly all specimens were dead, zero year class juveniles indicates an adverse habitat for newly metamorphosed individuals of this species.

Nephtys incisa was twelfth in numerical order (2.6 percent) but was found at 89.7 percent of the stations. In this faunal association *Nephtys* is a nonselective deposit feeder burrowing through the upper layers of the sediment, ingesting the substratum from which food materials are obtained. *Nephtys* was selected as a dominant because a *Nephtys-Nucula* community had been described from a similar faunal association (Sanders, 1956) and because *Nephtys* was the most uniformly distributed animal in the Sheepscoot survey. The comparatively low abundance may be ascribed to the great numerical fluctuations possible in some benthic communities as indicated by Thorson (1957).

The sampling period, July 29 to November 8, is assumed to have had no effect on the results of the survey, since no drastic environmental changes were observed, nor any important changes in faunal composition: Samples taken later in the year contained the same species typical of earlier samples. Possibly a slight increase in the abundance of some species may have occurred as small juveniles grew large enough to be retained by the screens. However, no change attributable to seasonal factors occurred in the order of species, ranked by abundance, during the survey period.

This, then, is a community of small animals including the bivalves *Nucula* and *Thyasira*, the

polychaete *Nephtys*, and the acorn worm *Stereobalanus*. The latter two species provide tubes and tunnels for commensals, such as the scale worm *Hartmania moorei*. Cumaceans and amphipods, particularly *Phoxocephalus*, *Corophium*, and *Dulichia*, are common and may be found as commensals, building tubes, or crawling freely about in the upper layers of bottom material. Most of the organisms are deposit feeders, ingesting the organic materials from the fine ooze layer of the sediments. The numerical abundance of the fauna is concentrated in relatively few species. Fifteen of the 108 species contributed over 80 percent of the total number of organisms. Seven species supplied nearly 60 percent of the animals collected.

This community in the Sheepscoot estuary, consisting of approximately 1,500 animals per square meter, is not heavily populated when compared with the 16,000 animals per square meter found by Sanders (1956) in the Long Island Sound community. Possibly the Sheepscoot fauna could attain comparable densities. Sanders used a finer screen size (1.0 mm.) for his study which would increase estimates of population density by retaining smaller forms of the dominant species: *Nucula*, *Nephtys*, *Yoldia*, and *Cistenides*.

TABLE 3.—Occurrence and abundance of selected* species, Ebenecook Harbor and Jewett Cove, Maine, July to November, 1955

Species	Ebenecook Harbor			Jewett Cove		
	Specimens	Stations	Average number	Specimens	Stations	Average number
	Number	Number	Per m. ²	Number	Number	Per m. ²
<i>Nucula proxima</i>	619	19	325.7	1,739	40	434.7
Cumacea sp. (4+species).....	828	17	487.0	1,145	38	301.3
<i>Stereobalanus canadensis</i>	168	13	121.5	610	21	290.4
<i>Thyasira gouldii</i>	98	13	75.3	619	38	187.5
<i>Phoxocephalus holbolli</i> ...	5	4	12.5	618	35	176.5
<i>Volsella modiolus</i>	129	27	47.7	444	41	108.2
<i>Corophium</i> sp.....	3	1	30.0	554	21	263.8
<i>Nucula tenuis</i>	73	11	66.3	442	35	126.1
<i>Dulichia</i> sp.....	188	12	156.6	219	27	81.1
<i>Scoloplos armiger</i>	173	17	101.7	229	30	76.3
<i>Aricidea</i> sp.....	272	19	143.1	123	24	51.2
<i>Nephtys incisa</i>	182	32	41.2	200	38	52.6
<i>Orchomenella pinquus</i>	4	4	10.0	288	24	120.0
<i>Ampelisca spinipes</i>	262	14	180.0	39	14	27.9
<i>Diplocirrus hirsutus</i>	4	4	10.0	249	15	166.0
<i>Retusa obtusa</i>	98	18	54.4	108	30	36.0
<i>Sternaspis scutata</i>	55	10	55.0	143	21	68.0
<i>Hartmania moorei</i>	48	13	36.9	107	26	41.1
<i>Ampharete acutifrons</i>	21	11	19.0	114	31	36.7
<i>Nemertea</i> sp.....	28	16	17.5	106	33	32.1
<i>Casco bigelovi</i>	3	2	15.0	131	14	93.5
<i>Nucula delphinodonta</i>	119	11	108.1
<i>Pholoe minuta</i>	18	10	18.0	82	30	27.3
<i>Cingula aculeus</i>	10	3	33.3	84	15	56.0
<i>Crenella decussata</i>	6	3	20.0	70	21	33.3

*First 25 from table 1.

COMMUNITY VARIATION

Although the two small areas studied produced nearly identical fauna, certain species were not found in both areas, and there were marked differences in occurrence and abundance (table 3). Greater average numbers of animals per sample were obtained in Jewett Cove than in Ebenecook Harbor (223.8 vs. 105.6) and more species per sample (24.9 vs. 14.8) were taken. The faunistic differences that exist between the two areas were found in fringe species that are incidental to the community (table 4). For example, 16 species were obtained in Jewett Cove that were not found in Ebenecook Harbor and Ebenecook Harbor provided 19 species not found in the other area. In Ebenecook Harbor, 15 of the 19 species were annelids, 2 species were mollusks, and 2 species were intertidal (epifaunal) gastropods. Only nine of the species in Jewett Cove were annelids, five were mollusks, and two were arthropods. Most of these animals were found in such small numbers that they appear to contribute little to community structure, but some species from each area were important to the bottom fauna. They were *Nucula delphinodonta* in Ebenecook Harbor and a three-species complex of the genus *Corophium* in Jewett Cove. *Corophium* was particularly important in the total abundance providing 4.3 percent of all fauna (table 2). Although *N. delphinodonta* contributed only about 1 percent to the combined fauna, the concentrated occurrence must be important in the bottom

associations of the deeper regions of Ebenecook Harbor, possibly in competition with *Nucula proxima*.

The faunal differences may be ascribed to physical and environmental conditions. Both Ebenecook Harbor and Jewett Cove were sampled essentially on the same grid plan. Ebenecook Harbor enclosed an area of 8,139 square meters, from which 36 one-tenth square meter samples were obtained, and Jewett Cove contained an area of 7,113 square meters, from which 42 one-tenth square meter samples were taken. Ebenecook Harbor is a more sheltered environment away from the main currents of the Sheepscot River and depends primarily on tidal exchange for circulation. Distinct environmental differences may be observed among the three coves in Ebenecook Harbor, probably as a result of their isolation from each other. Studies on the annual fluctuations in green crab, *Carcinus maenas*, populations have shown that winter mortalities—attributable to climatic factors—may be confined to one cove, but not necessarily the same cove, in successive years (W. R. Welch, oral communication). Jewett Cove, however, is hardly more than an indentation in the western bank of the Sheepscot River. The currents washing over the bottom are more pronounced than those in Ebenecook Harbor, water mass exchange may be more rapid, and probably more food material is available. These factors may also present an opportunity for a greater number of planktonic larvae to be brought into the area, and possibly provide for a more homogeneous distribution of the established animals. Differences in bottom slope, steeper in Jewett Cove and tending to compress the horizontal range of species with narrow depth requirements, may also be an important agent controlling faunal distribution.

TABLE 4.—Species not found in both Ebenecook Harbor and Jewett Cove, Maine, July to November, 1955

Ebenecook Harbor		Jewett Cove	
Species	Number	Species	Number
Annelida:		Annelida:	
<i>Polycirrus medusa</i>	2	<i>Eunoe nodosa</i>	7
<i>Polycirrus erimus</i>	5	<i>Goniada maculata</i>	1
<i>Praxillura ornata</i>	3	<i>Flabelligera affinis</i>	2
<i>Heteromastus filiformis</i>	3	<i>Scalibregma inflatum</i>	4
<i>Capitella capitata</i>	3	<i>Maldane sarsi</i>	13
<i>Eteone longa</i>	1	<i>Praxillella praeterrimissa</i> ..	6
<i>Phyllodoce mucosa</i>	1	<i>Phyllodoce groenlandica</i>	18
<i>Nereis virens</i>	12	<i>Euchone rubrocincta</i>	1
<i>Nereis caudata</i>	1	<i>Nereis pelagica</i>	1
<i>Arctidea</i> sp. 1.....	3		
<i>Paraonis gracilis</i>	2		
<i>Polydora</i> sp.....	1		
<i>Streblospio benedicti</i>	57		
<i>Nephtys caeca</i>	9		
<i>Prionospio malmgreni</i>	1		
Mollusca:		Mollusca:	
<i>Nucula delphinodonta</i>	119	<i>Clinocardium ciliata</i>	4
<i>Yoldia myalis</i>	2	<i>Amytilus edulis</i>	2
<i>Littorina littorea</i>	3	<i>Lyonsia arenosa</i>	1
<i>Littorina saxatilis</i>	5	<i>Lyonsia hyalina</i>	1
		<i>Cylichna alba</i>	8
		Arthropoda:	
		<i>Leptocheirus pinguis</i>	27
		<i>Anonyx liljeborgii</i>	6

DISCUSSION

Size composition

Apparently large animals are at a disadvantage in this community of small organisms and cannot establish themselves in this habitat. The marked small size of almost all animals in the *Nephtys-Nucula* community merits discussion, particularly with regard to some factors favoring small animals in this situation.

The possibility exists that the sampling equipment may not capture large animals either because

the animals live beyond the depth of sediment to which the grab can dig, or because the animals are too widely scattered. Neither of these appear to be valid objections, since the equipment has obtained larger animals from other local communities in soft sediments and other types of samplers have been used on the *Nephtys-Nucula* community without obtaining significant numbers of large animals (Sanders, 1956, 1960; Stickney and Stringer, 1957).

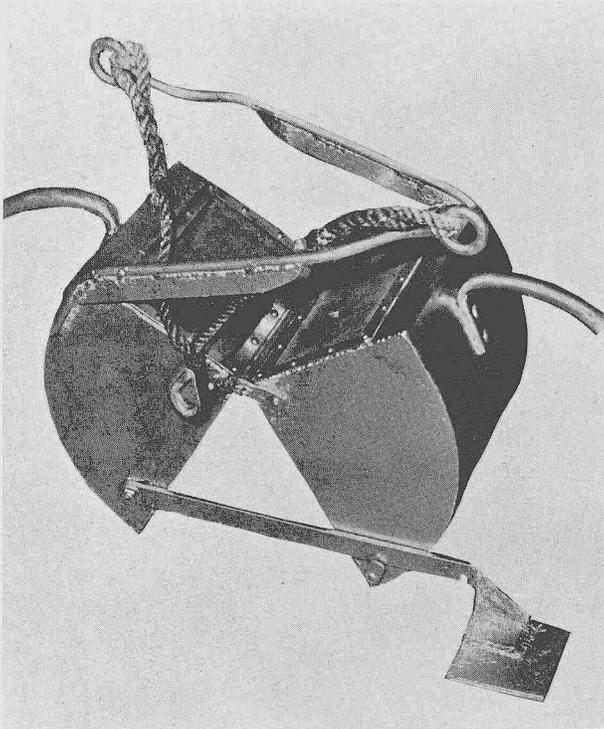


FIGURE 4.—Petersen-type dredge similar in construction to the grab used in this survey.

If the apparent size composition is not influenced by limitations of sampling then other selective factors must be operative. Juveniles of potentially large animals are occasionally taken in the sampler (for example, *Pitar morrhua* at 11 stations), but these animals rarely reach mature size in this community. The advantage gained by superior numbers alone may be favorable to small animals in the competition for habitat and the ability to mature rapidly can be very advantageous in colonization. High natality, rapid growth, and early maturity enables the species within a population to fill the ecological niche rapidly tending to exclude species with the slow

growth and late maturity characteristic of many large animals. If predation should become a dominant factor in controlling community size-composition, slow growth and late maturity expose prey to longer periods of predation and fewer individuals will reach adulthood. Recruitment of large animal species in the *Nephtys-Nucula* community tends to be at long intervals from sources outside the occupied area while recruitment is intensive and at shorter intervals from the endemic, smaller species.

Sediments conducive to the establishment of a population of small infaunal animals are probably not favorable to large organisms from the outset. Soil particle size may be an important selective factor in determining the size range of organisms in the community. The physical and chemical modifications (fecal deposition, tube construction, particle selection, etc.) of such sediments by a community of small animals would be expected to make the environment less attractive the longer the community successfully maintained itself.

Other environmental and ecological factors may regulate size composition within any animal community, and further research on this subject is needed.

Geographical distribution

The *Nephtys-Nucula* community was first described by Sanders (1956) from the benthos in Long Island Sound. Originally termed the *Nephtys incisa-Yoldia limatula* community, *Nucula* being rejected as a dominant because of small size, the name has been revised in recent papers on the basis of further study and now stands as *Nephtys incisa-Nucula proxima*. Sanders (1958, 1960) has also found the *Nephtys-Nucula* community in the soft mud bottoms of Buzzards Bay, Mass. He pointed out in these papers that although *Nephtys incisa* has often been classified as a carnivore, it is a nonselective deposit feeder in this association. This is particularly important if the animal is used to typify the community since predators are not considered to be stable members of an infaunal association (Thorson, 1957).

Stickney and Stringer (1957) have reported a faunal association from the soft mud bottoms of Greenwich Bay, R.I., which appears somewhat transitional between Sanders' *Ampelisca* community and the *Nephtys-Nucula* community. The *Ampelisca* community does exist in a large part of

TABLE 5.—Comparison of four "Nephtys-Nucula" communities

Rank	Sheepscoot River	Buzzards Bay ¹	Long Island Sound ²	Greenwich Bay ³
1	<i>Nucula proxima</i>	<i>Nucula proxima</i>	<i>Nephtys incisa</i>	<i>Ampelisca spinipes</i>
2	Cumacea sp.	<i>Nephtys incisa</i>	<i>Nucula proxima</i>	<i>Corophium cylindricum</i>
3	<i>Stereobalanus canadensis</i>	<i>Ninno nigripes</i>	<i>Yoldia limatula</i>	<i>Podarke obacura</i>
4	<i>Thyasira gouldi</i>	<i>Cylichna oryza</i>	<i>Cistenides gouldi</i>	<i>Tharyx acutus</i>
5	<i>Phorocephalus holboellii</i>	<i>Callocardia [= Pitar] morrhuana</i>		<i>Tornatina canaliculata</i>
6	<i>Volsella modiolus</i>	<i>Hutchinsoniella macracantha</i>		<i>Spiochaetopterus ocellatus</i>
7	<i>Corophium</i> sp.	<i>Lumbrineris tenuis</i>		<i>Macoma tenta</i>
8	<i>Nucula tenuis</i>	<i>Turbonilla</i> sp.		<i>Nucula proxima</i>
9	<i>Dulichia</i> sp.	<i>Spio filicornis</i>		<i>Pitar morrhuana</i>
10	<i>Scoloplos armiger</i>	<i>Retusa caniculata</i>		
11	<i>Aricidea</i> sp.	<i>Doreillea caeca</i>		
12	<i>Nephtys incisa</i>	<i>Tharyx</i> sp.		
Sediment	Very high percent silt-clay	Very high percent silt-clay	Greater sand content than other surveys.	Highly modified by <i>Ampelisca</i> tubes.
Equipment	Petersen-type Grab	Foster Anchor Dredge (modified).	Foster Anchor Dredge (modified).	Hayworth clamshell.
Sample size	0.1 m. ² x 10 cm. deep	7.6 cm. deep—calculated surface area from volume.	7.6 cm. deep—calculated surface area from volume.	0.5 m. ² x 30 cm. deep.
Finest screen	1.5-mm. openings	0.2-mm. openings	1.0-mm. openings	2.0-mm. openings—subsample only (0.5 m. ² x 8.0 cm.) remainder through 12-mm. openings.

¹ From Sanders (1960). ² From Sanders (1956). ³ From Stickney and Stringer (1957).

Greenwich Bay, but there is a strong indication from sedimentary and faunal evidence, that at least a section of the center part of the Bay could support the *Nephtys-Nucula* community.

The *Nephtys-Nucula* community has been recorded therefore from three locations on the Atlantic coast: Long Island Sound, Buzzards

Bay, and Sheepscoot Bay, with the possibility of a fourth in Rhode Island. These communities are compared in table 5. Characteristically, they are composed of small deposit-feeding species which live in the top few centimeters of the bottom sediments where a supply of organic food materials provides nutritional support for relatively large numbers of short-lived, but early maturing animals. The community appears to be endemic to the northern coasts of the United States in relatively protected bodies of water and is confined to the soft mud bottoms which have a high silt-clay sediment composition. The animals which it comprises are generally boreal. Species composition of minor community organisms will vary depending on the geographical location of the population.

The *Syndosmya-Alba* community described by Petersen and Jensen from Danish waters (see review by Thorson 1957, p. 510) appears to be a close counterpart of the *Nephtys-Nucula* community. The original definition of the *Nephtys-Nucula* community and comparison with communities from other geographical areas can be found in Sanders (1956).

SUMMARY

A *Nephtys-Nucula* community is described from a series of bottom samples taken with a Petersen-type grab. The community was found in areas of the Sheepscoot River estuary and has been previously described from similar soft mud sediments in Buzzards Bay, Mass., and Long Island

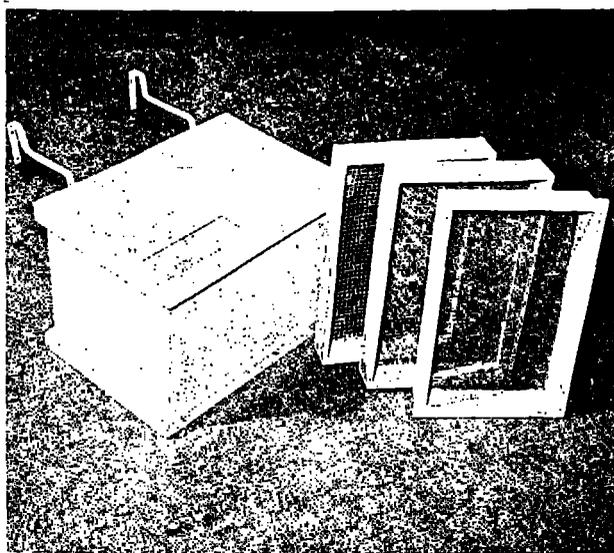


FIGURE 5.—Screen box and three nesting screens used to separate organisms from bottom sediments.

Sound. The faunal composition of the community is similar in all areas but incidental species composition varies with geographical location. *Nucula proxima*, a pelecypod, and *Nephtys incisa*, a polychaete, are the dominant organisms of the Sheepscot community with cumaceans, a hemichordate, a pelecypod (*Thyasira gouldi*), and an amphipod (*Phorocephalus holbolli*) also numerous and widely distributed.

The community is composed of small animals that inhabit the surface layers of the bottom sediment. They are mostly deposit or filter feeders. Their small size may be of advantage in competition with larger animals, at least in this environmental situation.

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H. L. Sanders and R. L. Wigley reviewed the manuscript.

LITERATURE CITED

- ALLEE, WARDER C.
1934. Concerning the organization of marine coastal communities. *Ecological Monographs*, vol. 4, pp. 541-554.
- BRYANT, FLOYD G.
1956. Stream surveys of the Sheepscot and Ducktrap river systems in Maine. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 195, 19 pp.
- COWLES, R. P.
1930. A biological study of the offshore waters of Chesapeake Bay. *Bulletin of the U.S. Bureau of Fisheries*, vol. 46, pp. 277-381.
- DEXTER, RALPH W.
1944. The bottom community of Ipswich Bay, Massachusetts. *Ecology*, vol. 25, No. 3, pp. 352-359.
1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bio-ecology. *Ecological Monographs*, vol. 17, pp. 261-294.
- HARTMAN, OLGA.
1955. Quantitative survey of the benthos of San Pedro Basin, Southern California. Part I, preliminary results. *Allen Hancock Pacific Expeditions*, vol. 19, No. 1, 185 pp.
- JONES, N. S.
1950. Marine bottom communities. *Biological Review (Cambridge Philosophical Review)*, vol. 25, No. 3, pp. 283-313.
- KINGSLEY, J. S.
1901. Preliminary catalog of the marine invertebrata of Casco Bay, Maine. *Proceedings of the Portland Society of Natural History [Portland, Maine]* vol. 2, pp. 159-183.
- KIRSOP, F. M.
1922. Preliminary study of methods of examining the life of the sea bottom. *Publications of the Puget Sound Marine (Biological) Station of the University of Washington*, vol. 3, pp. 129-139.
- LEE, RICHARD E.
1944. A quantitative survey of the invertebrate bottom fauna in Menemsha Bight. *Biological Bulletin*, vol. 86, No. 2, pp. 83-97.
- PARKER, ROBERT H.
1956. Macro-invertebrate assemblages as indicators of sedimentary environments in East Mississippi Delta region. *Bulletin of the American Association of Petroleum Geologists*, vol. 40, No. 2, pp. 295-376.
1959. Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. *Bulletin of the American Association of Petroleum Geologists*, vol. 43, No. 9, pp. 2100-2166.
1960. Ecology and distributional patterns of marine macro-invertebrates, Northern Gulf of Mexico. *Recent Sediments, Northwest Gulf of Mexico, 1951-1958*. [Published by the American Association of Petroleum Geologists, Tulsa, Oklahoma] pp. 302-337, 368-381.
- PETERSEN, C. G. JOHAN, AND P. BOYSEN-JENSEN.
1911. The valuation of the sea, Part I. Animal life of the sea bottom; its food and quantity. *Report of the Danish Biological Station*, vol. 20, 81 pp.
- PETERSEN, C. G. JOHAN.
1913. The valuation of the sea, Part II. The animal communities of the sea bottom and their importance for marine zoogeography. *Report of the Danish Biological Station*, vol. 21, 44 pp.
- SANDERS, HOWARD L.
1956. Oceanography of Long Island Sound, 1952-1954. X. Biology of marine bottom communities. *Bulletin Bingham Oceanographic Collection*. [Peabody Museum of Natural History, Yale University], vol. 25, pp. 345-414.
1958. Benthic studies in Buzzards Bay. I. Animal sediment relationships. *Limnology and Oceanography*, vol. 3, No. 3, pp. 245-258.
1960. Benthic studies in Buzzards Bay. III. The structure of the soft bottom community. *Limnology and Oceanography*, vol. 5, No. 2, pp. 138-153.

- SHELFORD, VICTOR E., ASA O. WEESE, LUCILE A. RICE,
DANIEL I. RASMUSSEN, N. M. WISMER, AND J. H.
SWANSON.
1935. Some marine biotic communities of the Pacific
coast of North America. *Ecological Monographs*,
vol. 5, pp. 249-354.
- SOIL SURVEY STAFF.
1951. Soil survey manual. U.S. Department of
Agriculture, Handbook 18. Government Printing
Office, Washington, D.C., 503 pp.
- STICKNEY, ALDEN P.
1959. Ecology of the Sheepscot River estuary. U.S.
Department of the Interior, Fish and Wildlife Serv-
ice, Special Scientific Report—Fisheries No. 309,
21 pp.
- STICKNEY, ALDEN P., AND LOUIS D. STRINGER.
1957. A study of the invertebrate bottom fauna of
Greenwich Bay, Rhode Island. *Ecology*, vol. 38,
No. 1, pp. 111-122.
- SUMNER, FRANCIS B., RAYMOND C. OSBURN, AND LEON J.
COLE.
1913. A biological survey of the waters of Woods
Hole and vicinity. *Bulletin of the U.S. Bureau of
Fisheries*, vol. 31 (1911) [In two parts] pp. 1-544,
545-860.
- THORSON, GUNNAR.
1951. Animal communities of the level sea bottom.
Annee Biologique, vol. 27, No. 7, pp. 249-257.
1956. Marine level-bottom communities of recent
seas, their temperature adaptation and their "bal-
ance" between predators and food animals. *Trans-
actions of the New York Academy of Science*,
Section II, vol. 18, No. 8, pp. 693-700.
1957. Bottom communities (sublittoral or shallow
shelf). *In* *Treatise on Marine Ecology and Paleo-
ecology*. Geological Society of America, Memoir
67, vol. 1, pp. 461-534.
- VERRILL, A. E.
1873. Report on the invertebrate animals of Vine-
yard Sound and the adjacent waters. Report U.S.
Fish Commission for 1871-1872, pp. 295-778.
- WIESER, WOLFGANG.
1960. Benthic studies in Buzzards Bay. II. The
meiofauna. *Limnology and Oceanography*, vol. 5,
No. 2, pp. 121-137.
- WIGLEY, ROLAND L.
1956. Food habits of Georges Bank haddock. U.S.
Department of the Interior, Fish and Wildlife
Service, Special Scientific Report—Fisheries No.
165, 26 pp.

UPWELLING IN THE COSTA RICA DOME

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ABSTRACT

The Costa Rica Dome is an area off the coast of Costa Rica where the strong tropical thermocline reaches to within 10 meters of the sea surface. The dome measures about 150 by 300 kilometers. It is situated near lat. 9° N., long. 89° W., at the eastern end of a ridge in the topography of the thermocline along the northern boundary of the Equatorial Countercurrent. This current, the Costa Rica Coastal Current, and parts of the North Equatorial Current form a cyclonic circulation around the dome.

At the surface the dome appears as an area of slightly reduced temperature, higher salinity and phosphate contents, and reduced oxygen saturation, which are indications of upwelling. The balance between the energy available for heating of the surface layer and the ascending of cooler water gives an average ascending velocity of 10^{-1} cm/sec. These movements add only 7×10^{10} cm.³/sec. to the surface layer, compared with

The eastern tropical Pacific Ocean is characterized by a very well-developed thermocline separating the warm surface water from the cooler subsurface water. The warm surface layer is comparatively shallow, and the topography of the thermocline is related to the currents in the surface layer as shown by Cromwell (1958). The divergences and convergences associated with the surface circulation, which result in the formation of ridges and troughs in the topography of the thermocline, have particular importance for the fertilization of the surface layer and for the distribution of the standing crop of zooplankton in the area, as shown by Brandhorst (1958) and Reid (1962). A feature of special interest in this connection is the Costa Rica Dome in which the top of the thermocline often comes to within less than 10 m.

transports of about 20×10^{12} cm.³/sec. of the horizontal circulation. The upwelling in the dome is caused by the cyclonic flow around the dome. When the Countercurrent strongly changes direction, the necessary adjustment of its velocity requires a cross-current velocity of about 0.9 cm./sec. which is sufficient to maintain the upwelling. During the Costa Rica Dome survey a deep-reaching eddy transporting 20×10^{12} cm.³/sec. appeared to be separated and to drift north with the Costa Rica Coastal Current.

Comparison of the topography of an isothermal layer during six surveys in the area showed that the dome was always present and maintained its position within 200 km. These observations indicate that the Costa Rica Dome, although a permanent feature, is subject to considerable fluctuations in its structure and circulation and may contribute essentially to large-scale mixing.

of the surface. This dome is situated off the coast of Costa Rica at about lat. 9° N. and long. 89° W. and has a diameter of approximately 200 km.

As pointed out to me by Milner B. Schaefer, the Costa Rica Dome was found in 1948, when bathythermograph (BT) observations from vessels en route between California and Panama were examined. Between 1952 and 1958 a number of expeditions crossed or partly surveyed this dome, and confirmed its existence and approximate posi-

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¹ Contribution from Scripps Institution of Oceanography, New Series.

tion. However, none of these expeditions succeeded in covering the area of the dome sufficiently to allow a detailed analysis. As a consequence of this, a survey of the Costa Rica Dome was undertaken in November and December 1959 under the leadership of M. J. Pollak and E. B. Bennett of the Inter-American Tropical Tuna Commission (Scripps Institution of Oceanography, 1960). The results of this survey, which covered the dome as well as the surrounding area, are used in this paper to analyze the structure of the dome and draw conclusions about its role in the circulation of the eastern tropical Pacific Ocean, except where other expeditions are mentioned.

The objectives of this expedition were to locate the position of the dome properly, to determine its extent, and to study its circulation and its effects on the distribution of biota. Upwelling is thought to occur near the center of the dome, and an analysis of the data of the expedition should give an estimate of its amount and an indication of the sources of the ascending water, as well as an explanation of the upwelling from dynamic principles. From the point of view of physical oceanography, the questions to be discussed in this paper are the following:

- i. Where is the upwelling area located, and what is its size?
- ii. What is the amount of upwelling?
- iii. Where does the ascending water come from?
- iv. How is the upwelling conditioned dynamically?
- v. Is the Costa Rica Dome a permanent or temporary feature?

These questions have a bearing upon the study of the tuna resources of the eastern tropical Pacific, which are exploited by United States fishermen. It could be expected that the spatial and temporal distribution of tuna would bear some relation to the distribution of upwelling, which, therefore, warrants investigation.

HYDROGRAPHIC STRUCTURE OF THE COSTA RICA DOME

The Costa Rica Dome appears as an area where the homogeneous surface layer is extremely thin and the top of the thermocline often comes to within less than 10 m. of the sea surface. Also, the thermocline itself is more strongly developed than in surrounding waters and temperature gradients usually exceed 1°C . per meter in the range

between 25° and 17° . As a consequence of this, the cooler subsurface water is found in a higher position than in the surrounding area. These conditions are shown in figure 1 where the topography of the 24° isotherm, as derived from BT-observations, is drawn, as are two BT-sections across the dome. The 24° isotherm, which coincides fairly well with the top of the thermocline in this region, ascends to less than 10 m. depth in several patches within an area of approximately 350×150 km. On the periphery of the surveyed area this isotherm is found in depths of more than 20 m., its deepest positions being in the southeast. A BT-section (A-A) running from northwest to southeast and drawn from the same data is shown in the upper part of figure 1. The dome is situated between stations 7 and 11 where the thermocline is highest and the temperature gradient is steepest, and also where the cooler subsurface water of 13° reaches its highest position, ascending to less than 90 m. depth. This section does not cut through the shallowest parts of the dome but runs between the two patches in which the top of the thermocline is highest. In the northwestern part of the section another area with a high position of the thermocline is found, but there are not enough observations to relate this feature to the Costa Rica Dome.

A much more satisfactory BT-section (B-B) across the dome was obtained in February 1960 by the vessel *Explorer* (Stewart, 1962). This section is drawn in the lower part of figure 1 and shows that the dome is situated between stations 331 and 369 in approximately the same position as during the Costa Rica Dome survey, with a diameter of about 230 km. The two sections run in the same general direction from northwest to southeast, but there is no shallow thermocline in the northwestern part of the *Explorer* section. Therefore, the shallow thermocline observed during the Costa Rica Dome survey in the northwest may be considered as a transient feature.

At the surface the dome appears as an area of slightly lower temperature, slightly higher salinity, reduced percent of oxygen saturation, and high phosphate concentration, although the centers of the areas defined by these properties do not completely coincide (fig. 2). Temperature near the center of the dome exhibits a more irregular pattern than on its periphery, where it usually exceeds 27°C . Near the center, patches of water of less than 25°C . are found beside patches

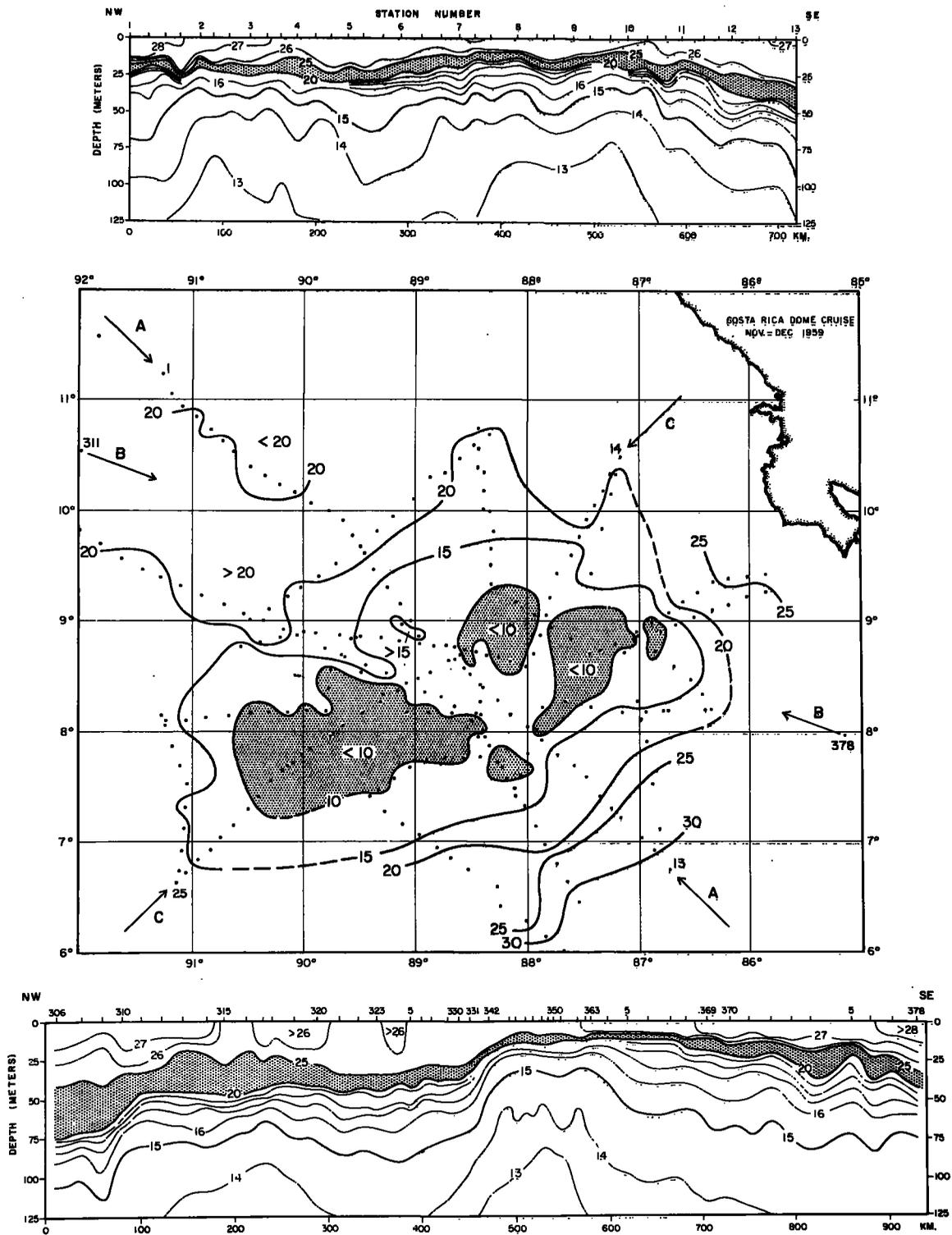


FIGURE 1.—The thermal structure of the Costa Rica Dome from bathythermograph observations. Center: Topography of the 24° C. isotherm during the Costa Rica Dome cruise, in meters, <10 m. shaded. Top: Distribution of temperature along section A-A during the Costa Rica Dome cruise; thermocline between 25° and 20° C. shaded. Bottom: Distribution of temperature across the dome in February 1960 according to observations of the vessel *Explorer* along section B-B; thermocline between 25° and 20° C. shaded.

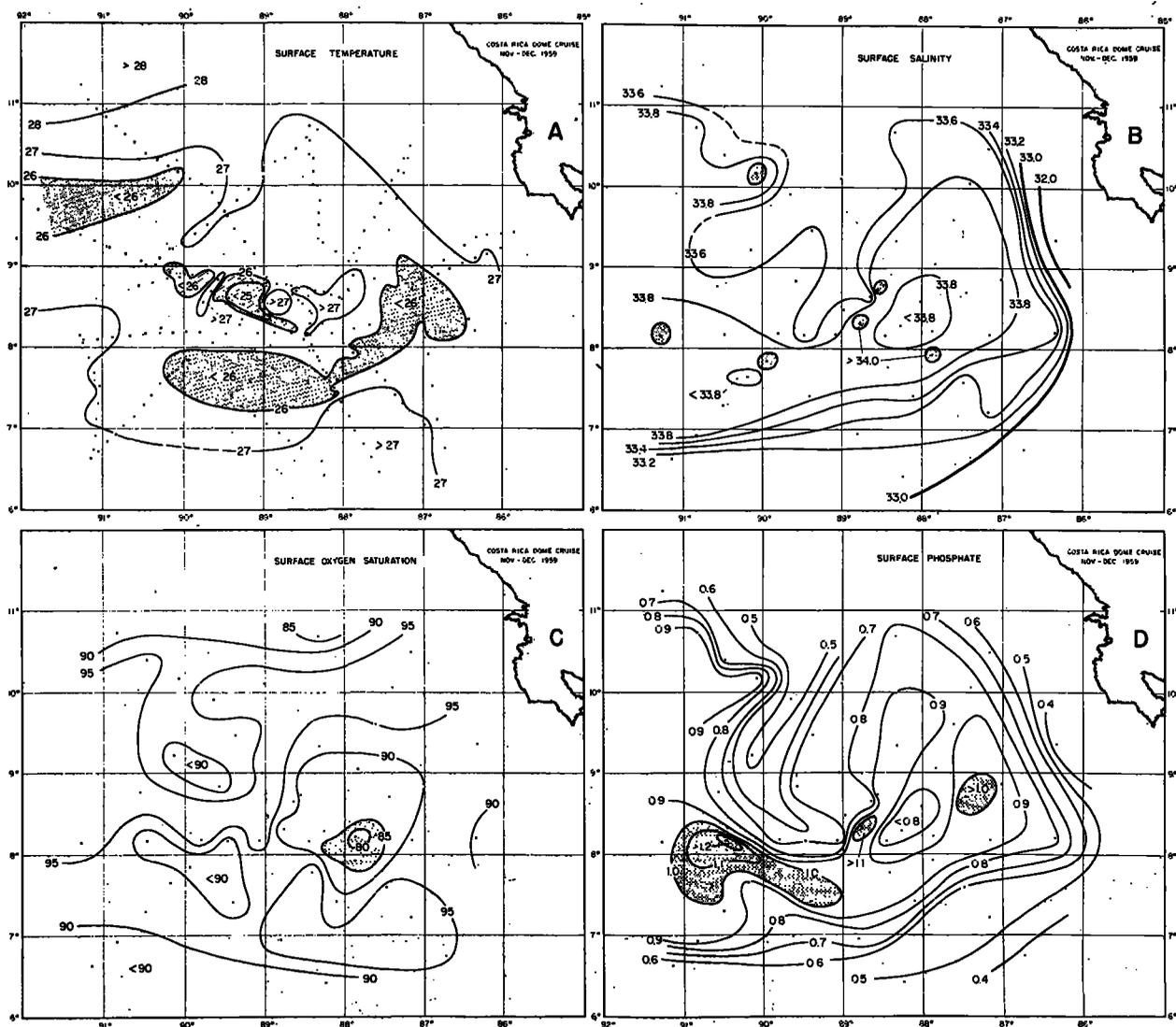


FIGURE 2.—Distribution of properties at the surface during the Costa Rica Dome cruise. (A) Surface temperature, $<26^{\circ}\text{C}$. shaded. (B) Surface salinity, $>34.0\text{‰}$ shaded. (C) Percent of oxygen saturation at the surface, <85 percent shaded. (D) Surface phosphate-phosphorus, $>1.0\ \mu\text{g.-atom/L}$. shaded.

with more than 27°C . (fig. 2A). This pattern indicates a patchiness of the actual upwelling, which occasionally and locally may bring the top of the thermocline right to the surface, but this is definitely an exception. The cooler water is situated between lat. 7.5° and 9°N . and between long. 87° and 90°W . Although the surface temperature shows a drop of as much as 2°C . in some places, it should be noted that during this survey no water within the temperature range of the thermocline reaches right to the surface and in all instances a shallow surface layer is shown in the BT-observations.

The distribution of surface salinity (fig. 2B) shows a tongue of high salinity extending eastwards between lat. 7° and 8°N . The salinity within this tongue is above 33.8‰ , and only in a few places is 34.0‰ exceeded. East of long. 89°W . the tongue turns north and its salinity is reduced. It seems to reach about lat. 11°N . To the south and to the east a sharp salinity gradient separates the tongue from the water of low salinity ($<33\text{‰}$) off the coast of Central America. This salinity gradient is not accompanied by a corresponding change of surface temperature.

The surface water is undersaturated with oxygen in the entire area, values being between 88 and 98 percent (fig. 2C). In a small area near lat. 8° N., long. 88° W., oxygen saturation at the surface drops below 85 percent indicating an advection of subsurface water of low oxygen content into the shallow surface layer. The phosphate concentration at the surface is high; only in the range of the low salinity water off Central America are the phosphate values less than 0.6 $\mu\text{g.}-\text{atom/L.}$ (fig. 2D). The distribution of the phosphate resembles closely that of surface salinity with a tongue of high phosphate coinciding with the tongue of high salinity. Within this tongue phosphate is in some places as high as 1.0–1.2 $\mu\text{g.}-\text{atom/L.}$

In the center of the tongue of water of high phosphate content, an area near long. 88° W. has phosphate values below 0.8 $\mu\text{g.}-\text{atom/L.}$ This area coincides with an area of reduced salinity (<33.8‰) within the tongue of high salinity, and with an area where the surface temperature is above 27°. Because upwelling in the dome should be indicated by low temperature, high salinity, and high phosphate, this patch of abnormal water in the center of the dome suggests that circulation and upwelling in the dome must be subject to fluctuations that can lead to the isolation of a patch of water of this size. The lowest oxygen saturation is found just to the southeast of this patch of abnormal water.

According to this analysis of the topography of the thermocline and of the distribution of properties at the surface, the Costa Rica Dome appears as the end of a ridge in which the thermocline is in a very shallow position. This ridge extends along the left or northern flank of the Equatorial Countercurrent, as shown by Cromwell (1958). When this current approaches the coast of Central America and turns north, the ridge is abruptly terminated, and the Costa Rica Dome is at its end. In this dome the thermocline comes even closer to the surface than is the case along the ridge at the northern boundary of the Countercurrent, indicating that upwelling occurs in the dome area. The dome was situated between lat. 7.5° and 9° N. and between long. 87° and 90° W. during this survey.

Within the strong tropical discontinuity layer, temperature decreases rapidly from about 25° to 15° C. within a depth interval of only 20 to 50 m.,

COSTA RICA DOME

and the other properties also change considerably. Salinity and phosphate content increase while oxygen content decreases, as shown by the distribution of these properties between the surface and 800 m. depth along a section crossing the dome area from southwest to northeast (fig. 3). This is section C-C in figure 1. Below 15° C. the

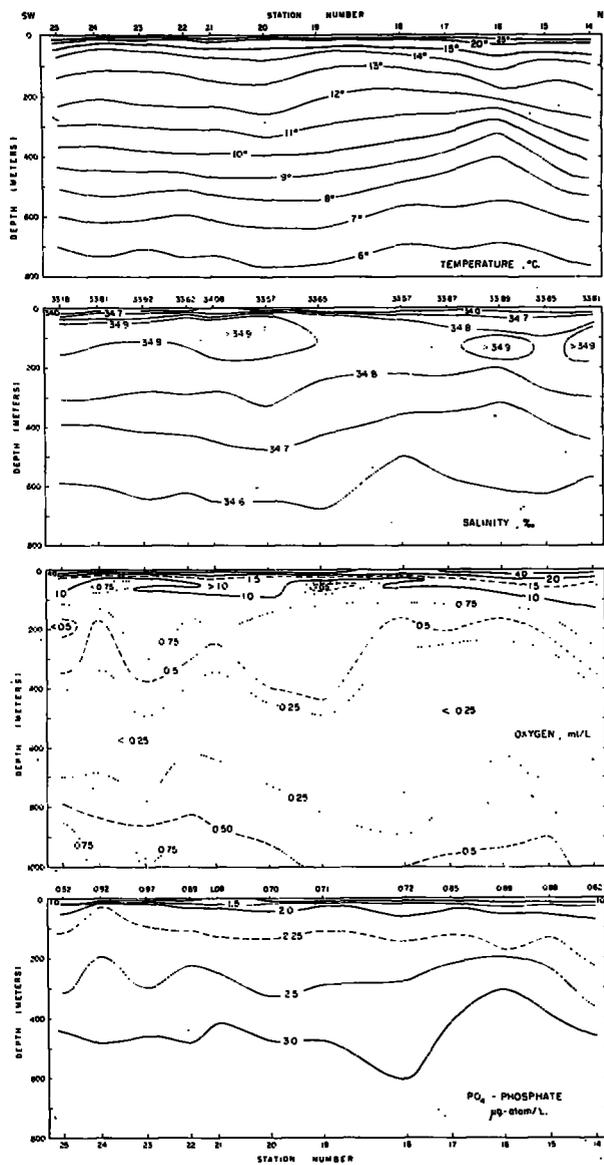


FIGURE 3.—Distribution of temperature, salinity, oxygen content (ml./L.), and phosphate-phosphorus between the surface and 800 m. depth along a section from southwest to northeast across the Costa Rica Dome, on the Costa Rica Dome cruise. The position of the section is shown in figure 1 by the line C-C.

temperature decrease is much slower and the salinity reaches a maximum near 100 m. depth in which salinities are close to 34.9‰. In the layer between 50 and 300 m. depth the oxygen content shows a number of maxima and minima before decreasing to values of less than 0.25 ml./L. and reaching the main oxygen minimum. These intermediate oxygen maxima and minima do not exhibit any uniformity with respect to the depth and temperature at which they are found. It is likely that this irregular oxygen distribution results from the local variability of the quantity and activity of oxygen-consuming material, as well as from the horizontal advection of smaller water bodies of higher oxygen content. The main oxygen minimum is found in depths between 400 and 700 m. in which oxygen content is everywhere lower than 0.20 ml./L. Below this layer oxygen increases again and the salinity reaches a minimum near 1,000 m. with salinities below 34.6‰ which are characteristic for the Intermediate Water. Phosphate, which is already unusually high at the surface, increases to 2.0 $\mu\text{g.-atom/L.}$ at about 50 m. and then much more slowly to values above 3.0 $\mu\text{g.-atom/L.}$ in the lower part of the oxygen minimum layer.

The vertical structure of the water masses in the area of the Costa Rica Dome is shown by the envelopes of all temperature-salinity and temperature-oxygen curves in figure 4. Below the surface layer of high temperature and comparatively low salinity, salinity increases to a maximum which is situated between 30 and 150 m. depth. The salinity in this salinity maximum is charted in figure 5a and varies only between 34.83 and 34.96‰. This subsurface salinity maximum is found everywhere in the eastern tropical Pacific Ocean and will be called the Equatorial Subsurface Water. A close analysis of the salinity maximum (not presented here) and of its depth shows that two branches are present in the area of the Costa Rica Dome. One branch is found east of long. 90° W. and the maximum is in depths between 80 and 150 m.; the other branch is found west of long. 88° W. and the maximum is between 30 and 60 m. depth. Between long. 88° and 90° W. the two maxima overlap and a double maximum is found. The salinities in the two branches are not different, and the small gradients seen in figure 5A do not allow one to draw conclusions

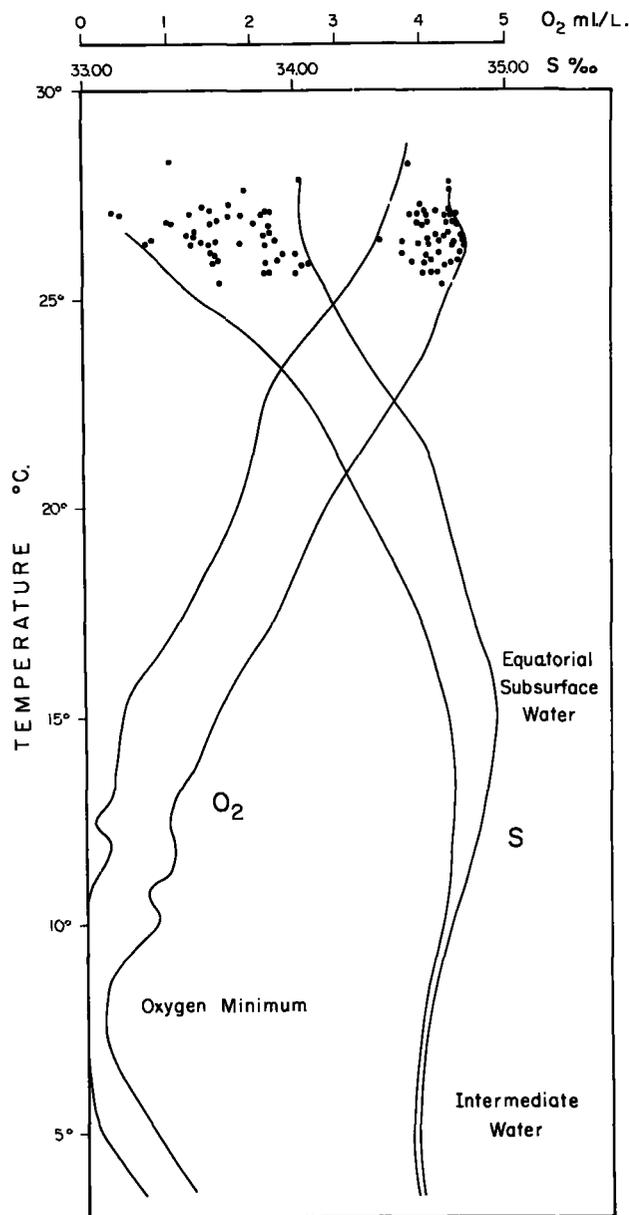


FIGURE 4.—Temperature-salinity and temperature-oxygen diagram showing the envelopes of all TS- and TO₂-curves during the Costa Rica Dome cruise. Surface values are entered by dots, and names of the main water masses are indicated.

about the spreading of the two branches. In the center of the dome, where the thermocline is highest, the salinity maximum is lowest and drops in some places below 34.85‰. This reduced salinity can be taken as an indication of upwelling in these localities because the ascending motion would tend to reduce the salinity in the maximum.

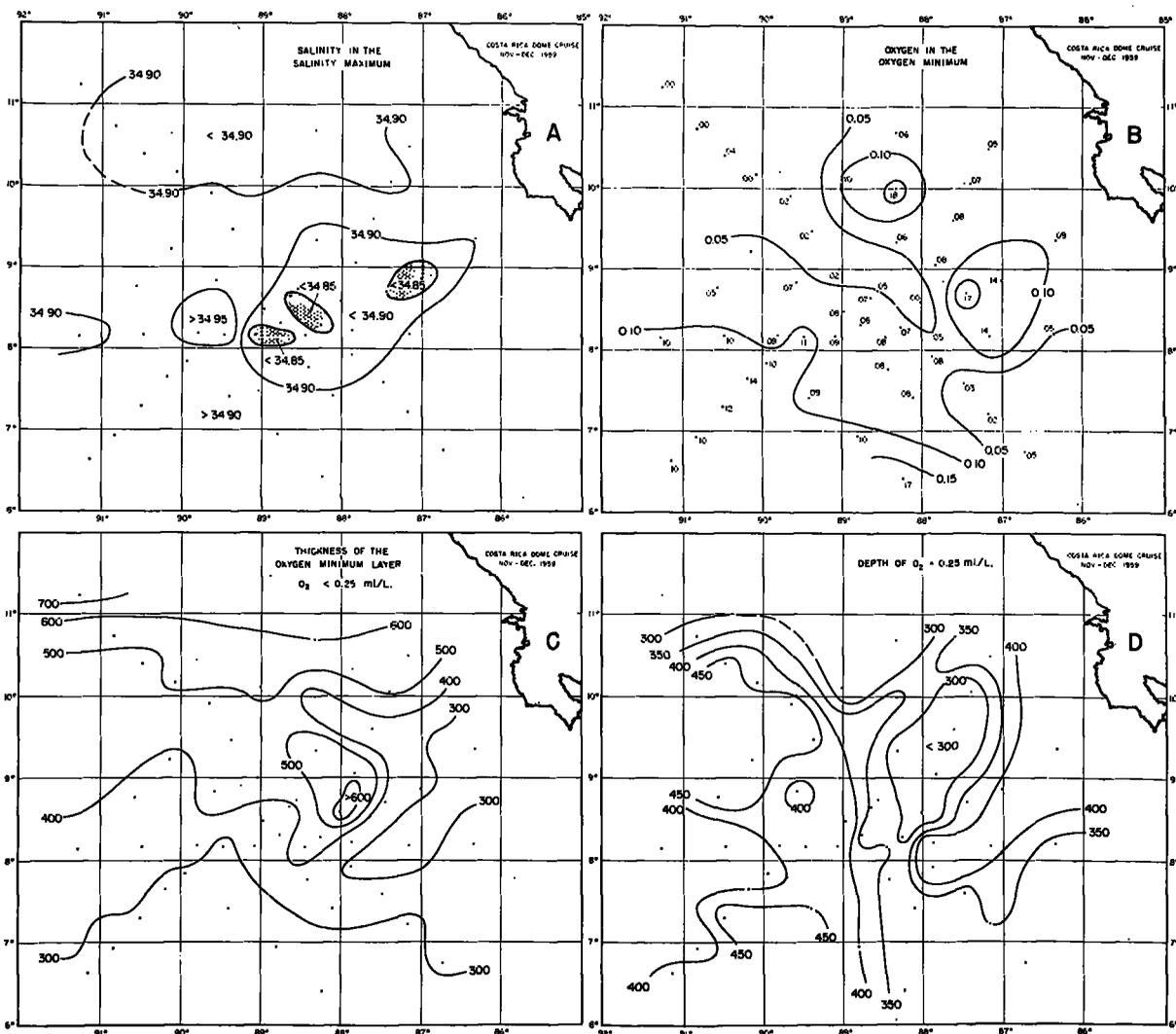


FIGURE 5.—(A) Distribution of salinity in the salinity maximum of the Equatorial Subsurface Water, $< 34.85\text{‰}$ shaded. (B) Minimal oxygen content in the oxygen minimum layer, in ml./L. Values at station positions are in 0.01 ml./L. (C) Thickness of the oxygen minimum layer (where $O_2 < 0.25$ ml./L.) in meters. (D) Depth of the upper boundary of the oxygen minimum layer, given by the depth of the 0.25 ml./L. surface in meters.

In the range of the Equatorial Subsurface Water, oxygen content varies widely but is, in general, low, between 2.0 and 0.25 ml./L., and shows intermediate maxima and minima.

In depths near 900 m. the Intermediate Water is found, characterized by a salinity minimum at a temperature of about 5° C. The salinities in the minimum are uniform and range only between 34.56 and 34.58‰ in the entire area surveyed.

The main oxygen minimum is situated between the Equatorial Subsurface and the Intermediate Water and extends over a considerable interval of

depth. Oxygen concentrations in the minimum are everywhere in the area below 0.20 ml./L. (fig. 5B) and in some places they are close to zero. Because the oxygen content remains at this low level within a fairly thick layer, it is not possible to chart the depth of the minimum with confidence and it is advisable to chart instead, the thickness of the layer that has an oxygen content of less than 0.25 ml./L. (fig. 5C) and the upper limit of the oxygen minimum layer as given by the depth of an oxygen content of 0.25 ml./L. (fig. 5D). The thickness of the oxygen minimum layer increases

from about 250 m. in the south to more than 600 m. in the north. Only underneath the dome, at lat. 9° N. and long. 88° W., is this regular increase in thickness interrupted and the oxygen minimum layer reaches a thickness of 600 m. in contrast to only 400 m. in the immediate vicinity. The upper limit of the oxygen minimum, as given by the depth where the oxygen content is 0.25 ml./L. shows a more irregular pattern. The highest position of this surface is found near lat. 9° N., and long. 88° W., considerably displaced relative to the position of the dome as indicated in the topography of the thermocline. This displacement will be discussed in detail when the dynamics of the system is treated. In the north of the area, the 0.25 ml./L. oxygen surface is also in a very high position but this is due to the great thickness of the oxygen minimum layer.

HORIZONTAL CIRCULATION

The Costa Rica Dome is north of the Equatorial Countercurrent. This current approaches the coast of Central America between lat. 4° and 8° N. during all seasons, with the exception of February and March when it seems to be absent or only weakly developed as shown in the surface current charts drawn by Cromwell and Bennett (1959). Along the coast of Costa Rica a coastal current flows northwest, separating the dome from the coast. It will be called the Costa Rica Coastal Current. This coastal current seems to carry away part of the water that is accumulated by the Countercurrent off the coast of Panama and Costa Rica. North of about lat. 10° N., the flow is to the west and the water movements are part of the system of the North Equatorial Current. The center of this cyclonic circulation off the coast of Costa Rica is the Costa Rica Dome as revealed from the topography of the thermocline.

The circulation in the vicinity of the Costa Rica Dome is shown in figure 6 by the topography of four surfaces relative to 1,000 decibars. The topography of the sea surface (fig. 6A) shows a strong current entering the region from the west and southwest turning north and later, northwest. The right flank of this current coincides with the strong salinity gradient seen in the chart of surface salinity (fig. 2B). This flow represents the northern part of the Equatorial Countercurrent

which is south of lat. 7° N. when entering the area at long. 91° W. East of long. 89° W. parts of the Countercurrent turn northeast and pass over into the Costa Rica Coastal Current. This map does not show how close this current reaches to the coast because the easternmost station is almost 100 km. offshore. In the northwestern part of the area the flow is from the north but turns west before reaching lat. 8° N. To the west of the Costa Rica Coastal Current an eddy has its center near lat. 8.5° N., long. 88° W., but the closed circulation in this cyclonic eddy is small compared with the strength of the coastal current. Another part of a cyclonic circulation can be seen at lat. 7.5° N., long. 91° W., where some water from the Countercurrent turns north and passes over into a flow to the west.

The circulation at 50 m. depth (fig. 6B) has substantially decreased in intensity as compared with the surface circulation. The Equatorial Countercurrent has lost in strength or may be found farther south. Also, the coastal current is weaker. However, the closed circulation in the eddy, whose center has shifted to about lat. 10° N., long. 88° W., has increased. This change in the circulation between the surface and 50 m. depth reflects the influence of the strong discontinuity layer situated between about 10 and 50 m. depth. The topography of the 100-decibar surface is almost identical to that of the 50-decibar surface if 10 dynamic centimeters are subtracted, so this chart is not shown.

The circulation at 200 m. depth (fig. 6C) is completely dominated by the huge eddy which is now centered near lat. 10° N., long. 88° W. The only other feature worth mentioning is the cyclonic circulation around a point near lat. 8° N., long. 91° W., which was already indicated in the topography of the sea surface. Below 300 m. depth velocities in the eddy decrease progressively, but even in depths near 700 m. this eddy is still shown in charts of the topography of isothermal layers. Thus, for instance, the 6° isotherm rises to less than 680 m. in the center of the eddy compared to more than 750 m. at its periphery, but the map is not shown here.

The vertical distribution of velocity and the transports across some sections are shown in figure 7 and the positions of the sections are

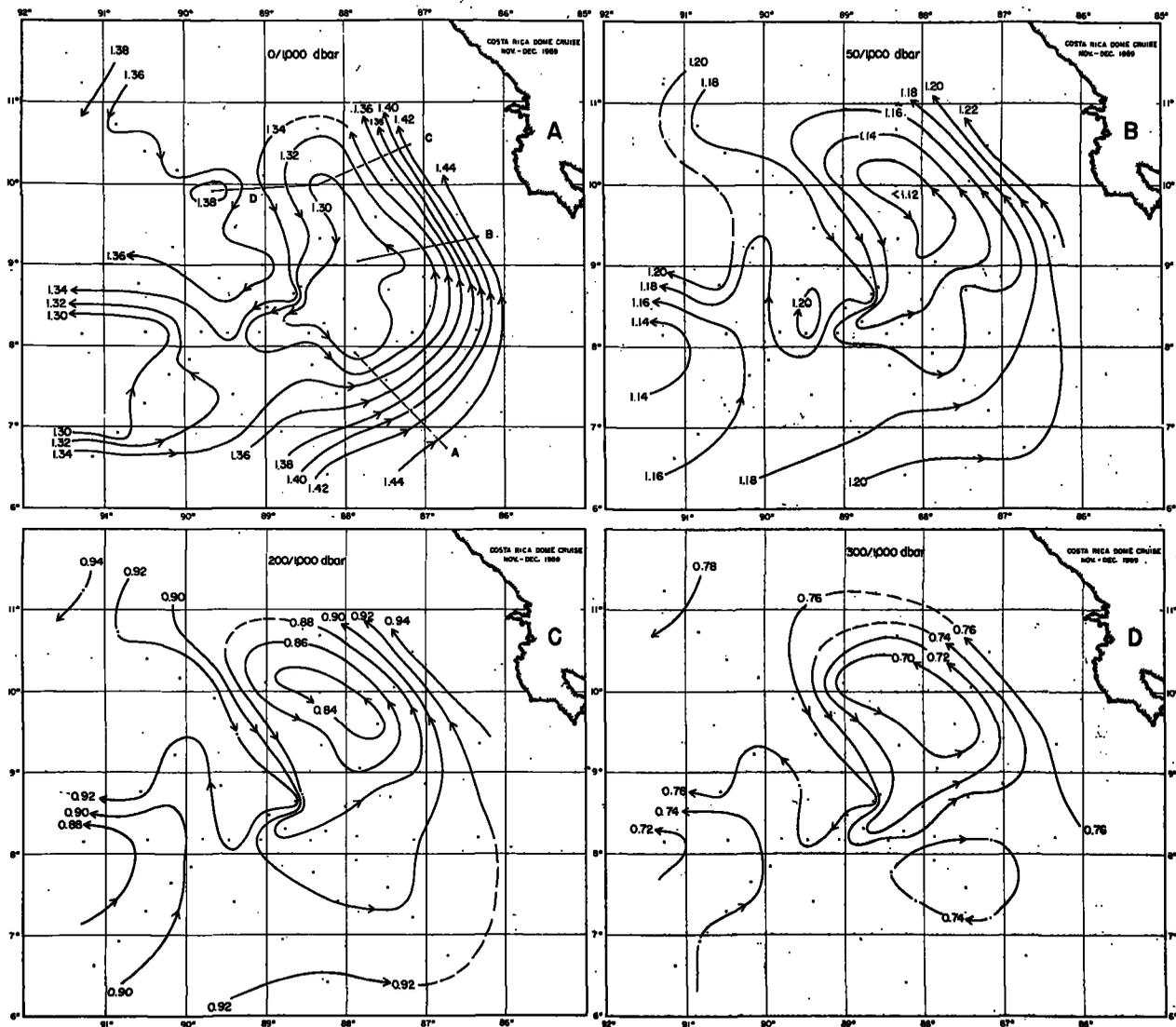


FIGURE 6.—Geopotential topographies of the sea surface, and of the 50-, 200-, and 300-decibar surfaces relative to 1,000 decibars during Costa Rica Dome cruise, in dynamic meters. The positions of sections for which transports have been calculated are marked in figure 6A by the lines A, B, C, and D.

indicated in figure 6A. Section A, between stations 10 and 13, crosses the Countercurrent just before it turns north. The average velocity at the surface is 43 cm./sec., but velocities of more than twice this value have been observed near the center of the current by surface drogues. The velocity decreases rapidly with depth and the total transport of 7.2 million $m^3/sec.$ between these two stations is chiefly concentrated in the upper 150 m. From the topographies of the subsurface layers it can, however, be seen that this section does not include the transport in the

east-going branch of the eddy in subsurface layers because station 10 is situated to the south of this flow. Section B, which cuts across the north-flowing part of the eddy, still shows a thin surface layer moving more rapidly than the subsurface layer, but most of the transport of 16.7 million $m^3/sec.$ is due to the flow in layers between 50 and 400 m. depth. Sections C and D have each a transport of about 20 million $m^3/sec.$ flowing north and south, respectively. These transports are concentrated between the surface and 400 m. depth, and the velocities are almost

uniform from the surface to that depth, especially in section D.

The circulation pattern in this area is characterized by the Equatorial Countercurrent flowing eastwards in the southern part of the area and by parts of the North Equatorial Current flowing west in the northern part of the area. Along the coast the northward flowing Costa Rica Coastal Current transfers water from the Countercurrent,

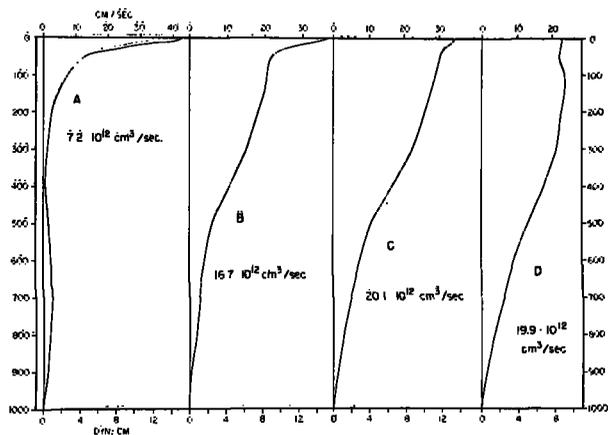


FIGURE 7.—Vertical distribution of the average geostrophic velocity (cm./sec.) relative to 1,000 m. depth in different branches of the circulation in the Costa Rica Dome. (The sections for which the transports have been calculated are shown by A, B, C, and D in figure 6A.)

which accumulates water off the coast, to the North Equatorial Current. A trough in the topography of the sea surface and a ridge in the topography of the discontinuity layer are developed between the flow to the east and the flow to the west. This trough is terminated by the north-flowing coastal current and does not reach the coast. The ridge in the topography of the thermocline is simultaneously terminated. The Costa Rica Dome is the very pronounced end of this ridge that separates the Equatorial Countercurrent from the North Equatorial Current. Around the eastern end of this ridge there is a strong cyclonic circulation.

Although this general picture of the circulation seems to be quite simple, there are some problems and observed features requiring an explanation. The flow in the North Equatorial Current, as well as the flow in the countercurrent, were

comparatively weak and shallow during this survey, and this is generally the case, as can be seen from surface current charts. Therefore, it is not obvious how these currents can maintain an eddy of considerable depth with a circular transport of the order of 20 million m^3/sec . If this eddy should be a stationary feature, it would require additional energy for its maintenance. Winds in this region, however, are weak and variable in direction, so that they cannot really be considered as a source of energy for such a strong, limited eddy. Moreover, there is little vertical shear in the eddy, as demonstrated by the weak velocity gradients between 50 and 300 m. depth in the eddy (fig. 7). Since there is no obvious source of energy to supply a stationary eddy in this position, the eddy may be considered as transient and the motion around the Costa Rica Dome as nonstationary. This assumption is partly supported by the fact that the center of the eddy in subsurface layers (fig. 6B, C, D) does not coincide with the center of the Costa Rica Dome (fig. 1) which is the area where the highest thermocline is.

To solve this problem, it should be investigated whether a similar eddy was found during other surveys of the same region. During the Eastropic Expedition in November 1955 (Scripps Institution of Oceanography, 1956) the area of the Costa Rica Dome was also surveyed although the station network was less dense. The data from that survey were used to plot the distribution of surface salinity and the topography of the sea surface relative to 1,000 decibars (fig. 8) for comparison with the situation during the Costa Rica Dome cruise. The difference is quite obvious. There is again a cyclonic circulation around a point at lat. $9^\circ N.$, long. $89.5^\circ W.$, but there is no separate eddy, at least not east of long. $90^\circ W.$ The water entering the area with the Equatorial Countercurrent turns north, and later, northwest, but nowhere is a flow to the south indicated as in figure 6a. The center of the cyclonic flow coincides with an area of lowest surface temperature ($<25^\circ C.$, fig. 8B) and highest surface salinity ($>33.8\text{‰}$, fig. 8A). The low salinity water of the Costa Rica Coastal Current occupies a larger area but is displaced to the northwest.

From this comparison it may be concluded that the cyclonic circulation around the eastern end of

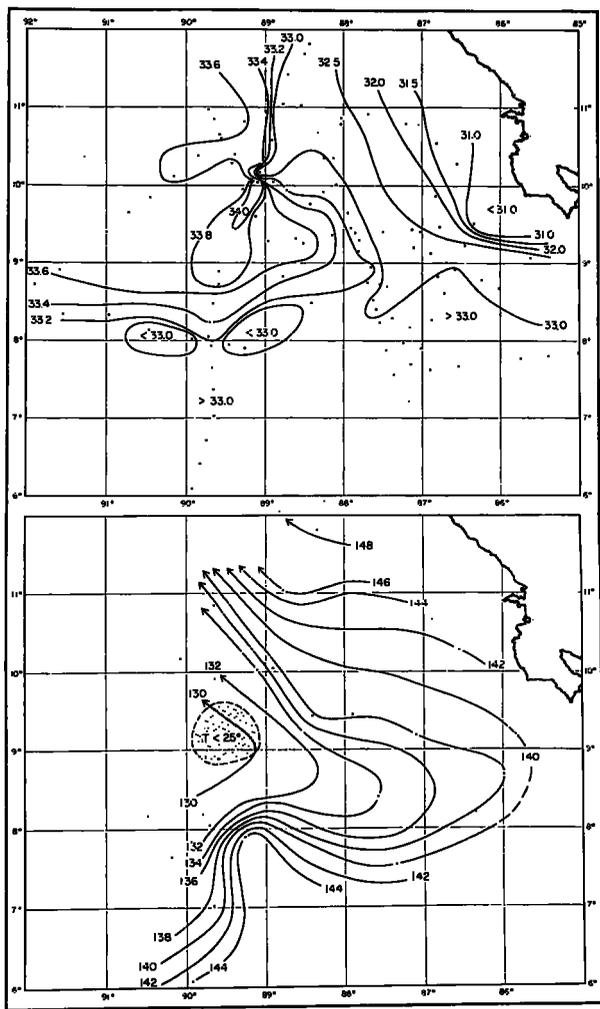


FIGURE 8.—A. Surface salinity (‰) during Eastropic Expedition. B. Geopotential topography of the sea surface relative to 1,000 decibars during Eastropic Expedition, in dynamic cm. (The area with surface temperatures below 25° C. is shaded.)

the trough separating the Countercurrent from the North Equatorial Current is not very stable and separates eddies from time to time. One of these eddies has been met during the Costa Rica Dome survey. This eddy seems to drift north or northwest on the left flank of the Costa Rica Coastal Current, as indicated by the displacement of its center towards the northwest, relative to the center of the dome. The reasons for the separation of such eddies are probably fluctuations in the strength and transports of the Countercurrent. Knauss (1961) has reported fluctuations in the transport of the Countercurrent by as much as

an order of magnitude, and it can be assumed that as a result of each of these major fluctuations one big eddy will be separated near the Costa Rica Dome where the Countercurrent ends. This eddy is similar in size to an eddy separate from the Gulf Stream which was observed by Fuglister and Worthington (1951).

The other feature to be explained is the different position of the center of the deep eddy and that of the thermal dome during the Costa Rica Dome cruise. Such a separation did not occur during the Eastropic Expedition when the lowest surface temperatures and the highest surface salinities coincided with the center of the cyclonic circulation (fig. 8). During the Costa Rica Dome survey, on the other hand, the center of the deep eddy was found near lat. 10° N., long. 88° W., while the thermal dome was situated between lat. 7.5° and long. 9° N. and between lat. 90.5° and long. 87° W. The discussion of the geopotential topographies mentioned that the circulation above the thermocline was substantially different from that at 50 m. depth, thus indicating the presence of a fairly independent surface layer. This finding leads to the conclusion that the thermal dome is related to the circulation within the thin surface layer and little or not at all influenced by the circulation in deeper levels. This conclusion will be substantiated in the next section.

The structure of the deep eddy, as well as the fact that the dome is developed in a different position, indicates that this eddy is already separated from the remainder of the circulation. This is also emphasized by the development of another cyclonic circulation near lat. 8° N., long. 91° W., where parts of the Countercurrent turn north and west into the North Equatorial Current (fig. 6). This cyclonic circulation is probably the start to re-establish the old circulation after the separated eddy in the northeast has decayed and disappeared.

UPWELLING

The structure of the thermocline, which comes to within a few meters of the sea surface, the lowered surface temperature, and the higher salinity and phosphate content are clear indications of upwelling in the Costa Rica Dome. The ascending movements bring water out of the range of the thermocline into the thin surface layer in

which it is removed horizontally. This continuous addition of cooler water from beneath requires that the ascending water be heated in order to maintain the temperature in the surface layer. The fact that the top of the thermocline does not reach to the surface but is, perhaps with occasional local exceptions, always covered by a thin surface layer demonstrates that the circulation in the dome area is in thermal balance and, therefore, the maximal possible ascending velocity is limited by the amount of energy available for the heating of the surface layer. In order to determine this maximal upwelling velocity a few calculations of the heat balance of the dome will be made in the following.

For the purpose of the calculations the dome will be considered as circular with the radius r . There will be a homogeneous surface layer of thickness D with the temperature T_o (fig. 9).

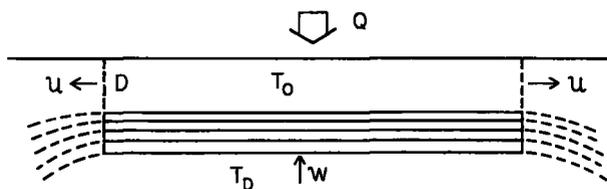


FIGURE 9.—Notations used for the calculation of the heat balance of the Costa Rica Dome.

Underneath this surface layer is the thermocline, and within this thermocline a constant ascending velocity w is assumed. The ascending water is assumed to come from the layer immediately beneath the thermocline out of a depth between 75 and 200 m. where the temperature is between 12° and 14° C. and the temperature gradient considerably weaker (figs. 1 and 3). This layer is assumed to form the reservoir for the ascending water, and its temperature is T_D . The water entering the surface layer from beneath is thought to flow horizontally away within the surface layer with the velocity u . The thermocline is assumed to be without horizontal motion. The water balance is then given by

$$2r\pi Du = r^2\pi w \quad (1)$$

and the heat balance by

$$2r\pi DuT_o = r^2\pi wT_D + r^2\pi \frac{Q}{\rho c} \quad (2)$$

where Q is the energy available for heating of the surface layer, ρ is the density, and c the specific heat of sea water. The energy available for heating the surface layer of the ocean results chiefly from the difference between incoming and outgoing radiation less the energy used for evaporation. Budyko (1956) has charted these quantities for the entire earth, and, according to his maps, about $110 \text{ cal.cm.}^{-2} \text{ day}^{-1}$ are available for the heating of the surface layer in the region of the Costa Rica Dome. Because the annual variations in the terms of the heat balance in this area are small, it is satisfactory to use the estimate by Budyko for the period of the Costa Rica Dome cruise.

Combining equations (1) and (2) gives the simple relation

$$w(T_o - T_D) = \frac{Q}{\rho c} \quad (3)$$

which is independent of the size r of the area. With $Q = 1.27 \times 10^{-3} \text{ cal.cm.}^{-2} \text{ sec.}^{-1}$, $T_o = 25^\circ \text{ C.}$ and $T_D = 13^\circ \text{ C.}$ the ascending velocity within the thermocline is $w = 10^{-4} \text{ cm./sec.}$ which is equal to 8.6 cm./day or 2.6 m./month. A velocity of this order will not disturb the temperature structure in the dome but will maintain it. A much greater velocity will be needed if "out-cropping" of the thermocline should occur, but this seems to be the exception in the Costa Rica Dome. The vertical velocity calculated above, however, represents an average value for the entire area and locally higher or lower values are possible. Also the vertical velocity does not give any information about the structure of upwelling, and it is not unlikely that the actual upwelling occurs in smaller patches, in which temperature anomalies disappear rapidly as a result of horizontal mixing.

The horizontal velocity at the periphery of the dome is given by $u = \frac{rw}{2D}$ and with a radius $r = 1.5 \times 10^7 \text{ cm.} = 150 \text{ km.}$ the velocity is $u = 0.38 \text{ cm./sec.}$ The total amount of upwelling in the dome is given by $T = wr^2\pi = 7 \times 10^{10} \text{ cm.}^3/\text{sec.}$ This is less than a tenth of a million $m.^3/\text{sec.}$ and very small compared with the strength of the horizontal circulation.

Knowledge of the approximate value of the vertical velocity within the thermocline allows the calculation of the vertical exchange coefficient A within this strong tropical thermocline. The

equation of the vertical diffusion of heat is given by

$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z} \left(wT - A \frac{\partial T}{\partial z} \right) \quad (4)$$

If the thermocline is considered to be stationary $\left(\frac{\partial T}{\partial t} = 0 \right)$, the advection of cooler water from below must be compensated by a turbulent flow of heat from above. Taking w and A as a constant within the thermocline, equation (4) can easily be integrated

$$T = T_D + (T_o - T_D) e^{\frac{w}{A} z} \quad (5)$$

where z has its origin at the top of the thermocline and is positive upwards. Taking $T_o = 25^\circ \text{C.}$, $T_D = 13^\circ \text{C.}$ and a temperature $T = 15^\circ \text{C.}$ at 25 m. below the top of the thermocline, as is observed, a value $w/A = 7.2 \times 10^{-4} \text{ cm.}^{-1}$ results. With $w = 10^{-4} \text{ cm./sec.}$ it follows that $A = 0.14 \text{ cm.}^2 \text{ sec.}^{-1}$. This value is reasonably close to that calculated by Montgomery (1939), who finds a maximal value of $A = 0.4 \text{ cm.}^2 \text{ sec.}^{-1}$ for the equatorial Atlantic Ocean.

The downward flow of heat Q_o is given by

$$Q_o = \rho c A \frac{\partial T}{\partial z} = \rho c (T_o - T_D) w e^{\frac{w}{A} z} \quad (6)$$

and decreases exponentially with depth. At the top of the thermocline ($z=0$) this flow is given by

$$\rho c A \left(\frac{\partial T}{\partial z} \right)_o = \rho c (T_o - T_D) w = Q$$

being the same equation as (3), which was derived from considerations of the heat balance of the entire dome, and shows that all the heat available in the surface layer diffuses down and that the heating of the ascending water takes place within the thermocline. At 25 m. below the top of the thermocline this vertical flow of heat has decreased to $0.2 \times 10^{-3} \text{ cal. cm.}^{-2} \text{ sec.}^{-1}$. Consequently, it can be stated that in areas with no upwelling, where such a downward flow of heat will not be opposed by ascending cooler water, either the layers below the thermocline will be heated, or, more likely, the thermocline will descend with time, as is usual in higher latitudes with summer heating.

With the application of these calculations, it follows from the observed temperature distribution that the upwelling in the Costa Rica Dome, at

least in the climatological average, is in thermal balance. This thermal balance limits the average ascending velocity to approximately 10^{-4} cm./sec. The amount of upwelling is of the order of $7 \times 10^{10} \text{ cm.}^3 \text{ /sec.}$ The ascending water is supplied from a layer immediately beneath the strong thermocline. The lower values of salinity in the salinity maximum, discussed in the section on "Hydrographic structure", indicate that water from these depths is ascending. All these results show that the Costa Rica Dome is a very shallow feature and must be closely related to and caused by the surface circulation. This is also strongly suggested by the fact that the circulation is appreciably different at the surface and below 50 m. depth as shown in the section on "Horizontal circulation".

The balance equations for phosphate can be studied now that the vertical circulation has been estimated from the heat balance equation. This is done by replacing the temperature in equation (3) with phosphate concentration, and the right-hand side then becomes the phosphate consumption

$$w(P_D - P_o) = X$$

Taking $P_D = 2.3 \text{ } \mu\text{g.-atom/L.}$ for the water ascending from the layer between 50 and 200 m. depth, $P_o = 0.5 \text{ } \mu\text{g.-atom/L.}$ for the water flowing horizontally away from the dome, and $w = 10^{-4} \text{ cm./sec.}$ as calculated from the heat balance, the phosphate consumption becomes $X = 155 \text{ } \mu\text{g.-atom/m.}^2 \text{ /day.}$ When this figure is converted into weight and a relation $P:C = 1:41$ is used the phosphate consumption is equivalent to $196.8 \text{ mg. C/m.}^2 \text{ /day.}$ Measurements of *in situ* organic production in the Costa Rica Dome give values between 160 and 440 $\text{mg. C/m.}^2 \text{ /day}$ (Holmes, personal communication), which agree very well with the calculated value of phosphate supply to the surface layer.

As the upwelling in the Costa Rica Dome has been found to be a very shallow process, its dynamics must be closely related to the circulation in the surface layer. This upwelling is situated at the northern flank of the Countercurrent in a position where this current turns sharply to the north. It will be assumed that the Countercurrent is in geostrophic balance when it approaches the area from the west. When turning to the north, the current has to attain a different balance and it will be shown that the

necessary adjustment results in upwelling along the left flank of the turning current.

Winds in this area are irregular and weak, and wind charts do not indicate a permanent feature in the wind field, with the overall dimensions of the Costa Rica Dome, that could locally be important for maintaining the upwelling in the dome. Therefore, an effect of the local wind on the circulation and the upwelling in the dome will not be considered in the following discussion.

To describe the motion, natural co-ordinates (s, n) will be used, ds being tangential, dn normal to a trajectory. V is the velocity along the trajectory, which in the stationary case is also a streamline. The equations of a stationary motion in this system are

$$V \frac{\partial V}{\partial s} = -\frac{1}{\rho} \frac{\partial p}{\partial s} \quad (7)$$

$$KV^2 + fV = -\frac{1}{\rho} \frac{\partial p}{\partial n} \quad (8)$$

where f is the coriolis parameter depending on the latitude, p the pressure and ρ the density. $K = \frac{1}{R}$ is the curvature of the trajectory, R the radius of curvature, both are functions of s .

It will be assumed that the current, represented by its isobars, enters the area from the west, as shown in figure 10. At point N the current may gradually start to turn north and reach its strongest curvature at point M . West of point N the curvature of the current is zero, $K=0$, and its velocity is given by

$$fV = -\frac{1}{\rho} \frac{\partial p}{\partial n} = f_0 V_g$$

as follows from (8). V_g is the geostrophic velocity and f_0 the value of the Coriolis parameter at the latitude of the Countercurrent. At point M the trajectory may have a radius of curvature $R=120$ km., as can be seen from figure 6A. It will be assumed that the normal pressure gradient remains constant along the trajectory, $-\frac{1}{\rho} \frac{\partial p}{\partial n} = f_0 V_g$.

With this assumption equation (8) becomes

$$KV^2 + fV = f_0 V_g$$

With $1/K=120$ km., $f=2.15 \times 10^{-5}$ sec.⁻¹ at latitude 8.5° , $f_0=1.65 \times 10^{-5}$ sec.⁻¹ at latitude 6.5° ,

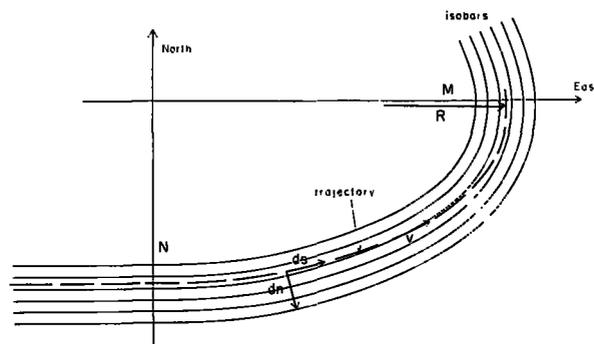


FIGURE 10.—Diagram showing schematically the isobars of a current flowing east and turning north. (The broken line is a trajectory, cutting the isobars under a small angle, R is the radius of curvature.)

and a geostrophic velocity $V_g=55$ cm./sec., it follows that $V=37$ cm./sec. at point M . This shows that the velocity decreases along the trajectory from 55 cm./sec. at point N to 37 cm./sec. at point M . The length of the trajectory between points N and M is approximately 450 km., thus the value of $\frac{\partial V}{\partial s}$ in equation (7) can be calculated.

It follows that $\frac{1}{\rho} \frac{\partial p}{\partial s} = 1.8 \times 10^{-5}$ cm. sec.⁻². Expressed in terms of dynamic topography, this means that the particle arrived at point M at a value 0.83 dynamic cm. higher than when it left point N , compared with a total difference of about 14 dynamic cm. across the current. The trajectory crosses the isobars at a very small angle, which is given by $\tan \alpha = \frac{\partial p / \partial s}{\partial p / \partial n}$. With $\frac{1}{\rho} \frac{\partial p}{\partial n} = 90.7 \times 10^{-5}$ cm. sec.⁻² it follows that $\alpha = 1.1^\circ$.

Because the trajectories cut the isobars, the velocity V along the trajectory can be split into one component v parallel to the isobars and another component u normal to the isobars. The angle between the two sets of curves is so small that v will be almost as big as V , while u can be calculated from the relation $u/v = \frac{\partial p / \partial s}{\partial p / \partial n}$, giving $u=0.92$ cm./sec. Over a distance of 450 km. and a depth of 20 m. this velocity normal to the isobars causes a transport of 8.3×10^{10} cm.³/sec. across the isobars from the left side of the current to its right side. This calculation of the cross isobar transport compares very well with the figure of 7×10^{10} cm.³/sec. calculated for the amount of upwelling from the thermal balance of the dome. Consequently, I

conclude that the upwelling in the Costa Rica Dome is an effect of the northward turning of parts of the Countercurrent. The cross isobar circulation associated with such a turning current causes the upwelling, which is situated along the left flank of this cyclonic flow. This upwelling is, however, especially effective in the Costa Rica Dome, because the thermocline along the left flank of the Countercurrent is already in a shallow position before the current starts turning. As a consequence of this, an intense enrichment of the thin surface layer with nutrients is possible in the Costa Rica Dome.

In order to conserve the mass transport of the current, the product VD , where D is the depth of the current, must remain constant along a trajectory. This increase in the depth of the current in the direction of its flow is well documented in figure 7, where its depths increase progressively as the current proceeds from section *A* to sections *B* and *C*. The difference of dynamic height across the current remains unchanged during its progress, while the surface velocity decreases and the depth of the current increases. Thus the transport across the isobars can be interpreted as upwelling on the left flank of the current and sinking on its right flank.

PERMANENCE OF THE COSTA RICA DOME

The above discussions of the structure of the dome and its circulation have been based chiefly on one survey, but it is worthwhile to investigate whether or not the Costa Rica Dome is a permanent feature of the circulation and how far it is subject to seasonal variations. So far eight expeditions (table 1) have crossed or touched the

TABLE 1.—Positions of the Costa Rica Dome on different expeditions

Expedition	Date	Position of the dome		Reference for data
		Latitude °N.	Longitude °W	
Shuttle.....	May 1952.....	9.5	89	Unpublished. ¹
Shellback.....	July–Aug. 1952.....	9	88	Unpublished. ¹
Eastrop.....	Oct.–Nov. 1955.....	9	89.5	Scripps Institution of Oceanography, 1956.
Scope.....	Nov.–Dec. 1956.....	8.5	89	Holmes and others, 1958.
Scot.....	May 1958.....	10	89	Holmes and Blackburn, 1960.
TO-59-1.....	Feb. 1959.....	9	89	Blackburn and others, 1962.
Costa Rica Dome.....	Nov.–Dec. 1959.....	8	88	Scripps Institution of Oceanography, 1960.
Explorer.....	Feb. 1960.....	9	89	Stewart, 1962.

¹ Data available at Scripps Institution of Oceanography, and will be included in Oceanic observations of the Pacific, 1952, to be published by the University of California Press.

area of the Costa Rica Dome, and all of them have found the dome in approximately the same position. As the dome is characterized by an extremely high position of the thermocline, the depth of the 19° C. isotherm, which coincides approximately with the center of the thermocline, is charted for six of the expeditions in figure 11. On the eighth crossing of the dome in February 1960 only BT observations were taken (fig. 1). During all these expeditions the 19° C. isotherm was found to be in less than 20 m. depth in the dome area. Along the periphery of the dome it was always below 40 m. Because some of the expeditions did only touch the dome or may not have crossed through its center, the size of the dome cannot be determined. The position of the dome during the different expeditions is given in table 1 and it can be seen that the dome maintains its position within 2° of latitude and longitude. It is situated between lat. 8° and 10° N. and between long. 88° and 90° W. Although the position of the dome was approximately the same during all these surveys, the circulation around the dome seems to have been considerably different, as indicated by the topographies of the 19° C. isotherm.

Six of these expeditions, made between 1952 and 1959, cover the months between May and December; during this period the Countercurrent is always present. During February and especially in March, the Countercurrent is absent in this area and the cyclonic circulation is only weakly developed, as indicated in the surface charts by Cromwell and Bennett (1959). Thus, it might be possible that the dome would not be developed during this period. In February 1959 the area of the dome was crossed on expedition TO-59-1, and in February 1960 it was crossed by the vessel *Explorer*. On both crossings the dome was found to be in about the same position as during the other expeditions, and the 19° C. isotherm was well above 20 m. depth, as can be seen from the BT section taken by the *Explorer* (fig. 1). It is, however, not known whether or not the Countercurrent was developed during these times, or whether the Costa Rica Dome is persistent enough to remain for an appreciable time during the period in which the Countercurrent is not indicated in the surface current observations.

From the comparison of the results of these eight expeditions it can be concluded that the

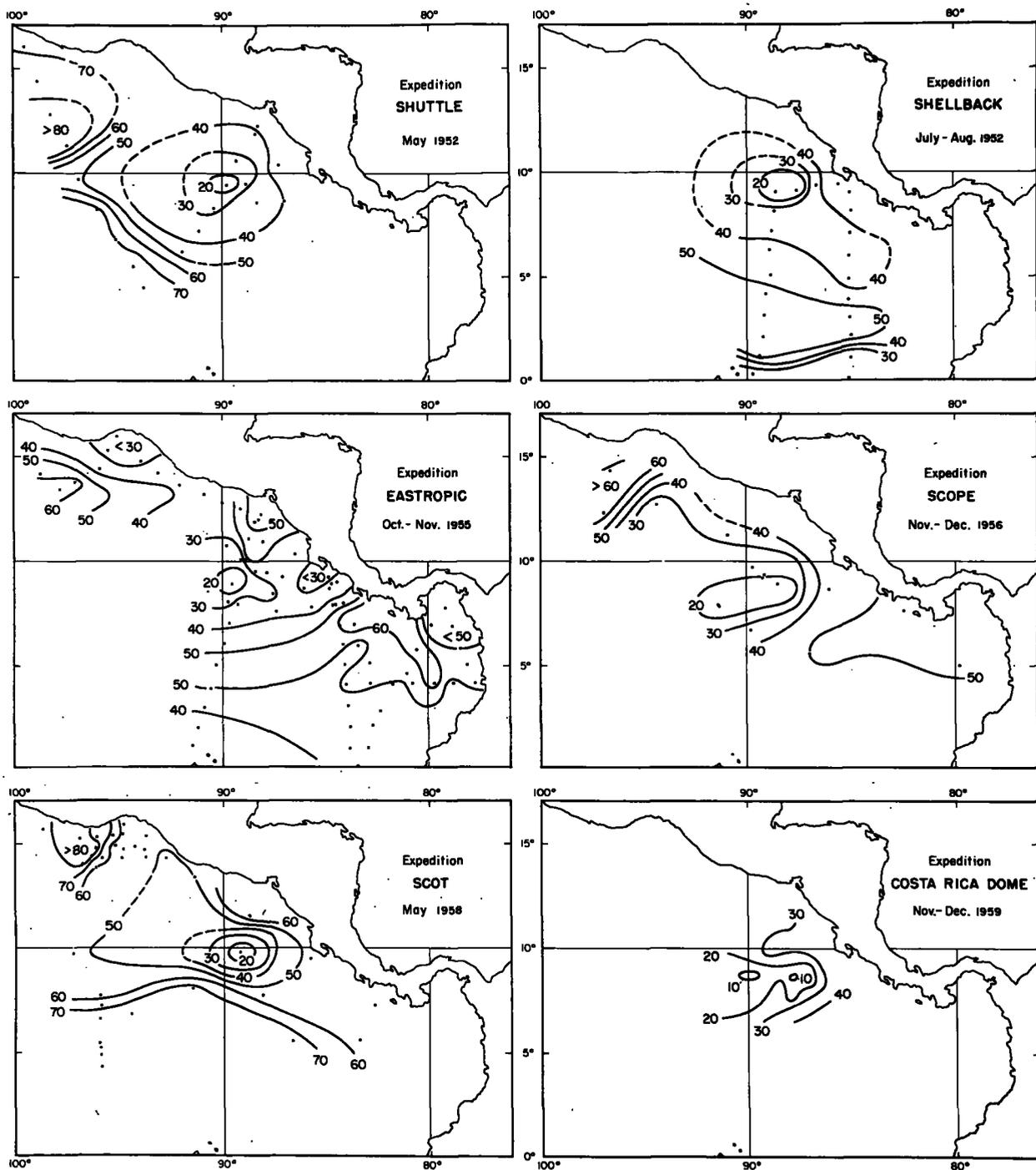


FIGURE 11.—Topography of the 19° C. isotherm in meters during six expeditions in the area of the Costa Rica Dome and its vicinity.

Costa Rica Dome is a permanent feature of the thermocline topography in the eastern tropical Pacific Ocean and that it varies very little in its position. A comprehensive survey of the Costa

Rica Dome in February and March would be desirable to confirm the existence of the dome during these months and to determine the character of the associated circulation.

CONCLUSIONS

The analysis of the hydrographic structure of the Costa Rica Dome and of its circulation, based on the Costa Rica Dome cruise and the comparison with seven less complete surveys, leads to the following conclusions:

1. The Costa Rica Dome is a more or less circular area where the thermocline is extremely high and extremely sharp and where the top of the thermocline reaches to within a few meters of the sea surface. This area, about 200 km. in diameter, is characterized by slightly lower surface temperatures, higher salinity and phosphate contents, and reduced percentage of oxygen saturation. The average position of the dome is lat. 9° N., long. 89° W., and the fluctuations of the center of the dome are within $\pm 1^{\circ}$ of latitude and longitude, as a comparison of eight surveys demonstrates. Thus, the Costa Rica Dome is a permanent feature of the circulation in the eastern tropical Pacific Ocean.

2. The circulation around the dome is determined by the Equatorial Countercurrent in the south, the Costa Rica Coastal Current in the east, and parts of the North Equatorial Current in the north. Off the coast of Costa Rica these currents form a cyclonic circulation in the center of which the dome is situated. The Costa Rica Dome is the very pronounced eastern end of a ridge in the topography of the thermocline extending along the northern boundary of the Countercurrent. From the cyclonic circulation around the dome large eddies seem to separate and to contribute to large-scale mixing. One of them was observed during the Costa Rica Dome survey transporting 20 million $m^3/sec.$

3. The northward turning of the Countercurrent requires an adjustment of its velocity distribution and causes a cross-circulation which produces upwelling in the dome. The upwelling in the dome must be in thermal balance which limits the average ascending velocity to 10^{-4} cm./sec. The total contribution of the upwelling is only 7×10^{10} $cm^3/sec.$, and the ascending water comes from layers immediately beneath the strong thermocline out of 75–200 m. depth where the temperature is 12° – 14° C.

4. The upwelling in the Costa Rica Dome is a shallow process restricted to the surface layer and

the thermocline. The amount of upwelling is very small because the intensity is less and the area much smaller than, for instance, that off the coast of Peru (Wyrtki, 1963). However, the effect of this upwelling on the enrichment of the surface layer in the Costa Rica Dome is considerable because of the much higher initial position of the thermocline and of the abundance of nutrient rich water immediately beneath the thin surface layer.

LITERATURE CITED

- BLACKBURN, MAURICE, RAYMOND C. GRIFFITHS, ROBERT W. HOLMES, AND WILLIAM H. THOMAS.
1962. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: three cruises to the Gulf of Tehuantepec, 1958–59. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 420, 170 pp.
- BRANDHORST, WILHELM.
1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 24, No. 1, pp. 16–31.
- BUDYKO, M. I.
1956. The heat balance of the earth's surface. Leningrad, 255 pp. Translated by U.S. Department of Commerce, Weather Bureau, 1958.
- CROMWELL, TOWNSEND.
1958. Thermocline topography, horizontal currents and "ridging" in the eastern tropical Pacific. Inter-American Tropical Tuna Commission Bulletin, vol. 3, No. 3, pp. 135–164.
- CROMWELL, TOWNSEND, AND EDWARD B. BENNETT.
1959. Surface drift charts for the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin, vol. 3, No. 5, pp. 217–237.
- FUGLISTER, FREDERICK C., AND L. V. WORTHINGTON.
1951. Some results of a multiple ship survey of the Gulf Stream. Tellus, vol. 3, No. 1, pp. 1–14.
- HOLMES, ROBERT W., AND OTHERS.
1958. Physical, chemical, and biological oceanographic observations obtained on Expedition Scope in the eastern tropical Pacific, November–December 1956. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 279, 117 pp.
- HOLMES, ROBERT W., AND MAURICE BLACKBURN.
1960. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: Scot Expedition, April–June 1958. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 345, 106 pp.
- KNAUSS, JOHN A.
1961. The structure of the Pacific Equatorial Countercurrent. Journal of Geophysical Research, vol. 66, No. 1, pp. 143–155.

MONTGOMERY, RAYMOND B.

1939. Ein Versuch, den vertikalen und seitlichen Austausch in der Tiefe der Sprungschicht im äquatorialen Atlantischen Ozean zu bestimmen. *Annalen der Hydrographie und Maritimen Meteorologie*, Band 67, pp. 242-246.

REID, JOSEPH L., JR.

1962. On circulation, phosphate-phosphorus content and zooplankton volumes in the upper part of the Pacific Ocean. *Limnology and Oceanography*, vol. 7, No. 3, pp. 287-306.

SCRIPPS INSTITUTION OF OCEANOGRAPHY.

1956. Data collected by Scripps Institution vessels on Eastropic Expedition. SIO Reference Report 56-28, 156 pp. (mimeo.)

SCRIPPS INSTITUTION OF OCEANOGRAPHY.

1960. Physical, chemical and biological data Costa Rica Dome cruise. SIO Reference Report 60-20 33 pp. (mimeo.)

STEWART, HARRIS B., JR.

1962. Oceanographic cruise report, USC & GS Ship Explorer—1960. U.S. Department of Commerce, Coast and Geodetic Survey, Washington, D.C. 162 pp.

WYRTKI, KLAUS.

1963. The horizontal and vertical field of motion in the Peru Current. *Bulletin of the Scripps Institution of Oceanography*, vol. 8, No. 4, pp. 313-346.

PRECONSTRUCTION STUDY OF THE FISHERIES OF THE ESTUARINE AREAS TRAVERSED BY THE MISSISSIPPI RIVER-GULF OUTLET PROJECT^{1, 2}

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ABSTRACT

Hydrographical and biological data were collected from April 1959 through March 1961 at selected stations in the marsh and bayou areas traversed by the Mississippi River-Gulf Outlet Channel between New Orleans and Breton Sound to provide preconstruction data needed for later assessment of the effects on the fauna of such a wide and deep channel connected at the Gulf end with water of high salinity. The channel

will raise salinities over most of the project area. This should not greatly affect the fishes of the area which are preponderately euryhaline. It should have an adverse effect on abundance of the blue crab. The possible effect on the white shrimp is obscured by their avoidance of the open waters of Lake Borgne and their preference for the shoal protected marshes.

The Mississippi River-Gulf Outlet Project of the Corps of Engineers is a deep-water navigation channel from New Orleans to the Gulf of Mexico (fig.1). The route traverses the marshes along the southwestern shore of Lake Borgne and then cuts across the intricate system of bayous to Breton Sound. The deep channel crosses Breton Sound just to the north of Breton Island. The completed channel will be 36 feet deep and 500 feet wide at the bottom. The channel was dredged in three stages: first, an access channel 18 feet deep by 140 feet wide, second, an interim channel 36 feet deep by 250 feet wide; and third, the full-scale channel.

The channel traverses a marsh and estuarine area of great value for waterfowl, muskrats, oyster culture, sport and commercial fishing, and, perhaps the most important, for a nursery area utilized by the young of fish and shrimp that are later harvested in great quantities in deeper water outside of the project area.

The principal aim of this study was to determine the environmental and biological conditions prevailing prior to channel construction from the fishery standpoint. A preconstruction study on such a large scale was lacking, and it was hoped that comparison with a later postconstruction study of the same area would be invaluable, both in deciding on what effects, if any, could be attributed to the present project, and in forming a basis on which to predict the effect of similar projects in the future.

NOTE.—Approved for publication April 9, 1963.

¹ The data on which this report is based were collected by the Texas A. and M. Research Foundation for the Bureau of Sport Fisheries and Wildlife of the U.S. Fish and Wildlife Service under Contracts No. 14-16-008-523; No. 14-16-008-572; and No. 14-17-008-119. The Foundation released three mimeographed reports referred to as Reference 59-5T, Reference 59-21T, and Reference 61-20F. The original data are archived at the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. All species identifications are by the Research Foundation. The author assumes sole responsibility for this analysis and the conclusions reached.

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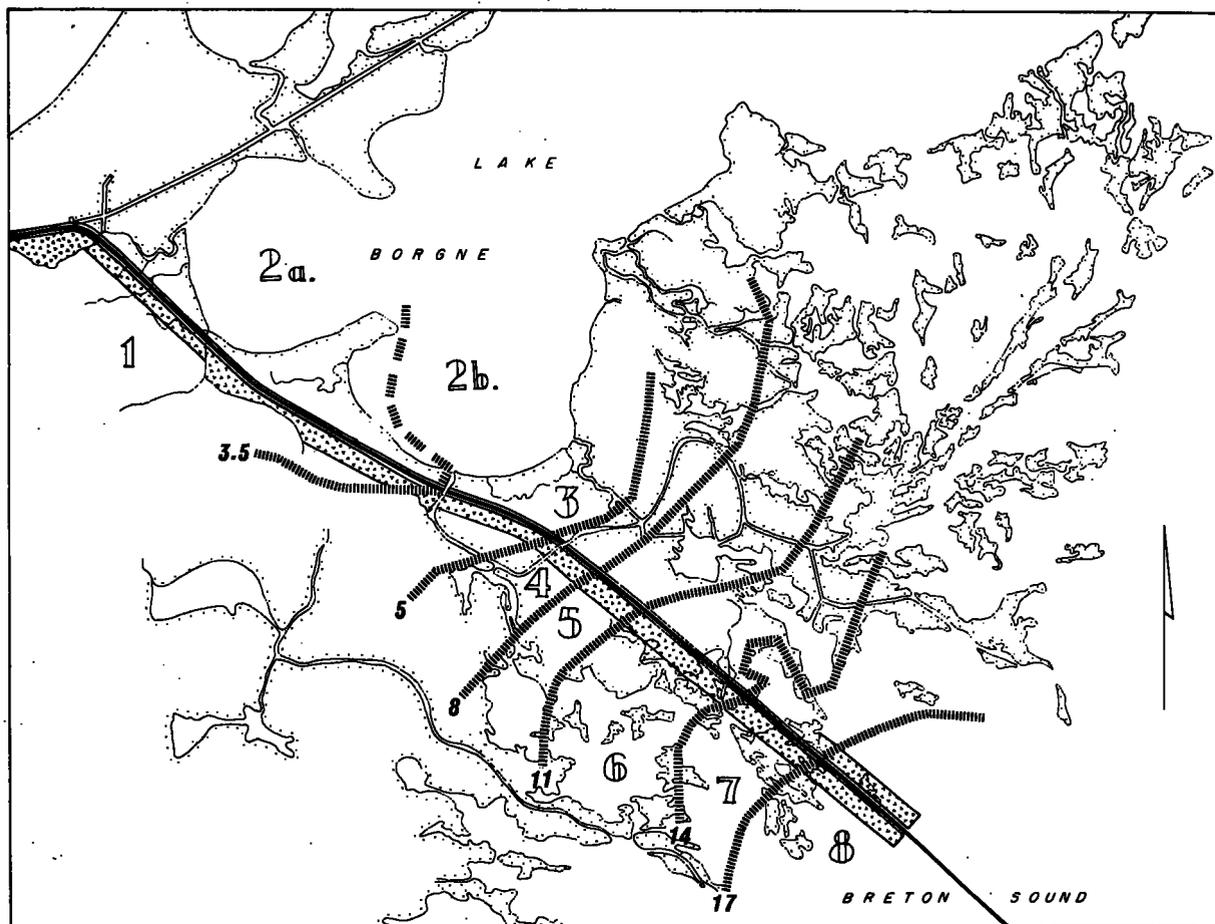


FIGURE 1.—The project areas showing the alignment of the Gulf Outlet channel as far as Breton Sound. (The shaded area along the southwest border of the channel is the 4,000-foot strip used as a spoil area. The shaded lines crossing the channel are isohalines that effectively divide the project area into smaller areas. The isohalines are based on average 24-month salinities.)

Dredging of the small access channel was commenced at the Gulf Intracoastal Waterway in May of 1959 and completed to Breton Sound by March of 1961. Some segments of the channel were dredged to the "interim" cross section during this period. Where they crossed the channel, certain bayous were kept open: Bayou Bienvenue, Bayou Villere, Bayou Dupre, Bayou Yscloskey, and Bayou La Loutre.

Following recommendations of the Fish and Wildlife Service, the Corps erected spoil retention dikes around a 4,000-foot strip along the southwestern boundary of the channel so that the solids could settle out from the liquid mud poured out from the hydraulic dredges. This measure effectively kept down sedimentation in the adjacent bayous.

HYDROGRAPHIC METHODS

Commencing in April 1959, stations were occupied at various points throughout the project area. At this time the exact route of the southern portion of the channel had not been decided but a route slightly northeast of the one finally chosen was then being favorably considered. Consequently, several stations occupied for a few weeks early in the study period were later abandoned, and a few more southerly stations added. The station locations are shown in figure 2. Table 1 lists the stations and the months each was occupied for hydrographical and biological observations.

Hydrographic observations were taken at each visit to a station (about once each 10 days through August 1960 and twice a month thereafter), and

TABLE 1.—List of stations by area and months sampled

Area	Station		Months sampled					
			Hydrography			Biology		
			1959	1960	1961	1959	1960	1961
Symbol	Name							
1.	BX	Bayou Bienvenue at Paris Road.	7	12	3			
	PRB	Intracoastal Waterway at Paris Road Bridge.	7	8				
	BV	Bayou Villere	3	12	3			
	BY	Bayou Bienvenue at Y	7	12	3			
	BD	Bayou Dupre	7	12	3	4	12	3
	RB	Rotten Bayou	2	12	3	4	12	3
	BDB	Bayou Dupre Beacon	7	12	3	4	10	3
	BWH	Bayou Lewis	7	12	3			
	BWA	Bayou Grand	7	8				
	2a.	BDL	Bayou Dupre Light	7	12	3	4	12
LB		Lake Borgne (off Bayou Dupre).	7	12	3		12	3
2b.	SBB	Shell Beach Beacon	9	12	3			
	BML	Bayou St. Malo Light	8	12	3	4	12	3
3.	SB	Shell Beach	9	12	3		8	3
	YC	Bayou Yscloskey	9	12	3			
	H	Hopedale	9	12	3			
4.	BM	Bayou St. Malo	9	12	3			
	BG	Bayou Guyage	9	12	3	4	12	3
	JDY	Jahnkes Ditch at Y	8	12	3	4	12	3
	BB	Bayou Biloxi	2	12	3	4	12	3
	MP	Mike's Pass	6					
	LL	Bayou La Loutre	6					
	LLBC	La Loutre-Bakers Canal, west.	9	12	3			
	TW	Bayou La Loutre Survey Tower.	9	12	3			
	HLE	Hopedale Lagoon entrance.	1					
	HL	Hopedale Lagoon	9	12	3			
5.	HLSE	Hopedale Lagoon, south-east.	2					
	EB	East Bayou	2					
	OB	Oyster Bay	9	12	3			
	LEG	Lake Eugene	6					
	CB	Crooked Bayou	6					
	LLBC	La Loutre-Bakers Canal, east.	9	8				
	CP	China Pass		5	3			
	LRO	Lake Robin-Oyster Bay	2	3			2	
	LR	Lake Robin	9	12	3			
	6.	TP	Treasure Pass	9	8			
BE		Bayou Eloi				1		
LE		Lake Eloi	9	12	3			
LEW		Lake Eloi, west				1		
BPPN		Bayou Pointe en Pointe, north.	9	12	3	4	12	3
BPPS		Bayou Pointe en Pointe, south.	9	6				
7.	LST	Lake of Second Trees	9	12	3			
	BP	Bayou Pisana	9	11	3			
	BLP	Blind Pass				1		
	LAS	Lake Athanasio, south	3	12	3	3	11	3
	LAN	Lake Athanasio, north	3	8		3	7	
	LAW	Lake Athanasio, west	2			3		
	LMN	Lake Machlas, north	2	12	3	2	11	3
8.	LFF	Lake Fortuna, at Bayou Frenepiquant.	2	12	3	1	11	3
	GPT	Grace Point		3	3		3	3

Zein-Eldin, May, and Lansford (1960) use 900 g. of NaI and 400 g. of NaOH in only 550 ml. of distilled water to overcome the errors produced from high turbidities.

Inorganic phosphate

Inorganic phosphate was determined by a colorimetric method. The values show great and erratic variations, which could be caused by partic-

ulate phosphate in the unfiltered samples. This explanation is corroborated by an apparent correlation between turbidity and phosphates.

Turbidity

Turbidity was measured with a Klett colorimeter. The readings were converted into grams per liter of oven-dried suspended solids by comparison with a predetermined curve. The samples were shaken vigorously before making readings so that the values include heavy particles which might not be transported any distance by the water, but be present in the samples wholly because of local wave action.

Average turbidities were slightly lower in general in areas of higher salinity. The dredging operations occasionally caused much higher than average turbidities. Thus, the turbidity at Shell Beach (SB) and Yscloskey (YC) was extremely high (twice the average) during February and March 1961. The interim channel dredging from Bayou Dupre to Bayou Yscloskey reached Bayou Yscloskey in February 1961 and might easily account for extreme turbidities in these closely adjacent stations.

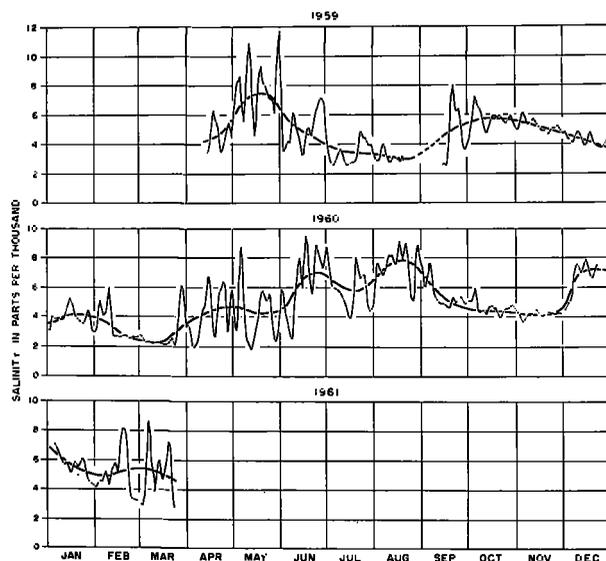


FIGURE 3.—Daily salinities at the base station (H) in Hopedale. (See text for details.)

SALINITY

The hydrographical changes that the Gulf outlet channel might be expected to cause would be chiefly changes in salinities and currents. For this reason, we have paid particular attention to these two features. The daily salinities at the

base station at Hopedale (see H, fig. 2) are given in table 2. These were smoothed by first interpolating for the missing weekend days and then smoothing by 3-s with double weight on the center item (fig. 3). The trend line has been drawn by eye.

TABLE 2.—Mean daily salinity at Hopedale, La.

[Parts per thousand]

Day	1959												1960												1961					
	Month												Month												Month					
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.						
1		5.64	9.95	3.87				4.38			4.85			8.01	2.67	4.21		6.66		4.87	8.09			4.14	4.42			4.14	2.98	
2		5.58	3.45	4.30				4.16			4.76			5.06	3.14			5.89		9.41	5.14			4.35	4.34			4.43	3.01	
3		5.63	3.18	2.85	2.78						5.33			5.97	2.25			12.94		9.61	5.00			3.87	4.35			4.67	2.82	
4		5.38	3.81		2.91						4.34			4.27	2.25	1.79	3.75			7.96	5.23			3.45				7.12		
5		5.62	4.24		3.23						7.69			3.70	1.95	10.20				5.61	6.68							4.59	9.28	
6		5.90		3.44	4.05						7.06			3.92	2.32	1.95	9.17	3.37	6.28		7.84	5.90			5.14	4.11	4.59	6.83	4.46	9.28
7		5.54	4.00	3.08							6.20			3.96	2.32	2.32		2.38	5.66		7.06	5.14			4.11	4.11	6.78	5.65	9.04	
8			4.54	7.35	3.45						6.73			3.89	4.23	2.25	2.62		2.33	5.95	7.03	5.29			4.31	7.08	4.31	5.22	5.22	
9			6.08	3.98							6.13				5.11	2.28		1.66	3.30		7.97	5.46			4.24	7.89	6.28	3.46	3.94	
10			11.48	4.55							5.53				8.20	2.17		2.76	5.14		8.51			4.59	4.14	4.14	5.60	4.98	3.33	
11			10.90	5.34							5.32				2.87	2.18		5.00	1.65		7.75			4.31	4.21		5.60			
12			3.01	7.42							4.87				2.80			5.53	1.75		8.41	4.79			4.06	6.72	5.91			
13			3.06	6.10							3.79				2.26	7.13		7.06	4.91		4.91	4.85			4.67	7.48	5.83	5.91	6.91	
14			3.68	3.36							5.37				2.22	7.12		3.77	3.60		7.05	4.91			4.85	4.02	4.78	5.68	4.67	
15			3.88								5.04				2.76	2.20		3.49	8.90		8.82			4.03	7.44	4.03	4.32	4.32	4.32	
16			5.30								4.79				2.43	2.12		4.77	10.20		9.65			4.58	4.11	4.00	6.17	8.18	5.44	
17			6.62	8.77							4.77				2.09	2.32	4.96		4.40	8.21			4.53	4.00		6.43	5.78	5.96		
18			10.80	10.80							5.91				2.51	2.12		7.51	7.62		4.51	4.56			4.11	6.43	5.86	8.13	3.24	
19			5.07	6.94							5.76				3.32	3.68	5.67	6.06	9.06		5.37	3.80			4.45	7.35	5.33	7.84	4.32	
20			5.82	3.92							6.08				2.29	6.21		5.06	6.75		5.57	3.88			4.32	7.44	4.96	4.96	3.28	
21			3.40	7.78							3.88				2.70	3.05	5.56	5.63	6.52		9.74	4.85			4.22	7.44	6.23	3.53	2.52	
22			3.33								3.70				2.43	2.02		4.83	8.88		6.44	4.88			4.18	7.55	6.18	8.32	2.67	
23			3.42								5.19				2.58	1.93		5.97	9.17		5.36			4.63	4.31		5.19			
24				6.93							6.42				2.82	2.44		6.92	5.65		6.83	5.57			4.78	4.78	5.00	6.18		
25				7.15							5.82				4.17	2.61		4.46	3.91		6.89	4.22			4.79	4.97	4.48	3.32		
26				7.17							5.73	5.32			4.85			2.56	2.09		5.05	4.37			4.50	4.14	4.48	3.04		
27				5.97							6.08				3.93	4.34		6.57	3.21		4.78	4.97			4.28					
28				4.82							5.71				4.59	2.99		6.33	7.38		7.00	4.36			4.28					
29				3.63							4.72				4.53			2.80	9.47		7.24	5.02			4.28					
30				11.25							2.82				2.12			2.12			7.39			4.45						
31				14							22				21			4.16			19	20			21	22	17	21	20	18
Days				25							15				14			22			25	20			21	22	17	21	20	18
Average salinity	4.36	7.87	5.30	3.43	3.24	4.37	5.70	5.27	4.19	4.11	3.44	2.77	4.17	4.41	6.27	5.76	7.51	5.59	4.64	4.17	6.68			4.17	6.68	5.76	5.06	4.84	4.84	
Number of observations	54	92	84	98	45	42	65	60	62	57	61	69	61	63	60	50	56	39	42	44	33			41	38	35	41	38	35	
Titrated observations	54	92	84	90	1	33	1	4	6	8	61	54	61	24	9	2	15	0	1	0	0			0	0	0	0	0	0	

¹ All nontitrated observations made with a portable conductivity meter.

Two facts are clearly shown by figure 3: the day-by-day variations in salinity are extreme, and over the 2-year period there is no consistent seasonal pattern.

The first step in determining the cause of salinity variations was to obtain as nearly as possible a picture of the average salinities in different sections of the project area over the entire 24-month period. The average monthly salinity at each station is given in table 3. In some cases, it has been possible to interpolate missing data on a proportional basis from adjacent stations with similar characteristics. These interpolated values are shown in parentheses.

TABLE 3.—Mean monthly salinity at each station

[Parts per thousand]

Date	Station 1																	
	BX		PRB		BD		BV		BY		RB		BDB		BDL		LB	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
<i>1959</i>																		
April		(1.50)		(1.91)		(2.21)		(2.26)		(2.32)		(2.53)		(2.58)		(2.74)		(2.82)
May	5	1.15	2	1.58	8	1.79		(1.48)	8	1.52		(1.70)	8	1.73	5	2.13		(2.20)
June	4	0.91	4	1.55	4	1.55		(1.42)	4	1.45		(1.68)	4	1.71	4	1.53		(1.89)
July	5	1.15	5	1.38	5	1.49		(1.44)	5	1.48		(1.55)	5	1.58	5	1.80		(1.86)
August	1	0.82	1	1.10	1	1.53		(1.46)	1	1.50		(1.50)	1	1.53	1	1.68		(1.73)
September		(1.00)		(1.27)		(1.47)		(1.51)		(1.55)		(1.69)		(1.72)		(1.83)		(1.89)
October	3	2.82	3	2.64	3	2.82	3	3.67	3	4.00		(4.78)	4	4.82	4	5.13		(5.29)
November	3	2.27	3	3.19	3	3.04	3	3.42	3	3.52	1	3.24	3	3.23	3	3.38		(3.48)
December	3	2.41	3	2.32	4	3.01	3	2.95	3	2.99	4	3.01	4	3.13	4	2.97		(3.06)
<i>1960</i>																		
January	3	1.37	3	1.87	2	2.36	3	2.47	3	2.03	2	2.60	2	2.53	2	2.74	1	2.26
February	3	1.02	3	1.32	3	1.62	3	1.85	3	1.46	3	1.62	3	1.70	6	1.99	3	1.79
March	3	0.80	3	1.37	3	1.58	3	1.86	3	1.48	3	1.62	3	1.59	3	1.58	3	1.68
April	3	0.95	3	1.06	3	1.09	3	1.23	3	1.46	3	1.28	3	1.54	3	1.36	3	1.21
May	3	1.11	3	1.25	3	1.29	3	1.18	3	1.29	3	1.27	3	1.82	3	1.31	3	1.25
June	3	1.37	3	1.36	3	1.67	3	1.53	3	1.51	3	1.53	3	1.62	3	1.37	3	1.69
July	3	2.23	3	2.45	3	3.09	3	3.62	3	2.71	3	3.36	3	3.23	3	3.63	3	4.08
August	3	1.63	2	3.38	3	3.39	3	3.31	3	3.45	3	3.80	3	3.88	3	4.23	3	4.83
September	2	2.82		(3.58)	2	4.79	2	4.18	2	4.38	2	4.49	2	5.26	2	5.34	2	5.72
October	2	1.56		(1.98)	2	3.13	2	3.04	2	3.40	2	3.54	2	3.53	2	3.98	2	4.16
November	2	1.98		(2.51)	2	3.35	2	3.35	2	3.26	2	3.40	2	3.54	2	3.64	2	3.35
December	2	4.16		(5.28)	2	5.97	2	5.59	2	5.48	2	6.20	2	6.30	2	6.48	2	6.87
<i>1961</i>																		
January	2	1.66		(2.11)	2	1.88	2	3.34	2	4.32	2	4.40	2	4.11	2	4.76	2	5.07
February	2	1.14		(1.45)	2	1.81	2	2.48	2	2.35	2	3.12	2	2.76	2	3.10	2	3.36
March	2	1.24		(1.57)	2	1.83	2	1.92	2	1.42	2	1.76	2	1.80	2	1.84	2	2.12

[Parts per thousand]

Date	Station 1																	
	BWA		BWH		SBB		SB		JDY		BML		BG		YC		BM	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
<i>1959</i>																		
April		(3.00)		(3.02)	3	3.49	10	3.77		(4.04)		(3.81)		(4.26)	11	3.78	2	4.42
May	2	2.26	2	3.24	2	3.71	3	7.15		(5.43)	1	6.07	3	4.62	3	7.59	4	5.63
June	4	2.23	4	2.22	4	2.79	4	3.88		(3.39)	4	3.31	4	3.50	4	3.98	4	3.70
July	5	2.00	5	1.96	5	2.83	5	2.70		(3.34)	5	3.13	5	3.30	5	2.73	5	3.65
August	1	2.08	1	1.92	1	2.97	1	3.02		(2.53)	1	2.66	1	3.21	1	2.82	1	2.77
September		(2.01)		(2.02)	1	2.33	1	3.25		(2.21)	1	2.31	1	2.54	1	2.29	1	2.41
October	3	4.98	3	5.26	3	6.21	3	6.42		(5.72)	3	6.50	3	5.96	3	5.91	3	6.25
November	3	4.67	3	4.72	3	5.14	3	5.10	1	4.85	3	5.19	3	5.48	3	4.68	2	5.24
December	3	3.66	3	3.57	3	4.07	3	4.29	3	4.14	3	3.93	3	4.17	3	3.99	3	4.07
<i>1960</i>																		
January	3	3.21	3	3.58	3	3.60	3	3.99	2	3.66	2	3.73	2	3.84	3	4.01	2	3.58
February	3	2.79	3	2.59	3	2.63	3	2.68	3	2.99	3	2.89	5	2.29	3	2.80	3	3.13
March	3	2.03	3	2.20	3	2.20	3	2.24	3	2.50	3	2.32	3	2.50	3	2.14	3	2.49
April	3	1.78	3	1.52	5	1.74	3	1.79	3	1.91	3	1.63	3	2.67	3	3.76	3	2.16
May	3	1.61	3	1.56	6	2.09	3	2.28	3	2.29	3	2.18	3	3.14	3	3.42	3	3.42
June	4	2.08	4	2.00	7	2.78	4	2.59	3	3.69	3	3.69	3	4.24	4	6.08	3	6.23
July	2	3.15	2	3.07	5	4.02	2	3.62	3	5.40	3	5.43	3	6.07	2	6.50	3	5.49
August	2	3.30	3	3.72	3	4.50	3	4.68	3	4.89	3	5.13	3	5.25	3	7.61	3	5.57
September		(4.95)		4.98	3	5.21	3	5.11	3	5.41	3	5.37	3	5.61	3	5.30	3	5.45
October		(4.27)		4.30	4	4.28	2	4.47	2	4.24	2	4.20	2	4.40	2	4.32	2	4.36
November		(3.75)		3.78	4	3.83	2	3.59	2	3.93	2	4.07	2	4.01	2	3.95	2	3.99
December		(7.73)		7.78	4	6.15	2	6.26	2	5.84	2	6.48	2	5.84	2	6.16	2	6.40
<i>1961</i>																		
January		(4.71)	2	4.74	4	6.42	2	6.29	2	6.60	2	6.80	2	6.54	2	5.83	2	6.70
February		(3.40)	2	3.42	4	4.24	2	5.23	2	4.74	2	4.52	2	5.04	2	3.02	2	4.90
March		(2.09)	2	2.10	4	3.12	2	3.15	2	4.48	2	3.38	2	4.98	2	3.99	2	5.02

See footnotes at end of table.

TABLE 3.—Mean monthly salinity at each station—Continued

Date	Station 1																	
	HLE		HL		TW		HLSE		LLBC ₁		EB		LL		BB		OB	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																		
April	4	5.38	12	6.24	4	5.93	7	6.31	5	7.27	4	6.62	5	7.33	1	7.88	4	7.58
May			4	10.77	5	10.67	1	8.71	6	14.98	1	9.06	5	13.96	2	12.52	4	12.38
June			4	8.90	4	3.70			8	9.79			4	11.09	4	9.06	4	10.44
July			5	4.95	6	5.26			40	6.27			7	6.37	5	7.24	5	6.83
August			1	4.87	1	4.28			1	7.49			1	6.67	1	6.70	1	6.97
September			1	4.59	3	5.44			3	4.64			1	8.73	1	9.03	1	5.41
October			2	5.28	2	6.16			4	5.66							2	5.74
November			3	5.69	2	-6.40			5	6.13							3	6.34
December			3	4.80	3	6.66			3	5.73							3	6.32
1960																		
January			3	5.02	3	4.93			3	5.49							3	5.87
February			3	3.92	3	3.78			2	3.13							3	5.24
March			3	2.66	5	4.73			3	3.30							3	4.26
April			3	6.28	2	4.76			3	6.47							3	6.44
May			3	3.94	3	5.71			3	6.61							3	6.80
June			3	9.21	3	10.85			3	11.91							3	11.67
July			3	9.55	3	10.60			3	11.96							3	11.08
August			3	9.72	3	7.50			3	8.40							3	12.57
September			3	7.10	2	5.61			3	6.86							3	9.82
October			2	5.54	2	4.68			2	5.60							2	7.04
November			2	4.07	2	4.18			2	4.74							2	4.36
December			2	6.81	2	7.88			2	7.84							2	8.14
1961																		
January			2	6.37	2	8.91			2	6.44							2	6.60
February			2	6.64	2	6.59			2	6.49							2	7.79
March			2	5.95	2	6.27			2	6.68							2	7.80

Date	Station																	
	MP		LRO		CB		LR		LEG		CP		LLBC ₂		BP		BPPN	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																		
April		(8.50)	5	8.13	1	8.72	4	9.43	1	8.57			4	10.68	2	12.30	2	12.96
May	3	14.00	2	14.02	2	14.36	2	11.89	2	15.63			4	18.49	3	16.20	2	19.58
June	4	11.74			4	11.86	6	6.38	4	12.61			4	14.08	4	14.12	4	16.49
July	5	7.82			5	8.82	5	7.70	5	9.34			5	11.61	5	9.75	5	11.22
August	1	8.35			1	9.09	1	7.45	1	8.35			1	11.18	1	9.39	1	12.37
September	1	10.00			1	10.12	1	8.45	1	10.00			1	6.02	1	8.77	1	8.38
October					2	7.68			2	7.68			2	8.40	2	9.75	2	10.92
November					3	8.19			3	8.19			4	8.25	3	11.98	3	9.64
December					3	7.60			3	7.60			3	8.90	2	11.99	3	9.47
1960																		
January							3	6.36					3	8.52	3	9.50	1	10.92
February							3	8.41					3	6.01	2	11.57	4	7.63
March							3	7.40					3	5.66	3	9.79	3	6.29
April							3	8.42					3	9.39	3	9.76	3	10.56
May							3	6.49					3	8.25	3	9.77	3	9.45
June							3	12.34					3	16.80	3	15.47	3	17.83
July							3	13.57					3	14.29	3	14.72	3	17.12
August			1	10.57			3	14.29			1	12.60	2	11.70	3	13.42	3	13.78
September			3	9.20			3	10.20			3	7.32		7.32	3	9.86	3	9.21
October			1	8.90			2	8.06			2	7.32		(6.83)	1	7.91	2	11.13
November							2	5.88			2	6.06		(5.34)	2	7.94	2	6.96
December							2	9.10			2	9.46		(10.74)		(16.50)	2	11.60
1961																		
January							2	8.40			2	10.19		(10.32)	1	12.60	2	11.76
February							2	8.40			2	9.52		(9.81)	1	9.97	2	11.78
March							2	9.49			2	8.59		(9.93)	2	11.64	2	11.69

See footnotes at end of table.

TABLE 3.—Mean monthly salinity at each station—Continued

Date	Station ¹																			
	TP		LST		LE		BPPS		LAW		LAN		LMN		LAS		LFF		GPT	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
<i>1959</i>																				
April	5	13.19	2	12.97	2	15.20	2	14.06				(15.12)		(16.39)		(17.12)		(18.85)		
May	4	20.88	3	17.23	4	22.39	3	20.39				(21.27)		(23.06)		(24.09)		(26.53)		
June	4	18.99	4	15.78	4	17.50	4	18.00				(17.86)		(19.37)		(20.23)		(22.28)		
July	5	13.64	5	11.38	5	13.56	5	13.51				(13.39)		(14.52)		(15.16)		(16.70)		
August	1	14.35	1	10.87	1	15.40	1	13.86				(14.11)		(15.29)		(15.98)		(17.59)		
September	1	10.40	1	10.40	1	14.30	1	13.00				(13.26)		(14.38)		(15.02)		(16.54)		
October	2	12.52	2	11.55	2	14.80	2	13.49	2	14.44	2	13.50	2	15.34	2	16.91	2	17.65		
November	3	10.12	3	12.83	3	12.05	3	12.30	1	13.00	3	12.76	2	12.36	3	13.14		(16.66)		
December	3	10.19	3	10.10	3	12.23	1	13.64			2	11.70	2	13.64	3	13.68	1	14.58		
<i>1960</i>																				
January	3	10.55	3	8.49	3	11.07	2	11.13			2	14.16	2	12.03	1	13.93	2	14.88		
February	3	8.12	3	11.36	3	8.47	3	12.16			3	11.97	3	12.43	3	12.41	3	13.39		
March	3	5.57	3	9.88	3	9.53	3	9.63			3	10.15	3	10.41	3	11.10	3	12.74		
April	3	12.13	3	11.26	3	12.73	3	11.97			3	11.90	3	12.53	3	14.77	3	15.18		
May	3	9.75	3	9.53	3	10.43	3	9.65			3	12.73	3	12.26	3	14.89	3	12.30		
June	3	17.12	3	16.59	3	18.85	3	18.14			3	19.16	3	20.48	3	21.83	3	20.79		
July	3	15.89	3	15.86	3	16.80		(18.03)			3	18.40	3	18.58	3	21.33	3	22.53		
August	2	15.43	3	15.20	3	15.30		(17.28)			2	13.84	3	15.41	3	16.73	3	17.61		
September		(9.09)	3	11.70	3	9.99		(13.30)				(11.47)	3	12.00	3	12.99	3	14.07		
October		(8.39)	2	8.05	2	9.22		(9.15)				(8.69)	2	9.76	2	9.84	2	10.64	2	9.98
November		(6.56)	2	9.08	2	7.21		(10.32)				(8.62)	2	10.32	2	9.76	2	10.76	2	11.05
December		(13.20)	2	17.59	2	14.50		(20.00)				(14.02)	1	17.80	2	15.88	2	22.33	2	20.36
<i>1961</i>																				
January		(12.68)	2	13.55	2	13.93		(15.41)				(17.25)	2	16.23	2	19.54	2	20.78	2	19.76
February		(12.05)	2	8.72	2	13.24		(9.91)				(11.69)	2	11.18	2	13.24	2	12.34	2	15.98
March		(12.19)	2	13.32	2	13.40		(15.14)				(13.49)	2	13.24	2	15.28	2	19.40	2	20.84

¹ Means in parentheses interpolated by comparison of observed data with adjacent stations. See table 1 for interpretation of symbols.

The data of tables 2 and 3 are summarized in table 4 by bimonthly periods. Observations are too scant, considering the degree of variation in respect to the mean, to be able to place reliance on means derived from any shorter period of time. A 24-month mean salinity is also shown for every station. Admittedly, the 24-month means may be somewhat unreliable when interpolated for stations with but a few months' data, but they are the best estimates available, and their consistency has given us considerable confidence in their use.

From the 24-month mean salinities of table 4, the isohalines of figure 1 are plotted. These have formed the basis for dividing the project area into the numbered areas shown, which will be referred to again under the discussion of the biology.

CURRENTS

The question now is what causes the observed 24-month salinity pattern and the short-term fluctuations therein. An attempt to utilize the data from hourly current observations taken for periods from 12 to 24 hours' duration was unsuccessful, chiefly because of the extremely limited

number of stations occupied. (All but 4 out of 42 observation periods were taken at stations H and YC.)

Thereafter, resort was had to the 568 observations on the direction of flow at 10 different stations made at the times these stations were visited by field observers (table 5).

From these field observations, figure 4 has been plotted to show the percent of time the current flowed in various directions at each station at which currents were observed. Figure 4 has been made semidiagrammatic to show the main routes water can follow as it moves across the project area. There appears to be a residual current flowing north in Bayou La Loutre from LLBC₂ that continues around the loop in the bayou past station LL. At LLBC₁ a portion of this water together with some from Lake Borgne turns south, but a portion continues west where it meets a residual eastward-flowing current from station YC. These observations are of great interest for they indicate the presence of a residual southerly current from Lake Borgne, entering the bayou system at both Bayou Yscloskey (SB) and Bayou St. Malo (BM).

TABLE 4.—Summary of mean salinities for all stations

[Parts per thousand]

Station	1959						1960						1961			
	24-month average	Apr.-May	June-July	Aug.-Sept.	Oct.-Nov.	Dec.-Jan.	Feb.-Mar.	Apr.-May	June-July	Aug.-Sept.	Oct.-Nov.	Dec.-Jan.	Feb.-Mar.	Mean of two bimonthly periods		
														High	Low	Difference
BX	1.62	1.32	1.03	0.91	2.54	1.89	0.91	1.03	1.75	2.22	1.77	2.91	1.19	2.72	0.91	1.81
PRB	2.06	1.74	1.46	1.18	2.91	2.10	1.34	1.16	1.90	3.48	(2.24)	(3.70)	(1.51)	3.59	1.17	2.42
BD	2.39	2.00	1.52	1.50	2.93	2.68	1.60	1.19	2.38	4.09	3.24	3.92	1.56	4.00	1.34	2.66
BV	2.45	(1.87)	(1.43)	(1.48)	3.04	2.71	1.86	1.20	1.58	3.74	3.19	4.46	2.20	4.10	1.32	2.78
BY	2.51	1.92	1.46	1.52	3.76	2.51	1.47	1.38	2.11	3.92	3.33	4.85	1.88	4.38	1.42	2.96
RB	2.73	(2.12)	(1.62)	(1.60)	3.98	2.80	1.57	1.28	2.44	4.14	3.47	5.30	2.44	4.72	1.42	3.30
BDB	2.78	2.16	1.64	1.62	4.02	2.83	1.64	1.43	2.42	4.57	3.54	5.20	2.28	4.88	1.52	3.36
BDL	2.95	2.44	1.82	1.76	4.26	2.86	1.78	1.34	2.50	4.78	3.81	5.62	2.47	5.20	1.55	3.65
LB	3.04	(2.51)	(1.88)	(1.81)	(4.38)	2.66	1.68	1.23	2.88	5.28	3.76	5.72	2.74	5.50	1.46	4.04
BWA	3.24	2.83	2.12	2.04	4.82	3.44	2.41	1.70	2.62	4.12	(4.01)	(6.22)	(2.74)	5.52	1.87	3.65
BWH	3.26	2.63	2.09	1.97	4.99	3.58	2.40	1.54	2.54	4.35	4.04	6.26	2.76	5.62	1.76	3.86
SBB	3.77	3.60	2.81	2.65	5.68	3.84	2.44	1.92	3.40	4.86	4.06	6.29	3.68	5.98	2.18	3.80
SB	4.03	5.46	3.20	2.64	5.76	4.14	2.46	2.04	3.10	4.90	4.03	6.28	4.22	6.02	2.25	3.77
JDV	4.09	(4.74)	(3.36)	(2.37)	5.28	3.90	2.74	2.10	4.54	5.15	4.05	6.22	4.61	5.75	2.24	3.51
BML	4.11	4.94	3.22	2.47	5.84	3.83	2.60	1.90	4.56	5.25	4.14	6.64	3.95	6.24	2.18	4.06
BG	4.31	4.44	3.40	2.88	5.72	4.00	2.40	2.90	5.16	5.43	4.20	6.19	5.01	5.96	2.64	3.32
YC	4.44	5.68	3.36	2.56	5.30	4.00	2.47	3.59	6.29	6.46	4.14	6.00	3.50	6.38	2.52	3.86
BM	4.47	5.18	3.68	2.59	5.74	3.82	2.84	2.79	5.86	5.51	4.18	6.55	4.96	6.20	2.69	3.51
Hopedale	4.95	6.12	4.36	3.80	5.48	4.15	3.10	4.29	6.02	6.55	4.40	6.22	4.95	6.38	3.45	2.93
HLE	5.34															
HL	6.20	8.50	6.92	4.73	5.48	4.91	3.29	5.11	9.38	8.41	4.80	6.59	6.30	8.94	4.01	4.93
TW	6.22	8.30	4.48	4.86	5.78	5.80	4.26	5.24	10.72	6.50	4.43	8.38	5.93	9.55	4.34	5.21
HLSE	6.81															
LLBC ₁	7.08	11.12	8.03	6.08	5.90	5.61	3.22	6.54	11.94	7.63	5.17	7.14	6.58	11.53	4.42	7.11
EB	7.11															
LL	7.17	10.64	8.73	7.70												
BB	7.24	10.20	8.15	7.86												
OB	7.58	9.98	8.54	5.69	6.04	6.10	4.75	6.62	11.32	11.04	5.70	7.37	7.80	11.18	5.22	5.96
MP	7.92	11.25	9.78	9.18												
LRO	8.32	11.08								9.88						
CB	8.69	11.54	10.34	9.60												
LR	8.82	10.66	7.04	7.95	7.94	6.98	7.90	7.40	12.96	12.24	6.97	8.75	8.94	12.60	6.98	5.62
LEG	8.90	12.10	10.98	9.18												
CP	9.85									9.96	6.69	9.82	9.06			
LLBC ₂	9.94	14.58	12.84	8.60	8.32	8.71	5.84	8.82	15.54	9.55	(6.08)	(9.87)	15.06	5.96	9.10	
BP	11.47	14.60	11.94	9.08	10.86	10.74	10.68	9.75	15.10	11.64	7.92	14.55	10.80	14.82	8.50	6.32
BPPN	11.61	16.27	13.86	10.38	10.28	10.20	6.96	10.00	17.48	11.50	9.04	11.68	11.74	16.88	8.00	8.88
TP	12.31	17.04	16.32	12.38	11.32	10.37	6.34	10.94	16.50	12.26	(7.48)	(12.94)	(12.36)	16.77	7.16	9.61
LST	12.22	15.10	13.58	10.64	12.19	9.30	10.62	10.40	16.22	13.45	8.56	15.57	11.02	15.90	8.93	6.97
LE	13.42	18.80	15.53	14.85	13.42	11.64	9.00	11.58	17.82	12.64	8.22	14.22	13.32	18.31	8.61	9.70
BPPS	13.90	17.22	15.76	13.43	12.90	12.38	10.90	10.80	18.08	(15.29)	(9.74)	(17.70)	(12.52)	17.89	10.27	7.62
LAW	14.63															
LAN	14.60	(13.20)	(15.62)	(13.88)	13.13	12.93	11.06	12.32	18.78	12.66	(8.66)	(15.64)	(12.59)	17.21	9.86	7.35
LMN	14.75	(19.72)	(16.94)	(14.84)	13.85	13.84	11.42	12.40	19.53	13.70	10.04	17.02	14.71	19.62	10.73	8.89
LAS	15.60	(20.60)	(17.70)	(15.50)	15.02	13.80	11.76	14.58	21.58	14.86	9.80	17.71	14.26	21.09	10.78	10.31
LFF	16.96	(22.69)	(19.49)	(17.06)	(17.16)	14.73	13.06	13.74	21.66	15.84	10.70	21.56	15.87	22.18	11.88	10.30
GPT	17.27										10.52	20.06	18.41			

TABLE 5.—Observations on current directions from regular sampling trips

[Percent of observations]

Direction	Station											Average
	SB	YC	HL	OB	TW	BM	LLBC ₁	LL	LLBC ₂	TP		
No current	1.4	7.0	10.9	4.6	13.6	7.1	4.9	52.2	2.0	9.8		11.4
Toward Lake Borgne	38.6	26.8				39.3	20.5					31.3
Away from Lake Borgne	60.0	66.2				50.0	45.5					55.4
Toward Bayou La Loutre (north)			39.1	52.3								
Away from Bayou La Loutre (south)			48.6	43.1								
Toward Bayou Guyago (west)						8.6						
Toward LLBC ₁ (east)			1.6									
Toward Hopedale (west)					74.2		30.6	39.1				48.0
Toward Stump Lagoon (east)					12.1		6.0	8.7				8.9
Toward LL (north)											49.0	
Away from LL (south)											6.1	
Toward Halfmoon Lagoon											33.7	
Away from Halfmoon Lagoon											7.1	
Toward Treasure Pass											2.0	
Away from Treasure Pass											73.0	
Toward Bayou Petre (north)												67.4
Away from Bayou Petre (south)												21.5
West on Bayou Petre												33.9
East on Bayou Petre												55.6
Number of days observed	70	71	64	65	66	28	81	23	49	51		56.8

¹ Toward Halfmoon Lagoon.

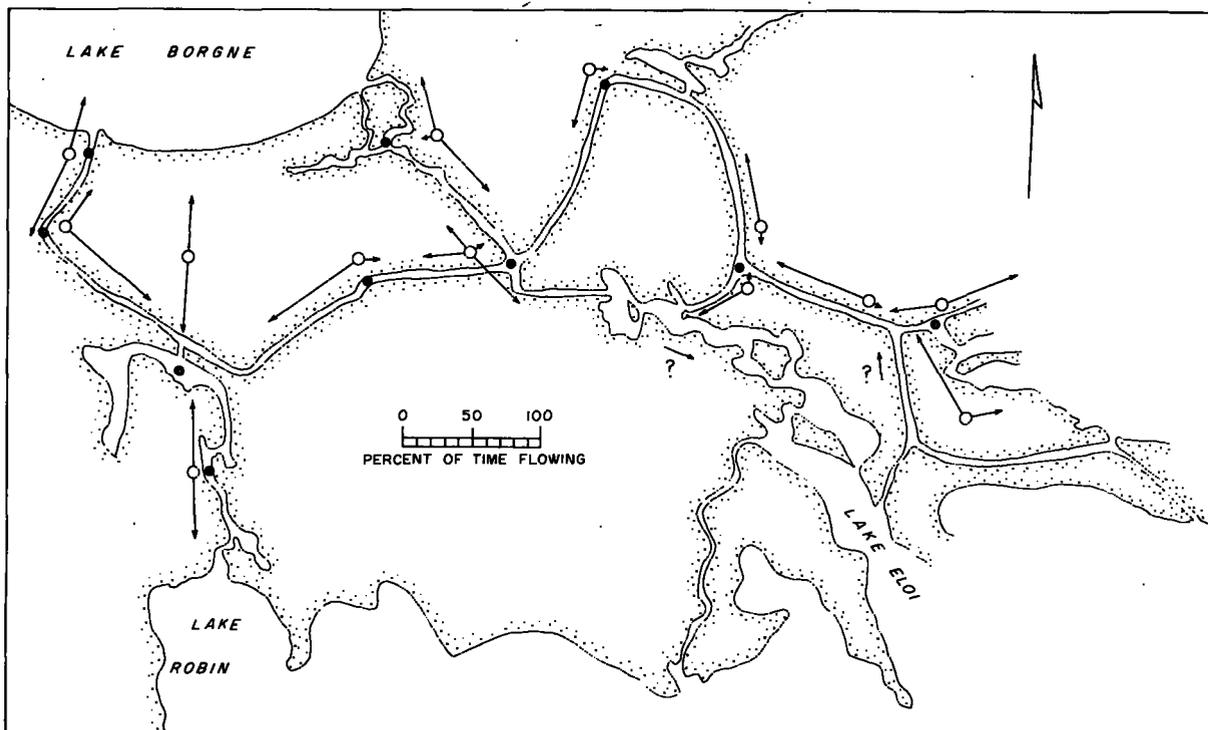


FIGURE 4.—Semidiagrammatic map of the project area showing the percent of time currents were flowing in each direction. Station locations shown by black dots. Length of arrows from adjacent open circles shows the percent of time in the indicated direction.

In addition to the two routes for water exchange between Lake Borgne and Breton Sound indicated in figure 4, there is a third route, via Bayou Biloxi, Lake Eugenie, Crooked Bayou, and Stump Lagoon (fig. 2), for which information is too scant to assess its actual significance. The effect of these main transport routes on mean salinities is shown in figure 5, in which 24-month salinities are plotted against distance from station SBB in Lake Borgne along the routes water would have to follow in order to circulate. The mean salinity along both the western and central routes between Breton Sound and where they meet the cross channels linking SB with LEG decreases at a rather uniform rate of 1‰ every 2 miles.

On the crosslinking channels running from LEG to SB the rate of decrease in salinity is also quite uniform but only 1‰ every 5 miles. This great contrast in the rate of decrease in salinity per mile between that of the two chief water routes from Breton Sound and that of the cross channel suggests that Lake Borgne dominates the water circulation north of Bayou La Loutre and

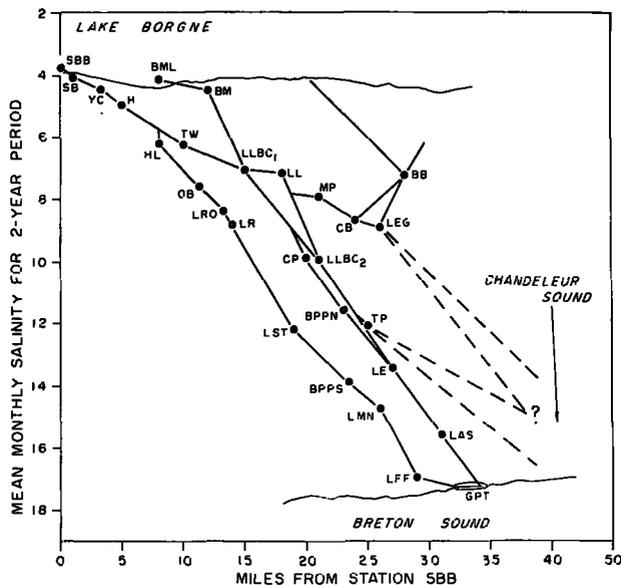


FIGURE 5.—Diagram to show the average relation between salinity and distance along the water exchange routes linking Lake Borgne with Breton and Chandeleur Sounds.

along Bayou La Loutre between Stump Lagoon and Lake Borgne.

The lack of data on the cross-sectional areas of the connecting waterways makes it difficult to estimate the relative importance of each route to the water exchange pattern. Some idea of their relative importance, however, can be gained by noting the relative variation in salinity, since the degree of variation should be positively correlated with the amount of water exchange.

Because of the paucity and nonorthogonal pattern of the sampling, I have been forced to utilize a very simple measure of variation; namely, the salinity difference between the average of the two highest bimonthly means and the average of the two lowest bimonthly means (table 4).

The logarithms of the resulting differences in salinity are plotted as the ordinate, labeled "salinity variation" in figure 6 using the mean monthly salinity for the entire 2-year period as the abscissa. Several features are of interest. The salinity variation in the central water transport system is considerably higher than in the western, indicating a greater water exchange. The great decrease in salinity variation between LLBC₁ and H on the linking stations tends to confirm this conclusion. It should also be noted that stations in Bayou Pisana (BP) and northern Lake Athanasio (LAN), which are in effect in cul-de-sacs without through movement of water, exhibit less variation than neighboring stations on the water transport route.

The four stations in Lake Borgne are similar in their degree of variation. The stations in area 3 (fig. 1) show approximately the same degree of variation as those of Lake Borgne. This tends to confirm my previous observation that a residual current flows southeastward from Lake Borgne since Lake Borgne obviously dominates these stations. In area 1, the stations exhibit a gradually lowering salinity coupled with decreased variation as they go from the lake shore toward Paris Road.

FACTORS AFFECTING SALINITY

Since the waters of Lake Borgne exert the major influence on salinities throughout the project area, I have attempted to determine to what extent certain measurable factors influence them. Table 6 gives data on the discharge of the Pearl River at Bogalusa, the intensity of the north and northeast wind components at the New Orleans Airport, and the average of the monthly salinities for four stations in Lake Borgne. As explained in the footnotes to the table, lagged averages have been used because both river discharge and wind take some time to effect major changes in salinity.

The isopleths for salinity of Lake Borgne plotted against these two variables are shown in figure 7. At low wind intensity from the north and northeast, there is a strong negative relationship between the discharge of the Pearl River and the resulting salinity in Lake Borgne. At higher wind intensities, the salinity rises considerably above the

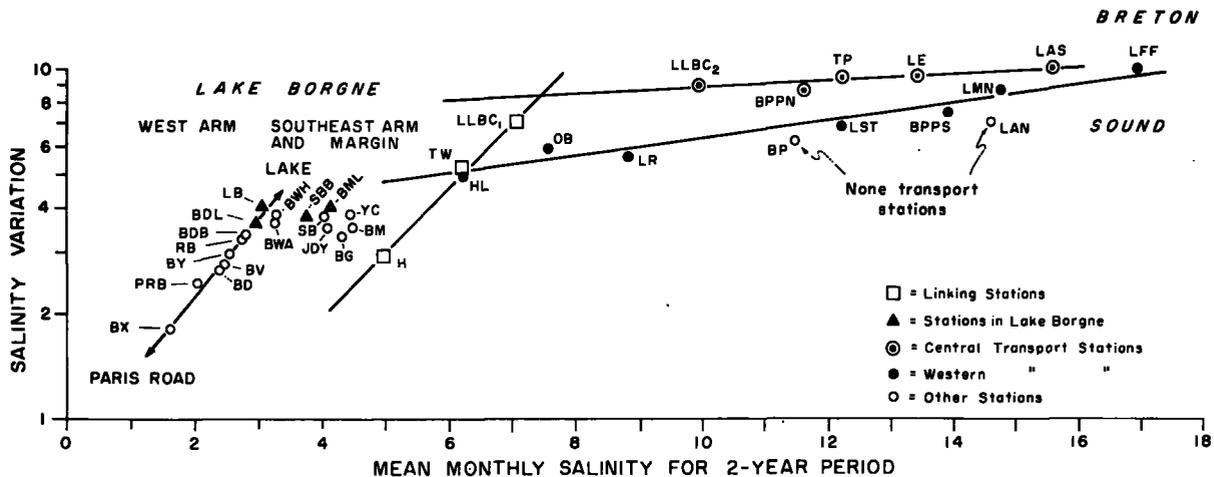


FIGURE 6.—Showing the variation in salinity in relation to mean salinity. The higher variation along the central transport route is indicative of a greater exchange of water through this system than through the western route.

TABLE 6.—Factors influencing salinity of Lake Borgne

Date	Fresh water		Wind		Salinity of Lake Borgne †
	Pearl River discharge		Wind intensity †		
	Month listed	Lagged average ‡	Month listed	Lagged average ‡	
<i>1959</i>	<i>Thousand c.f.s.</i>	<i>Thousand c.f.s.</i>			<i>‰</i>
February.....	18.86				
March.....	10.51				
April.....	10.86	12.32	71.7	(71.7)	3.28
May.....	7.93	9.62	22.9	39.2	3.54
June.....	9.05	8.96	31.1	28.3	2.54
July.....	4.29	6.92	17.2	21.8	2.43
August.....	3.01	4.73	41.3	33.3	2.28
September.....	2.66	3.13	69.2	59.9	3 (2.18)
October.....	3.18	2.94	121.8	104.3	5.78
November.....	4.44	3.58	121.4	121.5	4.60
December.....	6.99	5.21	60.1	80.5	3.64
<i>1960</i>					
January.....	11.50	8.28	86.2	77.5	3.41
February.....	20.91	14.36	57.6	67.1	2.54
March.....	24.48	20.46	71.4	66.8	2.08
April.....	9.47	17.76	45.3	54.0	1.56
May.....	9.95	12.66	50.4	48.7	1.79
June.....	2.27	6.78	31.0	37.5	2.46
July.....	1.85	3.64	42.4	38.6	4.04
August.....	4.30	2.91	26.2	31.6	4.40
September.....	2.39	3.05	96.5	73.1	5.22
October.....	1.88	2.57	53.1	71.9	4.19
November.....	2.06	2.05	90.1	83.4	3.83
December.....	2.39	2.16	83.8	87.9	6.72
<i>1961</i>					
January.....	7.41	4.33			5.68
February.....	22.75	12.54			3.82
March.....	39.47	26.37			2.61

† Number of days times mean speed in knots.
 ‡ For stations BDL, BWH, SBB, and BML.
 † Average for a period including month listed, previous month and half of second preceding month.
 ‡ Average for 6-week period, derived from average of month listed and half of preceding month's average times ½. Data are for New Orleans airport from U.S. Weather Bureau.
 † Unreliable, only 3 salinity observations for Lake Borgne.

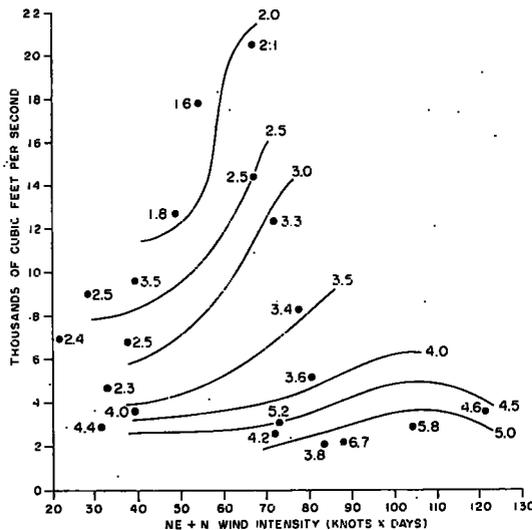


FIGURE 7.—Salinity isopleths in Lake Borgne under varying conditions of wind intensity and Pearl River discharge.

level dictated by river discharge. This is shown by the steep slope of the isopleths.

It would appear that the north and northeast direction of the wind causes intrusion into Lake Borgne of the more saline water of Mississippi Sound.

SUMMARY OF HYDROGRAPHY

In concluding the discussion of hydrography, several points can be noted:

1. Exchange between the low salinity waters of Lake Borgne and the higher salinity waters of Breton Sound takes place by three routes, the central route appears to carry more water than the western route.
2. Large, short-term fluctuations in salinity are especially pronounced in the bayous that form part of the water exchange route.
3. During the 24-month period of study, salinity trends at Hopedale were independent of season.
4. Salinity levels in Lake Borgne are controlled chiefly by fresh-water input (for which we used the discharge of the Pearl River) modified by wind direction and speed.
5. Pearl River discharge and wind intensity both require time to significantly affect salinities in the western end of Lake Borgne. This time lag appears to be several weeks for river discharge and about 2 weeks for wind intensity.
6. Salinity in areas 1 to 3 and the portion of area 4 from Bayou La Loutre northward is dominated by Lake Borgne salinity.

BIOLOGY

BIOLOGICAL SAMPLING

Biological sampling was carried out at selected stations since it was not considered feasible to collect at all stations. One of the major changes that could occur from the channel construction would be a change, probably a raising, in salinity levels. Therefore, it was decided to make collections in three areas that possessed relatively low, medium, and high salinity ranges. The mean bimonthly salinities for the stations actually sampled are given in table 7. It will be noted at once that hydrographical areas 4 and 5 shown in figure 1 were not sampled. Two-thirds of all of the otter trawl tows (the principal gear used) were made in areas 1 to 3 all of which are low salinity areas dominated by Lake Borgne.

TABLE 7.—Mean bimonthly salinities in areas of biological sampling during periods actually sampled

[Parts per thousand]

Date	Areas and stations							
	1	2a	2b	3	6	7	8	
	BD, RB, BDB	BDL, LB	SBB, BML	BM, BG, JDY	BPPN ¹	LAS, LAN, LMN ²	LFF ³	
1959								
June-July	1.59	1.85	3.02	3.48	13.86			
August-September	1.57	1.78	2.56	2.61				
October-November	3.64	4.32	5.76	5.58	10.28	14.00		
December-January	2.77	2.76	3.84	3.91	10.20	13.19	14.73	
1960								
February-March	1.60	1.73	2.52	2.66	6.96	11.41	13.06	
April-May	1.30	1.28	1.91	2.60	10.00	13.10	13.74	
June-July	2.41	2.69	3.98	5.19	17.48	19.96	21.86	
August-September	4.27	5.03	5.06	5.36	11.50	13.74	15.84	
October-November	3.48	3.78	4.10	4.15	9.04	9.50	10.70	
December-January	4.81	5.67	6.46	6.32	11.68	16.79	21.56	
1961								
February-March	2.09	2.60	3.82	4.86	11.74	13.55	15.87	
Monthly average	2.63	3.00	3.94	4.29	11.61	14.98	16.96	

¹ Also samples from adjacent stations BE, LEW, and BLP during July, 1959.

² Also samples from LAW in October and November, 1959.

³ Also samples from GPT from October 1960 to March 1961.

The number of otter trawl tows made in each area at different bimonthly salinities are shown in figure 8 and table 8. This concentration of biological sampling at one extreme of the salinity range has decreased the reliability of any prediction of the effects of moderate changes in salinity. Thus, table 7 shows no biological sampling in areas 4 and 5 leaving a gap between area 3 with an average salinity of 4.3‰ and area 6 with an average of 11.6‰.

TABLE 8.—Sampling effort by otter trawl in each area

[Number of 10-minute tows]

Date	Area							
	1	2a	2b	3	6	7	8	
1959								
June-July	9	2.7	2	8	13.5			
August-September	3	1	1	3				
October-November	18	6	6	17.8	6	18.3		
December-January	23	15.4	8	24.9	8	13	3	
1960								
February-March	8.7	16	5	19	9	21	7	
April-May	16.6	12	11	17.9	6	18	6	
June-July	16	12	12	17.9	6	18	5	
August-September	15	10	7	15	5	12	5	
October-November	12	8	8	12	4	8	8	
December-January	12	8	8	12	4	8	12	
1961								
February-March	12	8	8	12	4	8	12	
Total	147.3	99.1	76.0	159.5	65.5	124.3	58.0	

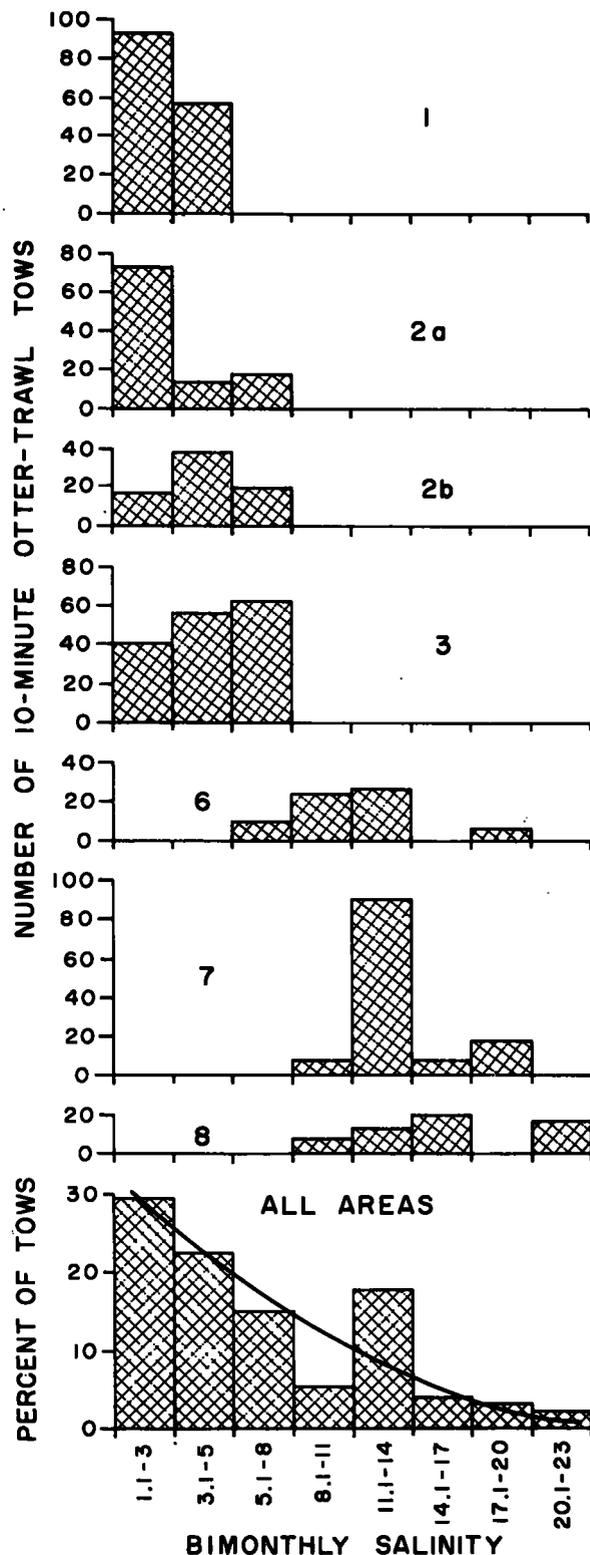


FIGURE 8.—Number of 10-minute otter trawl tows by the area and prevailing bimonthly salinity. The lower salinity sites are heavily oversampled.

GEAR

Several types of biological sampling gear were employed, but only the otter trawl could be called successful. The net measures 200 inches (16 $\frac{2}{3}$ feet) across the headrope and 212 inches (17 $\frac{2}{3}$ feet) along the footrope. The all cotton net has 9-thread 1 $\frac{1}{4}$ -inch mesh, stretched measure, except for the cod end which has 12-thread 1 $\frac{1}{8}$ -inch mesh. The otter boards measure 10 $\frac{1}{2}$ inches vertically by 24 inches horizontally by 1 inch in thickness with a steel reinforcing strap along the front and bottom edges. The boards were fastened directly to the ends of the wings. A galvanized iron chain, 13 links to the inch, and 18 feet long was suspended from the footrope. Four 3 $\frac{1}{2}$ -inch corks were attached to the headrope. The net was towed by two 75 foot lengths of $\frac{1}{2}$ -inch manila rope attached to a single warp.

A small net, described as a try net, was also used. It consisted of a triangle of $\frac{1}{8}$ inch mesh nylon netting, 3 feet across the bottom in front, and attached to a 1 $\frac{1}{2}$ -inch, 3-foot length of galvanized pipe. The catch consisted chiefly of slow-moving forms such as larval and very small juvenile fishes. Catches were insufficient for making any quantitative analysis.

A larger cone of the same description was used in two ways; either attached to a 6-foot length of 2 $\frac{1}{2}$ -inch galvanized pipe, or attached to a rectangular pipe frame about 4 $\frac{1}{2}$ feet wide and 13 inches high mounted on runners. Neither gear was used enough to provide sufficient material for analysis.

The small dredge used to collect mollusks had a mouth opening of only 16 inches. The bag was $\frac{1}{4}$ -inch wire screen. The dredge when new had long teeth soldered onto the front blade. Through use the teeth were completely worn away, thus seriously biasing any quantitative comparisons.

Plankton tows were taken with a $\frac{1}{2}$ -meter net, but plankton volumes were not measured.

EFFECT OF SALINITY ON FISH DISTRIBUTION

One simple basis for predicting changes in fauna that might occur with any major changes in salinity is to determine the ranges of salinity in which various species of fish are found in reasonable numbers. The numbers of each species caught by otter trawl are shown in table 9. The numbers taken in each area are influenced by the number of tows made. To discount this variable, the total

number of each species taken was distributed between areas on the basis of the number of tows. This gives the "expected" number that would be caught if tows alone were the deciding factor (ignoring for the moment, because of the paucity of sampling and low number involved, such other factors as seasonal occurrence). Determining the ratio of the observed to this expected number in each area and then comparing the ratios for all areas gives a rough measure of the areal distribution of each species.

The resulting relative abundance in numbers of all species of which 20 or more were taken by otter trawl is shown by area in table 10 and figure 9. The lack of samples from hydrographic areas 4 and 5 leaves a gap between the low salinity areas 1 to 3 and the higher salinity areas 6 to 8. It is quite obvious, however, that several species are confined to waters of low salinity; others to waters of higher salinity; with a larger number of species lying between that can apparently tolerate a fairly wide range of salinity.

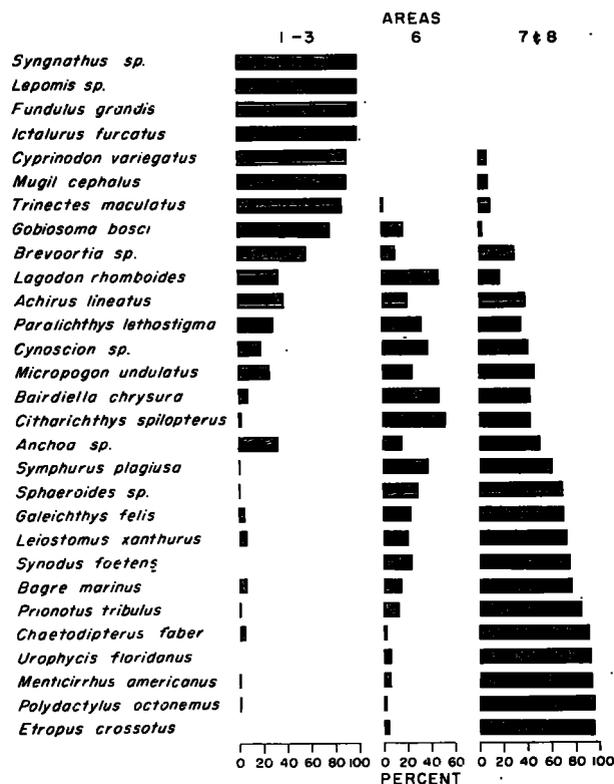


FIGURE 9.—Relative density of 29 species of fish in waters of low (areas 1-3), medium high (area 6), and high salinity (areas 7 and 8).

TABLE 9.—Fish taken by otter trawl shown by species and area of capture

[Number of fish]

Common name	Scientific name	Area of capture							Total
		1	2a	2b	3	6	7	8	
Spot	<i>Leiostomus xanthurus</i>	175	425	694	669	855	2,163	1,533	6,514
Croaker	<i>Micropogon undulatus</i>	547	1,518	581	320	375	449	311	4,101
Anchovy	<i>Anchoa sp.</i>	515	853	511	529	166	156	361	3,091
Sea trout	<i>Cynoscion sp.</i>	147	179	167	57	150	135	73	908
Blue catfish	<i>Ictalurus furcatus</i>	639	2	3	1	0	0	0	635
Sunfish	<i>Lepomis sp.</i>	5	0	0	722	0	0	0	727
Hogchoker	<i>Trinectes maculatus</i>	206	258	46	35	2	8	4	559
Menhaden	<i>Brevoortia sp.</i>	237	173	18	73	13	9	26	548
Sea catfish	<i>Galeichthys felis</i>	26	85	16	10	78	217	100	532
Fringed flounder	<i>Etropus crossotus</i>	0	0	0	0	11	133	146	290
Pinfish	<i>Lagodon rhomboides</i>	3	155	10	25	35	18	3	249
Spotfin whiff	<i>Citharichthys spilopterus</i>	2	22	9	2	83	57	34	209
Striped sole	<i>Achirus lineatus</i>	32	71	30	17	11	20	8	189
Eight-fingered threadfin	<i>Polydactylus octonemus</i>	0	4	12	0	4	65	86	171
Gulf killifish	<i>Fundulus grandis</i>	2	0	0	157	0	0	0	159
Puffer	<i>Sphaeroides (3 species)</i>	0	1	2	0	30	95	19	147
Silver perch	<i>Bairdiella chrysura</i>	7	8	17	21	42	29	19	143
Gafftopsail catfish	<i>Bagre marinus</i>	2	0	25	11	13	46	32	129
Sea robin	<i>Prionotus tribulus</i>	3	3	4	1	13	40	57	121
Spadefish	<i>Chaetodipterus faber</i>	2	2	2	8	1	20	22	57
Southern flounder	<i>Paralichthys lethostigma</i>	10	8	5	16	6	6	3	54
Lizardfish	<i>Synodus foetens</i>	0	1	0	0	9	23	11	44
Sheepshead minnow	<i>Cyprinodon variegatus</i>	1	0	0	41	0	1	0	43
Striped mullet	<i>Mugil cephalus</i>	2	0	0	39	0	1	0	42
Pipefish	<i>Syngnathus sp.</i>	3	1	3	29	0	0	0	36
Naked goby	<i>Gobiosoma bosci</i>	4	3	1	27	1	1	0	36
Tonguefish	<i>Symphurus plagiusa</i>	0	1	0	0	11	13	11	36
Southern hake	<i>Urophycis floridanus</i>	0	0	0	0	2	13	19	34
King whiting	<i>Menticirrhus americanus</i>	1	0	0	0	1	12	9	23
Sheepshead	<i>Archosargus probatocephalus</i>	2	3	3	8	1	0	0	17
Threadfin shad	<i>Dorosoma petenense</i>	7	0	0	0	0	1	8	16
Cutlassfish	<i>Trichurus lepturus</i>	0	0	1	0	2	8	5	16
Stingray	<i>Dasyatis sabina</i>	0	0	0	1	4	4	3	12
Sharp-tailed goby	<i>Gobionellus hastatus</i>	0	0	0	2	1	5	2	10
Toadfish	<i>Opsanus beta</i>	0	0	0	4	1	4	0	9
Miscellaneous species		22	3	4	27	12	12	26	106

TABLE 10.—Relative abundance of principal species of fish according to areas taken

Species	Areas			
	1-3	6	7	8
<i>Ictalurus furcatus</i>	100.0	0.0	0.0	0.0
<i>Lepomis sp.</i>	100.0	0.0	0.0	0.0
<i>Fundulus grandis</i>	100.0	0.0	0.0	0.0
<i>Syngnathus sp.</i>	100.0	0.0	0.0	0.0
<i>Cyprinodon variegatus</i>	91.5	0.0	8.5	0.0
<i>Mugil cephalus</i>	91.3	0.0	8.7	0.0
<i>Trinectes maculatus</i>	87.6	2.4	4.7	5.3
<i>Gobiosoma bosci</i>	78.5	18.2	3.3	0.0
<i>Brevoortia sp.</i>	58.7	11.5	4.3	25.5
<i>Achirus lineatus</i>	39.9	21.6	20.9	17.6
<i>Lagodon rhomboides</i>	35.0	47.6	12.9	4.5
<i>Paralichthys lethostigma</i>	30.4	33.8	18.9	16.9
<i>Micropogon undulatus</i>	27.7	26.0	21.9	24.4
<i>Cynoscion sp.</i>	19.8	39.4	19.0	21.8
<i>Anchoa sp.</i>	33.1	16.9	8.4	41.6
<i>Bairdiella chrysura</i>	8.3	48.0	18.0	25.7
<i>Citharichthys spilopterus</i>	3.1	53.2	19.3	24.4
<i>Symphurus plagiusa</i>	.4	36.4	22.7	38.4
<i>Galeichthys felis</i>	5.7	23.9	35.4	34.9
<i>Sphaeroides sp.</i>	.4	29.9	49.2	20.5
<i>Leiostomus xanthurus</i>	6.7	21.3	28.5	43.5
<i>Synodus foetens</i>	.3	24.4	35.6	39.7
<i>Bagre marinus</i>	6.6	15.8	30.6	46.9
<i>Prionotus tribulus</i>	1.6	13.2	21.3	63.9
<i>Menticirrhus americanus</i>	.9	6.2	37.2	55.8
<i>Chaetodipterus faber</i>	5.3	2.9	28.7	63.1
<i>Urophycis floridanus</i>	.0	7.3	23.7	69.0
<i>Polydactylus octonemus</i>	1.6	3.1	25.5	69.9
<i>Etropus crossotus</i>	.0	4.4	28.6	67.0
Bimonthly salinity (see table 7):				
Low	1.28	6.96	9.50	10.70
High	6.46	13.86	19.96	21.66
Average	3.48	11.61	14.98	16.96

In figure 9, an attempt has been made to rank the species of fishes in order of their preference

from low to high salinity as shown by their relative abundance in the areas depicted.

That errors can easily creep into this type of reasoning is illustrated by the fact that *Mugil cephalus* and *Brevoortia sp.* appear from the figure to be most abundant in waters of low salinity. Actually, this is possibly the case for the juveniles, which were easily captured in the small mesh trawl, but not true for the adults, which could usually escape the trawl. Barring such unusual circumstances, the order of ranking probably represents a fair approximation of the relative effect of salinity on the abundance of these species.

In considering further the subject of salinity tolerance it will be noted from table 9 that no *Lepomis sp.* or *Fundulus grandis* were taken in Lake Borgne (areas 2a and 2b). All but a very few were taken at the stations in area 3 (BM, BG, and JDY). Their occurrence at these stations was highly erratic; 146 out of 159 *Fundulus* were captured in a single haul. This causes me to speculate that these two predominately fresh-water species were living chiefly in some of the diked marsh areas; some occasionally escaping into the surrounding bayous, the salinity of

which, during portions of the year, could be tolerated by them.

FISH DENSITY BY AREA

An important question is how productive in finfish were the areas with different salinity levels. To answer this I show in table 11 the catch per tow in numbers and in biomass of five selected species, namely, spot, croaker, anchovy, sea trout, and menhaden. These five species were selected because of their widespread distribution, their high level of abundance, and their economic importance. Although the anchovy is not utilized directly, it is by far the most important forage fish in the area. Out of 20,013 trawl-caught fish (table 9), 15,162 or 76 percent belonged to this selected group.

TABLE 11.—Number and biomass of selected fishes by area and season¹

Date	1 and 2a	2b and 3	6	7 and 8	Sum
Biomass per tow (in grams)					
1959					
October–November	190.2	51.2	242.5	204.0	689.1
December–January	140.0	20.0	130.4	39.0	329.4
1960					
February–March	77.7	12.9	21.8	5.9	118.3
April–May	210.3	218.6	184.6	351.0	964.5
June–July	120.4	406.6	504.7	431.8	1463.5
August–September	138.6	58.4	53.4	442.9	703.3
October–November	113.4	162.8	336.0	308.5	920.7
December–January	306.0	55.8	183.9	399.0	944.7
1961					
February–March	130.4	101.3	204.1	162.9	598.7
Average	159.7	122.0	206.9	260.6	
Numbers per tow (5 cm. and over in length)					
1959					
October–November	12.5	2.4	15.2	9.6	
December–January	5.3	0.8	7.6	1.5	
1960					
February–March	13.7	1.7	2.6	1.5	
April–May	41.6	42.0	28.0	73.2	
June–July	17.5	38.1	78.8	56.1	
August–September	6.6	4.8	3.4	32.4	
October–November	5.9	8.5	16.0	12.9	
December–January	14.3	3.6	10.3	16.9	
1961					
February–March	15.7	9.8	13.8	12.5	
Average	14.8	12.4	19.5	24.1	

¹ Includes spot, croaker, anchovy, sea trout, and menhaden.

The numbers of fish per tow in table 11 are those of individuals 50 mm. or more in length. Smaller fish were captured in all areas, but because of the selectivity of the otter trawl mesh they were not captured consistently and so have been omitted.

The biomass per tow could only be obtained by estimation from the lengths of the fish, as weights were not taken. From length-weight data collected by C. R. Mock in Galveston Bay it was possible to estimate roughly what individual fish in each 5-cm. category should weigh during each 2-month period. The rough estimate of individual weight used in grams is:

Months	Fish lengths (cm.)			
	0-5	6-10	11-15	16 and more
February–March	1	2	27	74
April–May	1	4	24	60
June–July	1	6	15	66
August–September	1	9	18	55
October–November	1	12	21	66
December–January	1	12	24	72

In figure 10 are shown the estimated biomass (top) and the numbers of fish of 5 cm. and over (bottom), by area and bimonthly period. In both numbers and biomass the Lake Borgne and adjacent areas (1 through 3) were less productive than areas 6 through 8.

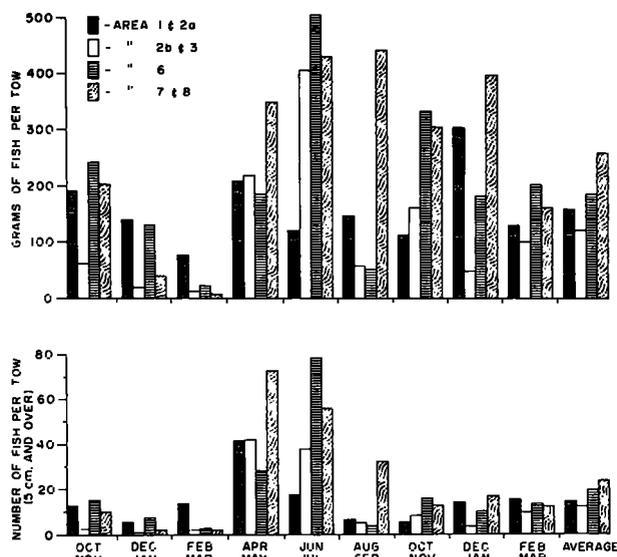


FIGURE 10.—Numbers and biomass of five selected species of fish by area and season.

CRUSTACEA

Enumerations and measurements were made of brown, white, and pink shrimp, and of blue crabs taken in the otter trawl samples. Only 122 pink shrimp were recorded; all were taken during the

last 6 months of the 24-month period. One may speculate that during the earlier months more may have been caught that were classified as brown shrimp.

Out of 9,187 shrimp of all sizes taken, only 419 under 50 mm. were retained by the otter trawl, or 4.6 percent. By contrast 3,059 out of 5,200 blue crabs, or 58.9 percent were under 50 mm. The catch per unit of sampling effort for shrimp of 50 mm. and over is shown in table 12 and in figure 11 for the 18-month period from October 1959 to March 1961. In contrast with the white shrimp, few brown shrimp over 100 mm. were caught. This reflects the Gulf-wide behavior of brown shrimp, which leave the protected waters for the Gulf at a smaller size than do the white shrimp.

There appears to be little salinity preference. Brown shrimp below 100 mm. were taken in all areas. White shrimp below 100 mm. were abundant in three areas, but very scarce in the open waters of Lake Borgne, and only moderately abundant in the rather open waters of areas 7 and 8. Young white shrimp thus appear to prefer shoal, protected waters.

Shrimp are transient residents of the marsh areas. Figure 12 shows the bimonthly catch per 10 tows of white and brown shrimp 50 mm. and

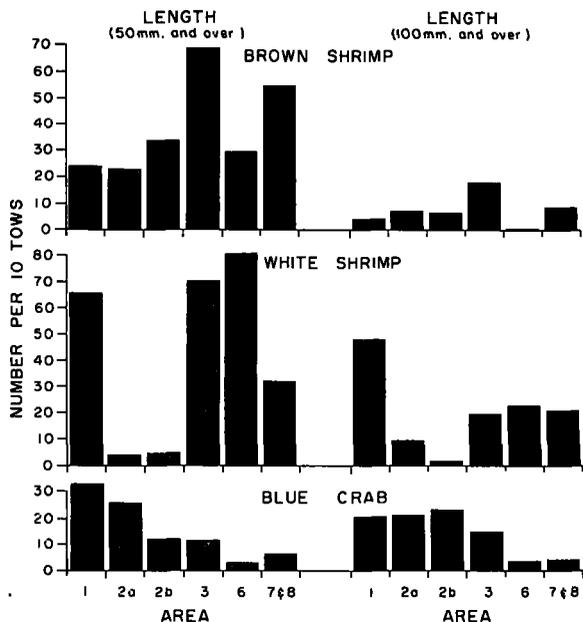


FIGURE 11.—Average catches by size of brown and white shrimp, and blue crabs, per 10 tows by area for the 18-month period, October 1959 to March 1961.

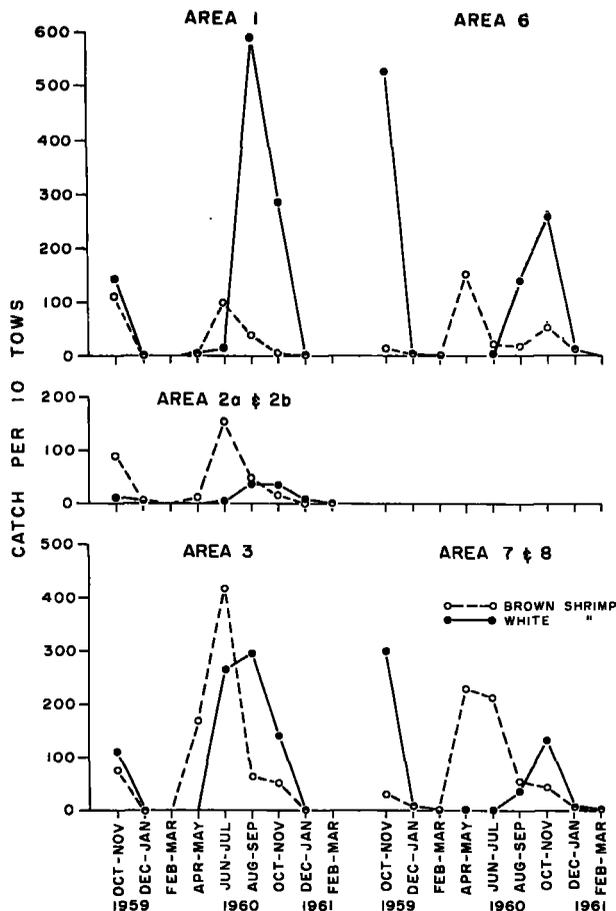


FIGURE 12.—Catches of brown and white shrimp per 10 tows by area and bimonthly period.

over. From December through March, shrimp are almost nonexistent in the areas. Brown shrimp appear in April and May and quickly increase in numbers. By the end of July the numbers of brown shrimp are falling rapidly as the larger sizes emigrate to the Gulf. The peak of abundance for white shrimp comes from 1 to 2 months later.

Blue crabs between 50 and 100 mm. (fig. 11) became progressively less abundant as salinity increased. The larger blue crabs (100 mm. and over) were about equally abundant in all of the areas bordering Lake Borgne, but like the smaller sizes they were scarce in areas 6 through 8. Mature female crabs are known to migrate considerable distances in a matter of a few days to reach higher salinity water for spawning (Fiedler, 1930). Salinities ranging from 23‰ to 30‰ were found by experiment to be optimal for hatching of blue crab eggs (Sandoz and Rogers, 1944). To

TABLE 12.—Number of shrimp caught per 10 tows of an otter trawl

Date	Area													
	1		2a		2b		3		6		7		8	
	Length of shrimp (millimeters)													
	50-99	100 and more	50-99	100 and more	50-99	100 and more	50-99	100 and more	50-99	100 and more	50-99	100 and more	50-99	100 and more
BROWN SHRIMP														
October–November 1959	111.7		53.3		121.7	3.3	76.4	2.2	16.7				30.0	1.1
December–January	1.7		0.6		1.3		0.8		1.3				7.5	
1960														
February–March			3.3		17.5	0.9	166.5	1.1	3.3				2.9	
April–May	6.6												226.3	2.9
June–July	71.7	25.6	94.2	38.3	127.5	46.7	288.8	129.6	21.7				173.9	38.3
August–September	26.7	10.7	38.0	26.0	27.1	5.7	44.0	20.0	18.0				20.0	33.5
October–November	2.5	2.5	21.3	1.3	8.8	1.3	40.0	12.5	47.5	2.5			36.9	3.8
December–January	0.8	0.8			2.5		3.3		7.5				3.0	
1961														
February–March					1.3								0.5	
Average	24.6	4.4	23.2	7.3	34.2	6.4	68.9	18.4	29.7	0.3			55.7	8.8
WHITE SHRIMP														
1959														
October–November	98.9	50.6	8.3		11.7	3.3	77.5	34.3	508.3	16.7			232.2	64.3
December–January	0.9		1.3		1.3				3.8				3.8	
1960														
February–March													0.8	
April–May													0.9	
June–July	16.1	0.6	9.2	1.7	5.0		362.0	3.9	1.7				11.8	23.5
August–September	365.3	223.3	12.0	45.0	17.1	4.3	236.0	60.0	98.0	40.0			30.6	102.5
October–November	118.3	163.3	6.3	41.3	10.0	8.8	56.7	85.0	107.5	152.5			9.5	
December–January			1.8				1.7		10.0					
1961														
February–March													2.0	1.5
Average	66.1	48.7	4.3	9.8	5.0	1.8	70.4	20.4	81.0	23.2			32.4	21.3

reach water of such salinity the female crabs in the project area would need to move at least as far as either Chandeleur Sound or Mississippi Sound. Darnell (1959) collected spawning females in Chandeleur Sound and the eastern end of Lake Borgne in a salinity range of 19.2‰ to 31.5‰.

Pearson (1948) says that the young blue crabs hatched in Chesapeake Bay begin to migrate toward brackish water and that this migration, halted by cold weather, is resumed in the spring. In the project area (table 13) crabs under 50 mm. are most abundant in winter (December through March). This difference between localities may be caused by the milder southern winters.

Since small blue crabs (under 50 mm.) were retained in large numbers by the otter trawl it is possible to arrive at some estimate of their abundance seasonally and by area (table 13 and figure 13). These very small crabs (under 50 mm.) are most abundant in the winter and early spring and extremely scarce from June through

September. They are abundant in the open (and low salinity) waters of Lake Borgne, and scarce in the semi-open (and moderately high salinity) waters of areas 6 to 8. Although crabs of this small size were not particularly abundant in areas 1 and 3, the slightly larger crabs (50–99 mm.) were more abundant in the low salinity waters of area 1 than in Lake Borgne. This seems to indicate a migration of these smaller crabs toward shallow and low salinity areas as they grow.

SUMMARY OF BIOLOGY

1. Only the otter trawl samples are sufficiently extensive and consistent to warrant quantitative treatment.

2. Lack of samples in areas of intermediate salinities (areas 4 and 5) precludes any precise conclusions regarding the effect on the fauna of salinity changes.

3. The bulk of the fish species taken were euryhaline. This included the species caught in greatest abundance.

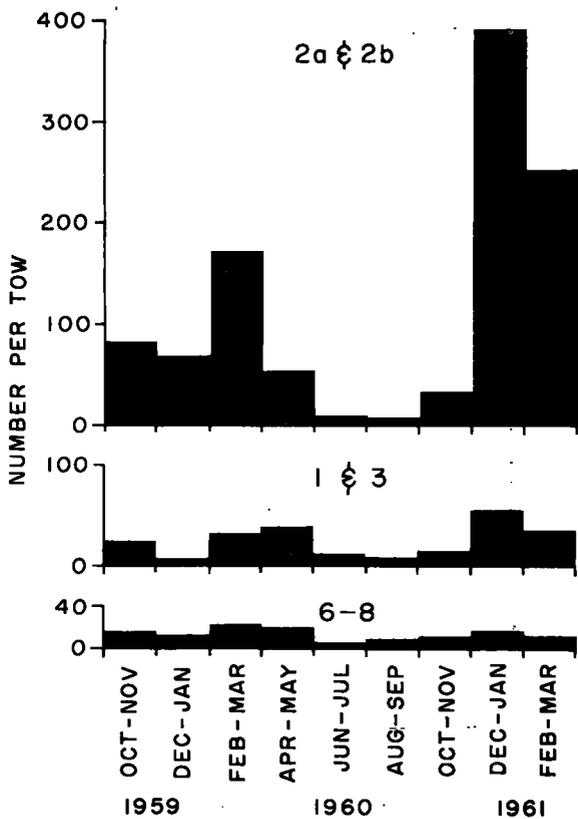


FIGURE 13.—Catches of very young blue crabs (under 50 mm.) by area and bimonthly period.

4. Seventy-six percent of the fish taken were of only five species.

5. In both numbers and biomass these five species were more abundant in areas 6 to 8 than in areas 1 to 3.

6. Neither brown nor white shrimp showed any significant salinity preference.

7. Smaller white shrimp were less abundant in open waters than in the shoal marshes.

8. From December through March shrimp are almost absent from the project area.

9. Smaller blue crabs (50 to 100 mm.) were most abundant in area 1 decreasing progressively to area 3; they were scarce in areas 6 through 8.

10. Larger blue crabs (100 mm. and larger) were about equally abundant throughout areas 1 to 3; but scarce in areas 6 through 8.

DISCUSSION

The Gulf outlet channel will apparently have some effect on the hydrography of the project area. Most probably the chief effect will be a raising of the salinity. This may be accomplished in three ways, first, by mixture of channel water with that of the surrounding bayous through intersection points. Secondly, by raising of the salinity in Lake Pontchartrain through movement of the denser and more saline water from the deeper layers of the channel into the lake. The higher salinities in Lake Pontchartrain would in turn raise salinities in Lake Borgne. The third means of raising salinities would be through the effect of the occasional abnormally high tides which would

TABLE 13.—Number of blue crabs caught per 10 tows of an otter trawl

Date	Area																	
	1			2a			2b			3			6			7 and 8		
	Length of crabs (millimeters)																	
	0-49	50-99	100 and more	0-49	50-99	100 and more	0-49	50-99	100 and more	0-49	50-99	100 and more	0-49	50-99	100 and more	0-49	50-99	100 and more
1959																		
October-November	37.2	31.7	12.8	88.3	53.3	3.3	73.3	6.7	23.3	11.2	12.9	22.5	8.3	1.7	5.0	23.5	2.2	3.3
December-January	13.0	24.8	2.2	108.4	7.1	19.5	27.5	13.8	37.5	2.8	21.7	19.3	11.3	-----	-----	12.5	5.6	1.9
1960																		
February-March	62.1	13.8	1.1	321.3	5.6	8.8	20.0	-----	6.0	3.2	3.7	3.2	3.3	-----	-----	44.3	2.5	0.7
April-May	39.8	46.4	15.7	61.7	25.8	21.7	45.5	21.8	20.0	37.4	14.5	20.1	6.7	5.0	1.7	32.9	15.8	4.2
June-July	7.8	21.7	16.7	4.2	21.7	21.7	10.0	21.7	21.7	17.3	8.9	7.3	5.0	15.0	10.0	1.7	7.0	7.0
August-September	8.7	34.0	29.3	8.0	34.0	49.0	1.4	2.9	24.3	7.3	12.0	6.7	10.0	2.0	8.0	-----	6.6	5.3
October-November	24.2	42.5	39.2	23.8	17.5	30.0	40.0	11.3	20.0	7.5	10.8	27.5	17.5	5.0	10.0	6.9	14.4	10.0
December-January	81.7	34.2	32.5	613.8	23.8	13.8	165.0	23.8	36.3	26.7	14.2	20.8	27.5	2.5	2.5	4.0	6.5	2.5
1961																		
February-March	55.0	50.0	48.3	277.5	46.3	27.5	227.5	11.3	22.5	14.2	10.8	10.0	15.0	2.5	-----	10.5	2.0	6.5
Average	36.6	33.2	20.9	167.4	26.1	21.7	67.8	12.6	23.5	14.2	12.2	15.3	11.6	3.7	4.1	15.1	6.9	4.6

be heightened by the close proximity of highly saline water in the channel.

The effect of the Gulf outlet channel on the salinity in Lakes Pontchartrain and Borgne has been studied in a large model at the Waterways Experiment Station, Vicksburg, Miss. The fishery aspects of these experiments have been reported upon by the Bureau of Sport Fisheries and Wildlife.³

This report shows that salt-water intrusion in the Gulf outlet channel will be severe. With the outlets to Lake Pontchartrain partially closed by hurricane protection structures but with no control in the Gulf outlet channel the model indicates (their figure 3) a rise in Lake Pontchartrain salinity of about 4.3‰ in years of high fresh-water inflow and about 5.5‰ for years of low inflow. The model indicates that this condition can be considerably corrected by placing control structures in the Gulf outlet channel where it intersects the Industrial Canal.

Heightened salinities in Lake Pontchartrain will in turn raise salinities in Lake Borgne by 1‰ to 2‰. However, the marsh lying between Lake Borgne and the channel instead of being dominated by Lake Borgne will now have direct and easy access to the waters of the Gulf. Thus the model studies indicate that under the best conditions of control of channel flow into Lake Pontchartrain (lowest salinities occurred in the model when channel flow was 60 percent of capacity) the salinity in the channel at a point close to station BWA was about 12‰ at a depth of 6 feet and about 26‰ at a depth of 12 feet.

Obviously, this marsh area (1 and 3) with a preproject salinity of about 2‰ to 5‰ is due for a pronounced rise in salinity.

The portions of the project area lying south of the channel will also experience a rise in salinity. Before the project, water from Lake Borgne and from Breton Sound was exchanged through the bayou systems resulting in the long-term salinity gradients shown in figure 5. With the project completed, water from Lake Borgne can reach this southerly portion of the project area only by crossing the wide channel at the few intersection points. Obviously, the future exchange of Lake Borgne water with the water south of the channel

will be very limited, and it will be mixed with channel water. Therefore, the areas southwest of the channel may be expected to experience a rise in salinity to a level higher than the portions of the project area between the channel and Lake Borgne.

Since the channel extends entirely across Breton Sound into the open Gulf the channel may have some elevating effect on the salinities in Breton Sound itself.

It is too soon to predict the final salinity changes engendered by the project, but it would appear that salinities in the project area with the optimum control of exchange at the northern end of the Gulf outlet channel will rise about 2‰ in Lake Borgne and at least 5 or more parts per thousand in the remainder of the project area.

The effect on the vertebrate fauna of such a rise in salinity will not necessarily be drastic. The principal species of fish in the area are obviously euryhaline, and of the remaining species, the majority are more adapted to higher than to lower salinities.

The brown shrimp shows no obvious salinity preference. The salinity preference of the white shrimp is somewhat obscured by the fact that the smaller juveniles apparently avoid the more open waters in favor of the shoal, protected marshes. On the whole the white shrimp may suffer some loss of what has been desirable nursery area, especially where the salinity rises appreciably above the 14‰ isohaline now separating areas 6 and 7.

The younger stages of the blue crab are now most abundant in the least saline waters (area 1), decreasing progressively and significantly as salinity increases toward area 3. Both young and adult crabs are scarce in areas 6 to 8. A rise in salinity should have an adverse effect on the abundance of crabs.

It is highly probable that a general rise in salinity will seriously affect the growing of oysters. Oyster beds, especially those used for collecting seed oysters, can be extensively harmed by only a slight rise in salinity, especially if it occurs when the salinity is at the borderline between suitability and unsuitability for oyster drills. Conversely, a rise in salinity may make some areas suitable for oyster growing where previously the average salinities have been consistently too low for successful oyster culture.

³ A detailed report on Hurricane Study Area No. 1: Lake Pontchartrain and vicinity, Louisiana. 32 p., 1 map, 9 figs., processed (issued in 1962 by Region 4, Bureau of Sport Fisheries and Wildlife, Atlanta).

The idea that a possible benefit could offset damage to existing oyster beds is highly speculative.

In evaluating losses attributable to the project one must consider the value of the areas occupied by the channel and the resulting spoil. The Branch of River Basin Studies of the Bureau of Sport Fisheries and Wildlife has furnished careful measurements of these areas:

Acres occupied by the project

Original state	Channel	Spoil areas	Total
Open water.....	1,680	4,518	6,198
Marsh.....	4,868	12,540	17,408
Total.....	6,548	17,058	23,606

The above tabulation of project area between the Intracoastal Waterway and Breton Sound shows that it occupies 23,606 acres or 36.9 square miles. The portion originally designated as marsh includes such shallow marginal areas as are occupied by emergent vegetation. Much of the remainder of the marsh is under water during extreme tides, which occur especially during late summer. Thus, in addition to the 6,198 acres of open water a fair portion of the 17,408 acres of marsh must be considered as nursery area for shrimp, crabs, and juvenile fishes.

Since the channel itself will be open water (6,548 acres), there will be little change in the total surface of open water. However, the pre-project open water consists of many shallow winding bayous that provide a very long shoreline adjacent to emergent vegetation—an ideal nursery area. The postproject open water is a deep channel along which the greatly reduced shoreline will be subjected to the constant wash of passing traffic. The shallow portions of the “marsh” areas bordering the bayous will be totally lost in the spoil areas.

The above losses of nursery habitat are permanent and irreplaceable.

It should be borne in mind that the effect of the project on the remainder of the area is not merely a narrowing of the coastwise belt of low salinity water. Such a situation would merely push the belt of marsh suitable for juvenile fauna farther inland. Instead, the channel carries saline water far inland so that Lake Pontchartrain will have higher salinity than Lake Borgne. Thus, fauna seeking to remain in the same salinity now prevailing in a large portion of the project area have lost the former bordering area of low salinity to which they could retreat.

This report is concerned wholly with the effect of the Gulf outlet channel on the commercial fisheries of the project area. The effects of salinity changes on the vegetation and directly or indirectly on waterfowl and furbearers is not touched upon.

LITERATURE CITED

- DARNELL, REZNEAT M.
1959. Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. Transactions of the American Fisheries Society, vol. 88, No. 4, p. 194-304.
- FIEDLER, R. H.
1930. Solving the question of crab migrations. Fishing Gazette, vol. 47, No. 6, p. 18-21.
- MARVIN, KENNETH T., ZOULA P. ZEIN-ELDIN, BILLIE Z. MAY, AND LARENCE M. LANSFORD.
1960. Chemical analyses of marine and estuarine waters used by the Galveston Biological Laboratory. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 349, 14 p.
- PEARSON, JOHN C.
1948. Fluctuations in the abundance of the blue crab in Chesapeake Bay. U.S. Fish and Wildlife Service, Research Report 14, 26 p.
- SANDOZ, MILDRED, AND ROSALIE ROGERS.
1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab, *Callinectes sapidus*, Rathbun. Journal of Ecology, vol. 25, No. 2, p. 216-228.

A MORPHOMETRIC STUDY OF YELLOWFIN TUNA *THUNNUS ALBACARES* (BONNATERRE)

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ABSTRACT

Morphometric measurements were compared for 4,180 yellowfin tuna from 28 locations in the Pacific Ocean; from off Angola, Africa, in the Atlantic Ocean; and from off Somaliland, Africa, in the Indian Ocean. The measurements used were head length; pectoral fin length; heights of second dorsal and anal fins; distances from snout to insertion of first dorsal fin, to second dorsal fin, anal fin, and ventral fin; distance from insertion of ventral to anterior edge of vent; and greatest body depth. Each measurement was related to fork length by regression analysis, and each relationship was considered a character. Curvilinear regression due to allometric growth was controlled by transforming some data to logarithms and by separating all samples into small, medium, and large size groups (less than 80, 80-120, and greater than 120 cm. fork lengths). Mean character sizes were determined for each sample at lengths of 65, 100, and 140 cm.

A comparison of mean character sizes revealed a cline in most characters from samples taken along the Pacific Equator between the vicinity of Costa Rica and the Caroline Islands. Yellowfin from the eastern Pacific have larger heads and greater distances from snout to insertion of first dorsal, second dorsal, ventral, and anal

fins; a greater distance from insertion of ventral fins to insertion of anal fin; and a greater body depth. On the other hand, they have shorter pectoral fins and much shorter anal and second dorsal fins. The samples from the more temperate parts of the Pacific and from off the coasts of Africa differed little from some part of this cline.

A multiple character comparison of overlap among samples from near the Pacific Equator showed less than 50-percent overlap between samples separated by 1,500 miles, less than 25-percent overlap between samples separated by 3,000 miles, and less than 6-percent overlap between samples separated by 6,000 miles. The possibility of long intermigrations among the equatorial stocks seems remote.

The full variation in length of the pectoral fin and heights of second dorsal and anal fins, which most authors have used to separate the species of yellowfin, occurs within the cline along the Pacific Equator. This occurrence, plus the continuous circumtropical high seas distribution of the yellowfin, indicates a single worldwide species. The appropriate name is *Thunnus albacares* (Bonnaterre) 1788.

A problem of immediate concern to us in investigation of the tuna fisheries of the Pacific is to determine the degree of intermingling of the tuna populations. Intermingling matters because tunas are being sought in different parts of the ocean by fishermen who are asking whether the catch by one nation in one area is affecting the population of tunas and catch by another nation in another area. In other words, do these tunas migrate thousands of miles, as do some of our migratory birds, or are they relatively localized, hatching, maturing, and

dying within an area of a few hundred miles? A closely related matter of secondary concern is to distinguish the species and subspecies of each kind of tuna in the oceans of the world.

Among the tuna fisheries of the Pacific, those for the yellowfin (*Thunnus albacares*)¹ are the most

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¹ The Pacific yellowfin tuna has been named *Neothunnus macropterus* (Temminck and Schlegel) by recent authors. I consider the yellowfin to be a single worldwide species, which I choose to call *Thunnus albacares* (see page 428).

important. The yellowfin is a major fishery resource from California to Chile and from Japan to Indonesia, especially near the Caroline Islands. Smaller fisheries also exist off Hawaii, Australia, and many of the islands of the central Pacific. In addition, exploration by the Bureau of Commercial Fisheries Pacific Oceanic Fishery Investigations (POFI)² in the central Pacific revealed major concentrations of yellowfin along the Equator from longitude 110° W. to 180°. These stocks were fished repeatedly by research vessels and subsidized commercial vessels between 1950 and 1955. The methods and results have been summarized by Sette (1954) and detailed by Murphy and Shomura (1953a, 1953b, and 1955) and Shomura and Murphy (1955). Since 1955 these populations have been fished with increasing intensity by Japanese commercial concerns.

One approach to the general problem of relations among Pacific tuna stocks has been through morphometric studies. Workers have included Schaefer (1948), who described the morphometric characteristics and relative growth of yellowfin off central America; Godsil (1948), who made a preliminary population study of yellowfin and albacore, *Germon alalunga* (Bonnaterre); Schaefer and Walford (1950), who compared yellowfin from off Angola, Africa, and the Pacific coast of Central America; Schaefer (1952), who compared yellowfin from the Hawaiian Islands with those from the Pacific coast of Central America; Royce (1953), who compared numerous groups of Pacific yellowfin; Tsuruta (1954), who compared yellowfin from the Gilbert Islands with those from Hawaii; and Schaefer (1955), who further compared yellowfin tuna from Central America and Hawaii with those of southeastern Polynesia.

A different technique, which may provide direct evidence of intermingling, has been applied by the California Department of Fish and Game, Marine Fisheries Branch, and used subsequently by other groups. Yellowfin, albacore, and skipjack, *Katsuwonus pelamis* (Linnaeus), have been tagged with plastic tags, as reported by Wilson (1953), and have already shown some remarkable migrations. One albacore released 18 miles south of Los Angeles, California, was recovered nearly 1 year later about 5,000 miles distant at latitude 31°30' N., longitude 149°40' E., off the coast of

² Now the Biological Laboratory of the Bureau of Commercial Fisheries, Honolulu, Hawaii.

Japan (Ganssle and Clemens, 1953) and two other albacore, tagged near Guadalupe Island, were recovered about 6 months later in the vicinity of Midway Island (Blunt, 1954). Yellowfin also were tagged off the Line Islands from March 1955 to February 1956 (Iversen and Yoshida, 1957). Of the 1,056 that were released, 2 were recaptured locally and 1 was recovered 800 miles east of the point of release after being at liberty 13 months. But these tag returns are as yet too few to provide good evidence of the extent of intermingling or of any different migratory behavior of the several species.

Much interest in these problems of intermingling of tuna populations has been expressed at various meetings of the Indo-Pacific Fisheries Council, and the collection of data has been a matter of major concern to its Tuna Subcommittee. Through this organization the aid of numerous people in the Indo-Pacific area has been enlisted in the collection of data, which have been used in this report. This interest has also been expressed by some independent studies along the same lines in other countries, particularly in Japan by Tsuruta (1954) and in Australia where morphometric studies are underway.

STATISTICAL COMPARISON OF MORPHOLOGICAL DATA

The following section is a summary of a general review of the problem involved in statistical comparisons of morphological data previously made by Royce (1957).

In all morphometric studies of yellowfin tuna the authors have used essentially the same methods. All have used measurements of body parts, especially lengths and heights of the fins and distances from the snout to insertion of the fins, as principal characters. All have used regression analysis to relate part size to fork length and then have compared samples by covariance analysis. All have found much larger differences between samples than would be expected from chance variations, and from such differences there has been a tendency to conclude that the populations were distinct.

But this method of analysis is not wholly satisfactory. It provides a test of whether a difference is significant, but this conclusion may be trivial, because significant differences can be found commonly between even the most closely related

natural populations (Mayr, Linsley, and Usinger, 1953: 151). It does not show how great the differences are in terms that can readily be compared. It does not provide evidence of clines or character gradients, which are to be expected in tuna populations because of their continuous distribution and which are useful indicators of relations of the populations. Neither do the methods in current use provide information on the key problem of the amount of intermingling.

Use of regression analysis to relate size of body parts to fork length does provide basic data needed for finding clines according to the method described by Hubbs and Hubbs (1953). The regression statistics provide the mean character size estimated for a fixed length of fish; the measure of dispersion about the mean, which is the standard deviation from regression; and the measure of reliability, which is the standard error of the estimated mean. I showed that clines exist among yellowfin tuna populations (Royce, 1953), but I did not use the method of Hubbs and Hubbs nor employ sufficiently precise methods of regression analysis. In this paper I will use more refined methods of regression analysis and try to show fully the nature of the clines.

The problem of intermingling will be approached through an extension of the concept of overlap, which has been applied to comparison of natural populations by many taxonomists. The methods in current use have been summarized by Mayr, Linsley, and Usinger (1953: 142). They have indicated overlap between populations by a coefficient of difference (CD), which is computed according to the formula—

$$CD = \frac{\bar{x}_1 - \bar{x}_2}{s_1 + s_2}$$

The overlap is the difference between means \bar{x}_1 divided by the sum of standard deviations s_1 of the two populations. I prefer to change this formula slightly to—

$$D = \frac{\bar{x}_1 - \bar{x}_2}{s}$$

in which s is the within-sample standard deviation computed from the pooled variance, and D is the distance between the means in the standard measure of statistics, i.e., in units of the standard deviation. It is obvious that $CD \approx \frac{D}{2}$.

The concept of overlap of two frequency distributions is shown graphically (1A and 2A) in figure 1. The mutual area (1B and 2B) of

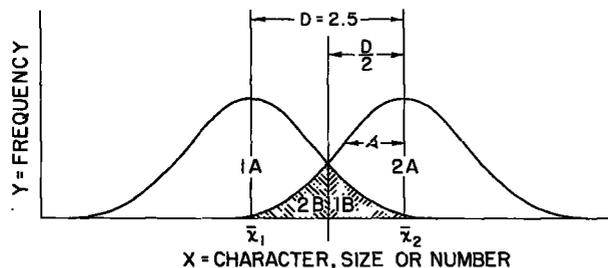


FIGURE 1.—Overlap of normal distributions. 1A and 2A indicate normal populations which overlap in the shaded areas 1B and 2B; s indicates one standard deviation, \bar{x}_1 and \bar{x}_2 indicate means; D is the distance between means in units of the standard deviation.

the two curves is shaded; one-half of the shaded area, or tail of one distribution, which I designate as p , may be determined readily from a table of the probability integral, such as table 2 in Pearson (1948). The table is entered with the value of

$\frac{D}{2}$. The value of p represents the probability

of misclassifying the individuals on the basis of the character used. When the two means are identical and the chances of making a proper choice are equal, p will range from 0.5 to essentially zero when the two curves are widely separated, and for all practical purposes there is no overlap. However, the value p , while indicative of overlap, is not fully satisfactory because it approaches a maximum of 0.5 and because it must be considered properly as a probability of misclassification rather than a measure of the mutual area of the frequency curves.

A more satisfactory measure of overlap may be obtained if one considers the area of one frequency curve and within it the proportion ($2p$) that might belong to another specified frequency curve. I have designated this by $\Omega = 200 p$, expressed as a percentage. It is a measure of overlap which will be 100 percent when the curves have the same mean and will approach zero as the means become widely separated.

The particular usefulness of Ω is in the concept that it is an estimate of the proportion of one sample with the characteristics of another. If the samples are representative of populations in

a specific time and place, it follows that Ω is that proportion which might have come from another population, and thus the value of the overlap indicates a maximum for the amount of intermingling. The overlap Ω does not show that intermingling has occurred, and when large it merely shows that a large amount of intermingling may have occurred. Whether intermingling did occur must be determined by other means. When Ω is small, however, and we can establish that the characters used do not change during migration, we may then be able to establish that no significant intermingling occurs.

The most satisfactory measure of overlap is obtained from several characters simultaneously, which requires a substantial extension of the computations. The measure in current use by most taxonomists has been applied merely to comparisons of single counted characters. I have shown (Royce, 1957) that it may be applied readily to single measured characters through substitution of the regression statistics. The much greater extension to multiple characters is based on D as already defined. The use of D as a distance between populations has been generalized for multiple characters by Mahalanobis (1936). In his generalization, each additional character adds to D only to the extent that it is not correlated with previously considered characters. Thus, all arbitrary combinations of characters as ratios or indices are avoided. Rao (1947, 1952) pointed out that D satisfies two fundamental postulates of distance: (1) the distance between two groups is not less than zero; (2) the sum of distances from one group to two other groups is not less than the distance between the two other groups (triangle law of distance). The further empirical requirement that the distance must not decrease when additional characters are considered is also satisfied.

AVAILABLE DATA

There were available for this study 28 samples of yellowfin from the Pacific Ocean, 1 from the Atlantic Ocean off Angola, Africa, 1 from the Indian Ocean off Somaliland in northeast Africa, and 1 of only 3 specimens from off Ceylon.³ The data include the measurements of yellowfin

³ This sample was compared with the Pacific samples by Royce (1953) and found to be most like the Phoenix Islands sample. It will not be further considered here.

from off the American coast published by Godsil (1948), whose 13 samples have been combined into 6; those from off Costa Rica by Schaefer (1948); from Angola by Schaefer and Walford (1950); from Fiji, Palmyra, and Hawaii by Godsil and Greenwood (1951); from Hawaii by Schaefer (1952); and those from the Gilbert Islands by Tsuruta (1954). The original measurements of most of the remaining samples were published by Dung and Royce (1953). The remainder, a sample from the Pacific Equator near longitude 110° W. and another from northeast Africa, are listed in appendix tables 1 and 2.

The geographic distribution of Pacific samples is shown in figure 2. There is an excellent series from about 8,000 miles along the Pacific Equator between the American coast and the central Caroline Islands. In addition, there are samples from the South Pacific off the Fiji and Society Islands, and from the North Pacific off the Philippines, Japan, Bikini Island, Hawaii, Mexico, and Guatemala. All major areas of the Pacific where yellowfin are known to occur are included except the South American coast and the southwest Pacific from Australia to the coast of Asia.

It was necessary to omit four samples from the Pacific. Those from the western Marshall, western Caroline, and Fiji Islands have not been further considered, because they contain less than 20 fish, the number I arbitrarily established as the minimum. In another sample from near the Gilbert Islands, reported by Tsuruta (1954), measurements of one specimen are questionable (No. 2 in his table 1), and I have been unable to verify the computations shown in his table 2. Fairly large discrepancies occur in the regression statistics, apparently because enough digits were not carried during the computations. This sample was obtained on only 3 days from a limited area. For these reasons I have not further considered it.

Certain basic statistics about the samples will be needed repeatedly in the ensuing discussion and are presented here. The length distribution of all samples is shown in table 1. Pertinent data on how the samples finally used were collected are shown in table 2. The sums, sums of squares, and sums of products for all characters of all samples which have not been published are given in appendix table 3. Included, also, are the means, regression constants, and estimated character sizes at certain lengths for all samples.

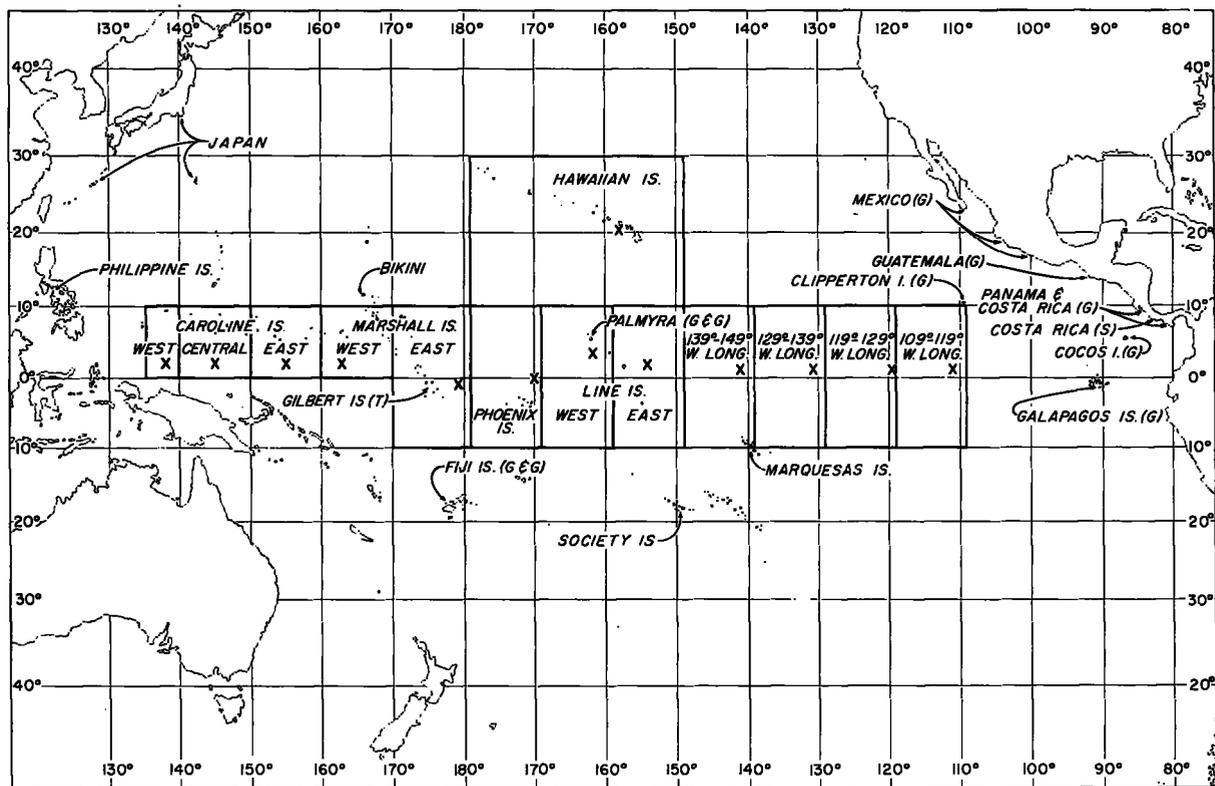


FIGURE 2.—Geographic distribution of Pacific samples of yellowfin tuna. (X indicates approximate center of distribution of fish comprising each sample from Hawaii and the equatorial area. (G) indicates Godsil, 1948; (G & G) Godsil and Greenwood, 1951; (S) Schaefer, 1952; (T) Tsuruta, 1954.)

MORPHOLOGICAL CHARACTERS USED

The morphological characters I have used in this study were selected through precedent and experience. The precedent was established by several workers who attempted thorough morphometric studies. None of the recent workers (Schaefer, 1948; Godsil, 1948; or Schaefer and Walford, 1950) explained how they selected their characters, but undoubtedly they were guided by previous research reported in the literature in which yellowfin tuna had been differentiated largely on the basis of fin length. Godsil (1948) defined 16 measurements but presented data on only 6: fork length; head length; and distances from the snout to insertion of first dorsal, second dorsal, anal, and ventral fins. He states that he investigated counts but discarded them because they were unsatisfactory. Schaefer (1948) used five of these measurements (he did not measure snout to insertion of ventral fin). He added the greatest body depth; length or height of the pectoral, second dorsal, and anal fins; longest dorsal

finlet and dorsal ray; distance from pectoral fin insertion to insertion of first dorsal fin; length of the base of first dorsal fin; diameter of iris; and length of maxillary. In addition, he obtained four counts: number of dorsal fin rays (including spines if any), dorsal finlets, anal finlets, and gill rakers.

Schaefer and Walford (1950), for part of the specimens measured off Angola, Africa, used the same measurements as Schaefer (1948), but added spread of caudal fin, length of first dorsal spine, least depth of caudal peduncle, greatest width of caudal peduncle at keels, and snout to insertion of ventral fins. They also obtained the same four counts and recorded the sex of some of the fish. Subsequently, this list of measurements was markedly reduced by Schaefer (while he was directing the morphometric program at POFI) to fork length; head length; snout to insertion of first dorsal, second dorsal, anal, and ventral fins; length or height of pectoral, second dorsal, and anal fins; greatest body depth; and diameter of the

TABLE 1.—Number of tuna measured, by size interval and place of collection

Area	Number of fish in fork length (cm.) interval of—														Total	
	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9	90-99.9	100-109.9	110-119.9	120-129.9	130-139.9	140-149.9	150-159.9	160-169.9		170-179.9
Mexico ¹			52	143	155	8	3									361
Guatemala ¹			49	54	16	1										120
Panama and Costa Rica ¹		1	29	283	282	36	43	43	48	20	3					887
Costa Rica ²			8	7	3	6	11	6	6	2		2	1			46
Cocos Island ¹		6	8	36	128	80	28	2		4	10	5	4			311
Galapagos Island ¹			97	14	9	65	9									194
Clipperton Island ¹			1	21	7	4	2	1	2							38
109°-119° W.....					1	2		1	2	3		7	5	6		27
119°-129° W.....										3	10	16	14	4		47
129°-139° W.....				1	1		1			5	5	12	10	11		46
139°-149° W.....										4	25	29	33	20	2	113
East Line Islands.....					4	4	8	16	5	12	35	48	52	10		195
West Line Islands.....		1	5	16	22	28	22	19	17	11	21	18	7	1		188
Palmyra Island ²			1	10	24	18	27	10	2	1		1				94
Phoenix Islands.....			4	19	14	16	19	9	15	15	21	7	2	1		142
East Marshall Islands.....										2	6	16	16			40
Gilbert Islands ³										2	3	13	14	1		33
West Marshall Islands.....	2	2	7	1									4	2		18
Bikini Island.....			21	6	4	5	4	3	1							44
East Caroline Islands.....		1	18	23	18	19	16	6	14	12	21	9	13	1		171
Central Caroline Islands.....		1	6	11	19	21	21	33	27	33	24	13	2			211
West Caroline Islands.....				2	1	1	3		2	7	1					17
Philippines (SW. Panay).....		1	58	131	62	47	19	9	6	15	11	5	2			356
Japan.....		11	6	6	7	8	6	1								46
Hawaii ²		16	15	3	2	4	9	15	6	17	29	22	15	32	18	203
Hawaii ³			42	5		11			1		7	11	1	1		70
Society Islands.....		2	15	3	2	7	1					2				32
Fiji Islands ³			1	2		3	1	6								13
Northeast Africa.....				5	12	30	1									48
Angola, Africa ⁴		1			11	11	1		9	8	9	6	2	2		60
Total.....	3	43	537	793	804	435	253	181	167	181	261	243	168	91	20	4,180

¹ Godsil (1948). ² Schaefer (1952). ³ Godsil and Greenwood (1951). ⁴ Schaefer and Walford (1950). ⁵ Tsuruta (1954).

iris. But another measurement was added—the distance from insertion of the ventral fins to the anterior edge of the vent.

This reduction was undertaken without conclusive evidence that the omitted characters were less satisfactory than those retained; but some reduction was clearly necessary in order to have a manageable number of characters, and we think that the selection was good. The characters retained are, in general, external measurements that differentiate several species of tuna closely related to the yellowfin. Of special importance are length of the pectoral fin, length of the anal and second dorsal fins, and the general body proportions, which are reflected by length of the head and distance to the insertions of several fins. It is reasonable to assume that if these characters have differentiated during evolution of these other tuna species, they may well be differentiating in the evolution of the yellowfin group.

Some characters were excluded because they were troublesome to measure or count. For example, the counting of dorsal and anal finlets is complicated occasionally by the apparent absence of a finlet in the midst of the series. Sometimes it is obvious that a finlet has been torn off, at other times it is uncertain whether there had been

a finlet in the space. The diameter of the iris has been omitted because of confusion among our workers between measuring the diameter of the iris and that of the eye. When plotted, these measurements seemed to fall into two groups and we found that measurements had been taken in different ways. We also have not used the gill raker counts, even though we obtained considerable numbers of them, because of uncertainty that our numerous field people were counting gill rakers in the same way. The difficulty is that gill rakers become progressively smaller on one side of the gill arch until covered by skin and, in any gross examination such as must be made in the field, it is always necessary to decide whether certain gill rakers are big enough to be counted. In addition, the number of gill rakers is not entirely independent of length of the fish. In one long series of counts made with great care in the laboratory on yellowfin from a single area, we found a statistically significant association between number of gill rakers and length of the fish.

Thus, the selection of characters has obviously been haphazard and I cannot claim to have selected the best ones. I can say only that they are the principal external characters which have served to differentiate the species of tunas and they

TABLE 2.—Characteristics of yellowfin tuna morphometric samples

[Size groups: S, < 80 cm., M, 80-120 cm., and L, > 120 cm.]

Area and size group	Number	Mean fork length (cm.)	Sampling effort				Numbers of fish by gear ¹			Remarks
			Years	Months	Days	Examiners	Long-line	Pole and line	Troll	
Mexico: 2 S.....	361	68.46	2	2	5	1				(2)
Guatemala: 2 S.....	120	62.26	1	1	2	1				
Panama and Costa Rica: 2										
S.....	887	75.19	3	5	?	1			887	
M.....										
Costa Rica: 2 M.....	29	99.88	1	6	?	4			29	
Cocos Island: 2										
S.....	311	82.16	2	2	<6	1			311	
M.....										
L.....										
Galapagos Island: 2 S.....	194	68.32	1	1	?	1			194	
Clipperton Island: 2 S.....	38	73.89	1	1	3	1			38	
109°-119° W.: L.....	21	149.82	1	1	5	4	2	21		
119°-129° W.: L.....	47	146.72	1	4	12	4		46		
129°-139° W.: L.....	47	144.67	1	3	15	5		45		2
139°-149° W.: L.....	113	148.73	1	3	23	6		109		1
East Line Islands:										
M.....	33	102.51	3	8	13	9	17		16	From catches of POFI vessels.
L.....	157	145.35	4	9	36	9	149		3	
West Line Islands:										
S.....	44	68.68	4	9	28	9	1		7	From catches of POFI vessels.
M.....	87	97.76	4	8	31	9	7		8	
L.....	58	138.13	4	8	23	8	46		1	
Palmyra Island: 4										
S.....	35	72.49	1	1	Ca.	1				All fishing done close to Palmyra, Fanning and Christmas Islands.
M.....	57	94.38	1	1	12	1				
Phoenix Islands:										
S.....	37	67.67	3	5	16	5	1	9	27	From catches of POFI vessels.
M.....	59	98.23	2	6	24	7		16	42	
L.....	46	133.53	3	6	26	7	19	13	9	
East Marshall Islands: L.....	40	136.34	1	1	8	3	32			
Bikini Island: S.....	31	59.03	1	2	?	1			31	Measured by J. C. Marr.
East Caroline Islands:										
S.....	60	65.27	2	6	24	4	59	1		Obtained by POFI observers on Japanese mothership expeditions.
M.....	55	98.26	2	4	20	4	55			
L.....	56	139.95	2	5	21	4	56			
Central Caroline Islands:										
S.....	37	67.94	1	3	17	4	36	1		Contributed by D. V. Villadolid, Philippine Bureau of Fisheries.
M.....	102	100.88	1	3	22	4	102			
L.....	72	132.29	2	4	17	4	72			
Philippines:										
S.....	242	65.19								Measured by POFI observers in Japan.
M.....	81	90.74								
L.....	33	132.99								
Japan: S.....	31	57.73	1	2	7	1	1	28		
Hawaii:										
S.....	36	52.35	2	7	17	4		19	5	From POFI catches and Honolulu fish market.
M.....	34	101.95	1	7	21	4	15	15	2	
L.....	133	150.04	1	7	77	4	129	1		
Hawaii: 5										
S.....	47	57.01	1			1				From near Johnston Island and near islands northwest of Kauai.
L.....	20	142.96	1			1				
Society Islands: S.....	22	57.30	1			4		22		From Honolulu market.
Northeast Africa: S.....	48	79.15	1	2	9	1				From frozen fish landed in Honolulu. Courtesy of FAO, measured by A. Fraser-Brunner.
Angola, Africa: 4										
M.....	21	97.64	1	1	4	1				
L.....	27	137.67	1	1	4	1				

¹ A few specimens lacked record of gear used. ² Statistics based on curvilinear regressions, Godsil (1948). Additional information from correspondence.³ Schaefer (1952). ⁴ More than half of samples measured by one person. ⁵ Godsil and Greenwood (1951). ⁶ Schaefer and Walford (1950).

appear to be the most variable ones within the yellowfin group that can be measured with precision and consistency by different people.

METHODS OF MEASUREMENT

Our methods of measuring tuna follow the specifications given by Marr and Schaefer (1949). I think we have measured the fish exactly as they intended, but we slightly modified their definitions to overcome some confusion existing among our measurers. The most recent instructions given POFI workers have been as follows:

The measurements described are all made in millimeters with calipers or dividers, depending on the size of the fish and the distance to be measured. All distances are straight lines. The tip of the fixed arm of the calipers (or one point of the dividers) is applied to the first point mentioned and the tip of the sliding arm of the calipers (or the other point of the dividers) is applied to the second point mentioned. Where a choice of sides is involved, all measurements and counts are made on the left side of the fish. Fin insertions are to

be determined while holding the fin approximately perpendicular to the contour of the fish.

Fork length.—(Total length of Marr, Schaefer, and Godsil.) The distance from the tip of the snout (most anterior point on upper jaw), with jaws closed, to the cartilaginous median part of the caudal fork (seating the sliding arm of the caliper firmly and thus depressing the small fleshy flap extending posteriorly).

Head length.—Distance from the tip of the snout to the most posterior point on the margin of the subopercle (depressing the fleshy flap extending posteriorly).

Snout to insertion of first dorsal fin.—The distance from the tip of the snout to the insertion of the first dorsal. The insertion of the first dorsal is the intersection of the anterior margin of the first dorsal spine, when the fin is held erect, with the contour of the back. This point is identical with the most anterior point of the first dorsal fin slot.

Snout to insertion of second dorsal fin.—The distance from the tip of the snout to insertion of the second dorsal. The insertion of the second dorsal is not so clearly defined as the insertion of the first dorsal, particularly on larger fish; but it is the intersection of the anterior margin of the second dorsal with the contour of the back when the fin is held erect. When the second dorsal is raised, the determined point should be marked with thumbnail or scalpel.

Snout to insertion of anal fin.—The distance from the tip of the snout to the insertion of the anal fin. The insertion of the anal fin is determined in the same manner as the insertion of the second dorsal.

Snout to insertion of ventral fin.—The distance from the tip of the snout to the insertion of the ventral. The insertion of the ventral is the intersection of the anterior margin of the ventral, when the fin is extended, with the contour of the body.

Insertion of ventral fins to anterior edge of vent.—The midline distance from the insertion of the ventrals to the anterior edge of the vent.

Greatest body depth.—The greatest distance between the dorsal and ventral contours perpendicular to the axis of the fish. The measurement is taken from the dorsal body contour to the ventral body contour, with the first dorsal fin depressed in its slot. It is oriented by reference

to the dorsal spine, the insertion of which is at or nearest to the upper end of the vertical. Dorsal spines are counted posteriorly, the most anterior spine being the first.

Length of pectoral fin.—The distance from the anterior end of the fin slot to the most posterior point, taken with the pectoral fin extended posteriorly and opposed to the side.

Height (length) of second dorsal fin.—The distance from the insertion of the second dorsal fin to its distal end, with the fin in a normal position. Note that this fin is often extended in a long filament, especially in large *Neothunnus*, and care should be taken to notice if this extension is frayed.

Height (length) of anal fin.—The distance from the insertion of the anal fin to its distal end, with the fin in a normal position. Remarks under height of second dorsal fin apply here.

Diameter of iris.—The greatest diameter measured to the margin of the yellow iris and the adjoining black tissue. This is generally not a line parallel to the median line of the body.

Number of gill rakers.—The number of anterior rakers on the most anterior gill arch on the left side of the fish (some species also have posterior rakers on this same arch). The counts of the rakers on the two arms of the arch are kept separate. For example, 10+20=30 gill rakers with 10 on the upper arm and 20 on the lower. The counts include all rakers that project above the surrounding epithelium. We have encountered no difficulty in assigning rakers near the angle of the arch to one arm or the other.

Sex.—Determined by inspection. Very immature males and females may be difficult to distinguish. Ovaries, which are tubular, may often roll between the fingers, while testes, which are solid, will turn over. The testes of ripening or ripe males are enlarged, solid, white bodies, not round in cross section. The ovaries of ripening or ripe females are enlarged, turgid, pink or yellow-orange bodies, round in cross section. Ova may often be distinguishable with the naked eye. The testes of spawned-out males are less turgid, tougher, and pinker than those not spawned, and are difficult or impossible to distinguish from maturing testes in early stages. The ovaries of spawned-out females are hollow, more or less flabby, saclike tubes.

Weight.—Should be determined in pounds on steelyards of proper range. Do not weigh on

steelyard having capacity greater than about three times the weight. Be sure to subtract the weight of any hooks used to hold the fish. Record weight to smallest unit on steelyard. Note if fish is weighed in pieces.

IMPORTANT

Check steelyards before each cruise. Errors must not exceed 1 percent.

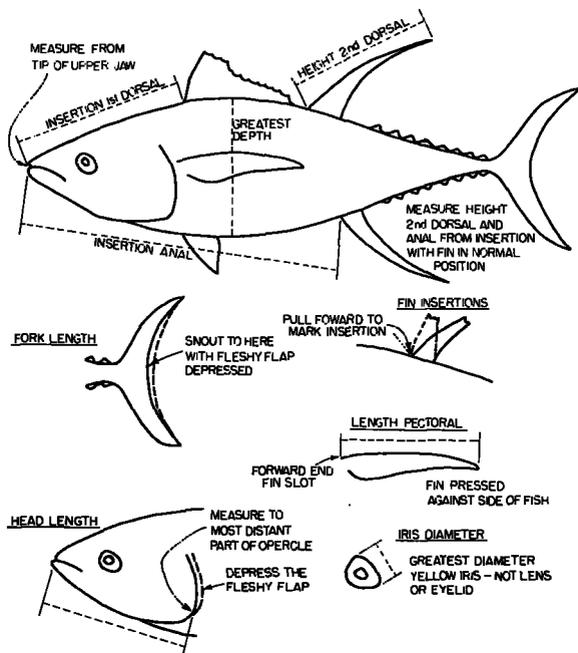
Check calipers each time they are used. Errors must not exceed 1 mm.

In addition to these instructions, diagrams were provided on the back of each field sheet (fig. 3).

All measurements of distances exceeding about 55 mm. have been obtained with sliding calipers. This lower limit occurs because some of our calipers will not measure closer than that and hence the shorter distances have been measured with dividers and millimeter rule. All measurements are the actual distance between two points and not the distance parallel to the midline of the body and between perpendiculars as specified by LeGall (1951) for body measurements of European tunas.

Our calipers have usually been of two sizes, 1 m. and 2 m. They evolved through brass and aluminum to standard wooden meter sticks.

DIAGRAMS SHOWING CERTAIN MORPHOMETRIC MEASUREMENTS OF TUNA



MAKE ALL MEASUREMENTS WITH CALIPERS OR DIVIDERS WHILE FISH IS LYING ON ITS RIGHT SIDE

FIGURE 3.—Diagrams on the back of the field data sheet showing certain morphometric measurements of tuna.

YELLOWFIN TUNA

The 1-m. caliper consisted simply of a fixed jaw and a slider on a standard meter stick. If the meter sticks are selected with care to get straight ones, we find it easy to maintain the accuracy within 1 mm. by checking the caliper prior to each use. (We found this checking equally essential with the metal calipers because of the ease with which they can be bent.) For the 2-m. calipers we put two meter sticks end to end in a sheet aluminum channel. The channel was made slightly longer than the two meter sticks to permit a third meter stick with a movable jaw to be inserted when we were measuring large sharks or marlins more than 2 m. long.

Almost all of our measurements were obtained in the field and usually on shipboard. In equatorial areas on POFI vessels it was customary to measure up to about 10 tuna of all species during the course of a day's fishing. During longline fishing operations, which were usually carried out along a line of stations, this ensured that the sample included tunas from a wide-spread area. On the Japanese mothership expeditions in the Caroline Islands area, POFI observers measured fish on the deck of the mothership a few days after capture by catcher vessels.

The original measurements not obtained on POFI vessels came from a variety of sources. In the Honolulu area most measurements were from specimens received at the fresh fish market. The Japanese specimens were measured by members of the POFI reconnaissance team that visited Japanese markets in 1949. Specimens from the Society Islands were measured from the catch of the vessel *Hawaiian Tuna* when they were landed at the Honolulu market and after they had thawed.

METHODS OF COMPUTATION

As indicated in the general discussion on the comparison of morphometric data, I have not considered ratios or indexes but have used regression analysis entirely in order to control the effect of size of fish in our comparisons. I have used the regressions for yellowfin tuna proposed by Schaefer (1948), who stated that the original measurements provided a satisfactory straight-line relation with fork length in the case of head length, snout to insertion of first dorsal fin, snout to insertion of second dorsal fin, snout to insertion of anal fin,

and greatest body depth.⁴ For the length of the pectoral fin he used the actual length of the fin with the logarithm of fork length, and for heights of the second dorsal and anal fins he used the logarithm of length of fin with the logarithm of fork length. For the other character, the distance from the insertion of the ventral fins to the anterior edge of the vent, which Schaefer (1948) did not use, no transformation is needed to obtain a reasonably straight line.

After accumulating several thousand sets of measurements for several species of tunas, we found that the labor of analysis was beyond our facilities and we turned to the International Business Machines Corporation for assistance. On most of our material, in which the original field data sheets had one fish per sheet, codes were added for species, locality, 10-cm.-length group, month, year, sex, and the examiner. Certain measurements were transformed to logarithms and the code and measurements were punched on cards. It was then possible to square, cross multiply, and tabulate automatically. A complete tabulation of sums, sums of squares, and sums of the products for regression analysis was obtained, arranged according to species, locality, and 10-cm.-length group. Subsequently, special tabulations of the material were made as needed.

After the data had been completely tabulated and totaled, scatter diagrams were made for each character on all specimens from each area to permit an immediate judgment of aberrant observations. If any data were obviously aberrant,⁵ they were checked with the original field data, and, if plotted as recorded, they were assumed to be in error and were discarded. The regression line was then computed and plotted along with parallel lines plus and minus three standard deviations from regression. At this time, any remaining points more than three standard deviations from regression were assumed to be in error and were dropped. Then, final regression and the standard deviation from regression were computed. I have not tabulated the number of discarded observations, but I estimate it to be less than 2 percent of the total.

⁴ An evaluation of the regression formulae will be found in the following section.

⁵ This was usually more than about 15 percent (about four standard deviations) of the size of the character away from the general trend.

Discarding any data is questionable because correct but unusual observations may be discarded. By my method, however, most of those dropped were far removed from the line. The rejected values frequently were so located that one suspected that digits had been transposed or errors made in the decimeter digit. I believe that few if any correct observations were discarded. Furthermore, some culling is desirable for all data of this kind which have been collected under difficult field conditions where it is not practical to check original measurements.

Checks were made at all stages of computations. All IBM card punching was verified. All desk calculator operations that could not be independently checked were repeated. Finally, the plots of the regression line and standard deviations from regression provided a visual check which detected any but trivial errors.

SELECTION OF REGRESSION EQUATIONS

In the analysis of yellowfin tuna morphometrics, two fundamental statistics, mean and variance, are required. Both must be unbiased estimates of corresponding population parameters. These statistics are estimated from the best regression formulae. If I apply straight line regressions to data that are curvilinear, then my estimates of the means may diverge an unknown amount from the population parameter and the estimates of variance will tend to be excessive. On the other hand, curvilinear regression techniques tremendously increase already laborious calculations and for practical reasons should be avoided unless fully justified.

The two authors who have dealt with relative growth of the yellowfin tuna are in fundamental disagreement on whether curvilinear regression is needed for several characters. Schaefer (1948: 117) stated, "Over the range of sizes considered, all the characters measured, with the exception of the lengths of the pectoral, second dorsal and anal fins, bear a linear relationship to the length of the fish." For the length of the pectoral fin he used the logarithm of fork length and for the other two fin dimensions he used the logarithm of both fin length and fork length and simply states, without offering proof, that these transformations are appropriate. Schaefer later (1952) cautioned that the relationships were only approximations that did not completely describe the relation between

fork length and size of the body part. On the other hand, Godsil (1948: 7) stated—

Plotting to a large scale the actual measurements of a given character against body length in each case, revealed that the sample regressions were nearly but not quite linear. Of the various functions tried, the expression $Y=a+bx+c\frac{1}{2}$ (where x =body length in each case and Y =the dependent variable) resulted in the best fit.

The other functions tried included $y=a+bx$, $y=a+bx+cx^2$, $y=a+bx+cx^2+dx^3$, $y=ax^b$, and $y=ae^{bx}$. He also stated that the reduction in the sum of the squared deviations from the above expression when compared with the sum from the linear regression was in most cases highly significant. He offered no statistical data supporting this assertion; but his graphs, with the plotted points and curved lines, show clearly that the data for head length and snout to the insertions of first dorsal, ventral, second dorsal, and anal fins are slightly curvilinear and the computed lines fit well. The curvilinearity in Godsil's data is further puzzling because Schaefer and Walford (1950) presented data for characters used by Godsil that show no curvilinearity.

Therefore, it is desirable to examine in greater detail the source of curvilinearity in Godsil's data. This may be done by comparing the mean-square deviations from linear regression with those from curvilinear regression (table 3). When such comparisons are summed for the 13 samples for each character, I find that curved lines significantly reduced the mean square of pooled data as well as the mean square of within-sample data for each character. I notice, however, that for

all characters reduction in the mean square from linear to curvilinear regression is much greater for pooled data than it is for within-sample data. Such differences between pooled and within-sample data suggest that a major part of the curvilinearity is between samples rather than within samples.

More conclusive evidence of the source of curvilinearity is to be found by examining the significance of the reduction in the mean square, character by character and sample by sample (table 3). Here significant or highly significant curvilinearity for most characters occurs in samples 1, 3, 4, 5, 6, and 7. In the remaining seven samples, 2 and 8 through 13, only four instances of a significant but not highly significant reduction in mean square occur in 35 comparisons. Since two significant reductions would be expected to occur by chance in this number of comparisons, little importance can be attached to the four. Clearly, curvilinearity is associated with certain samples and not with certain characters for all samples, as would be expected from a truly curvilinear regression of body part on fork length.

One characteristic of the samples that might be associated with curvilinearity is size, since it is obvious that very large samples ($DF=385, 348$) show curvilinearity whereas small samples ($DF=25, 36, 67$) do not. Among the eight samples of intermediate size, however, four, with degrees of freedom equaling 192, 121, 98, and 96, show no more than one character with significant curvilinear

TABLE 3.—Mean-square deviations from linear and curvilinear regressions of yellowfin morphometric measurements
[Measurements from Godsil, 1948]

Sample number	Degrees of freedom ¹	Length of head		Snout to insertion of—								Date of collection ²
		Linear	Curvilinear	First dorsal fin		Second dorsal fin		Anal fin		Ventral fin		
				Linear	Curvilinear	Linear	Curvilinear	Linear	Curvilinear	Linear	Curvilinear	
1.....	92	7.84	**0.69	14.53	**13.49	20.15	**19.22	20.26	**17.66	13.07	**11.41	Mar. 13, 1939.
2.....	96	5.71	5.68	10.06	10.21	12.83	12.45	19.59	*18.47	11.89	11.79	Mar. 8, 1939.
3.....	106	10.80	*10.58	12.40	12.10	21.17	**19.29	26.93	*26.44	16.87	17.10	Apr. 25, 27, 1940.
4.....	385	11.06	**10.34	20.98	**19.70	32.46	**29.91	29.40	30.63	25.07	**24.70	Nov. 5 to Dec. 7, 1936.
5.....	348	11.08	**8.91	18.97	**15.72	22.95	**15.69	22.63	**19.70	20.06	**19.07	Jan. 14 to Feb. 13, 1937.
6.....	118	5.82	**5.32	10.66	**9.24	13.27	13.21	13.40	13.44	12.86	*12.32	Mar. 26, 27, 1939.
7.....	141	18.40	**14.19	25.57	**22.22	38.00	**32.30	34.09	**30.69	31.75	**28.29	Jan. 16 to 19, 1937.
8.....	192	7.73	8.37	12.01	12.49	11.62	12.55	16.56	16.85	14.07	15.71	Apr. 1 to 19, 1940.
9.....	67	6.37	6.29	4.84	14.55	12.81	13.06	16.07	16.15	8.42	8.58	May 12, 1940.
10.....	121	5.45	*5.26	9.91	10.30	11.19	11.03	15.74	16.43	13.79	14.16	Jan. 21 to Feb. 10, 1937.
11.....	36	7.81	7.83	9.94	*8.83	21.92	21.03	13.97	14.17	18.63	19.32	Mar. 22 to 24, 1940.
12.....	25	6.92	7.21	7.84	8.17	15.16	15.75	23.60	24.54	21.12	21.96	Apr. 29, 1940.
13.....	98	8.28	8.32	14.99	15.11	13.04	*12.66	16.72	16.84	14.27	14.28	Mar. 30, 31, 1940.
Pooled-sample variance.	1909	12.07	**9.53	19.07	**15.78	24.93	**20.40	27.25	**25.85	19.91	**19.31	
Within-sample variance.	1885	9.71	**8.80	16.14	**14.94	21.69	**19.24	22.65	**21.99	18.73	**15.34	

¹ Varies slightly with different characters.

² Supplied by Godsil in personal communication.

* Statistically significant reduction in mean square

($0.05 > p > 0.01$). ** Highly significant reduction in mean square ($p < 0.01$).

earity. The other four samples of intermediate size show highly significant curvilinearity in at least one character and significant curvilinearity in more than half of the characters. It is likely that something other than sample size alone has caused curvilinearity.

Another source of curvilinearity may be accidents of sampling. Such accidents appear to be rather likely because most of Godsil's samples (table 2) were obtained on a single day or over a period of a few days. It is well-known that yellowfin school by size, and when one of the larger samples includes a considerable range in sizes it is probable that it was obtained from only a few schools of different average size. If the sample included schools of slightly different morphological characteristics and also of different mean size, there would be two sources of regression—one within schools fished and the other between schools fished. The combined regressions might appear to be curvilinear.

Therefore, when I examined our data for curvilinear regression I turned first to the sample that I considered had the best coverage of the area sampled and that contained a good size distribution of fish. It was the sample from the western Line Islands area, obtained during 13 different months with the majority of the fish caught by longlining and trolling and measured by 12 different measurers. During both longlining and trolling operations, it was customary to measure only a few fish a day (rarely more than 10), and thus these fish came from several dozen different schools and as many different locations within the area. There are 188 sets of measurements available in this sample, with good numbers in most 10-cm. length groups from 50 to 160 cm.

Evidence of curvilinearity was sought in the plots of complete data that were made to check each sample. Some evidence of curvilinearity appeared in the plots for certain characters, but the scatter of points around the line made interpretation difficult. Hence, I sought a way to magnify any curvilinearity and plotted the deviations of the 10-cm. group means from the rectilinear regression equations for each character in the sample (fig. 4). These equations were based on the transformations, proposed by Schaefer (1952), which are log fork length and log height of second dorsal fin, log fork length and log height of anal fin, and log fork length and length of pectoral fin.

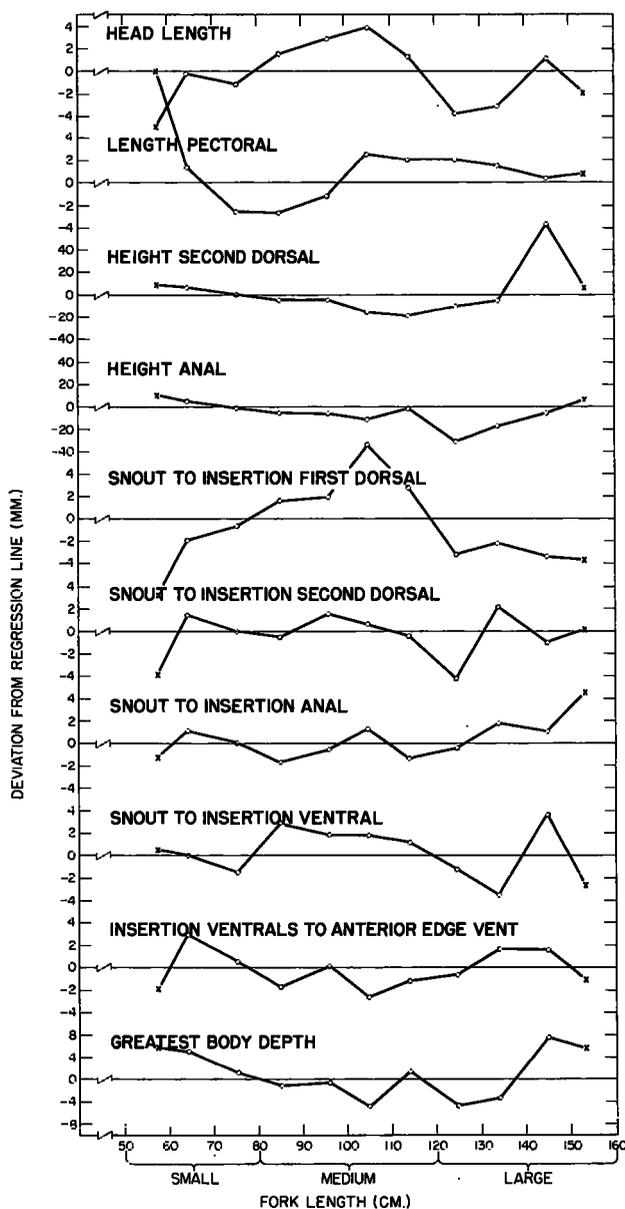


FIGURE 4.—Sample of yellowfin tuna from western Line Islands area. Deviations of 10-cm. group means from regressions were used. (X, average of less than 10 fish; O, average of 10 or more fish.)

The data for all other characters were not transformed.

The graph suggests that some curvilinearity occurs in several characters. If a random distribution of 10-cm.-group means about the regression line is assumed, a line connecting the group means would be expected to cross the regression line an average of five times (with 11 points). To the contrary, for four characters—

length of pectoral, height of second dorsal fin, height of anal fin, and snout to insertion of first dorsal fin—the lines crossed only twice. In the case of only one character—the snout to insertion of second dorsal fin—did the lines cross more than the most probable number of times.

The question then arose whether the curvilinearity prevailed in other samples, and I made a similar analysis of our other two large samples

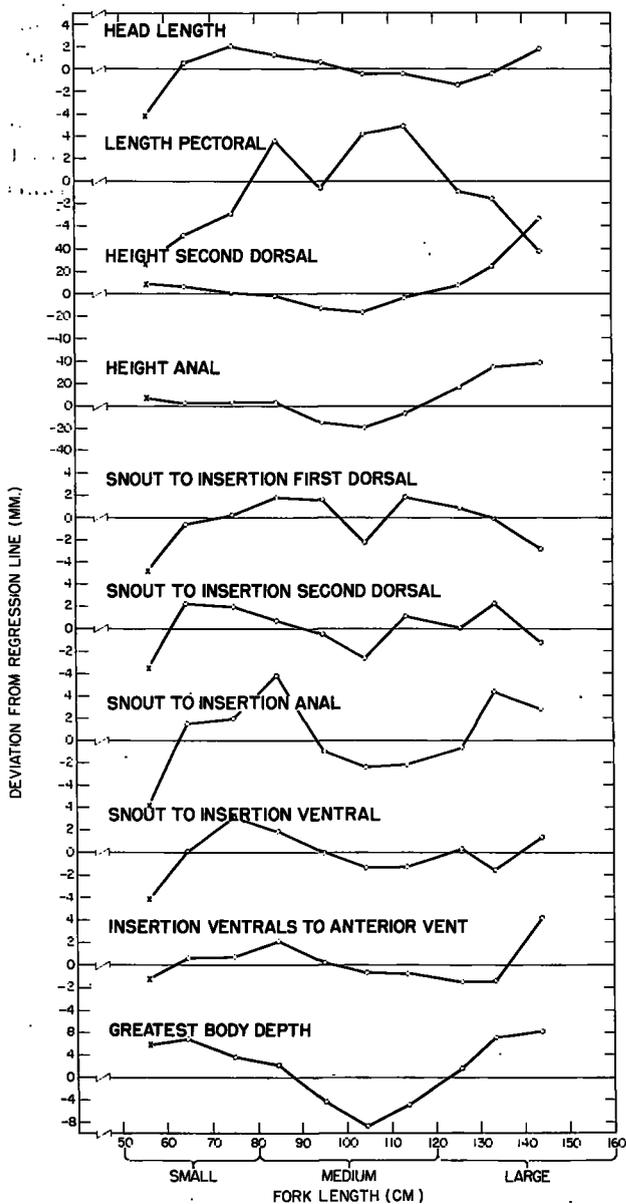


FIGURE 5.—Sample of yellowfin tuna from central Caroline Islands area. Deviations of 10-cm.-group means from regression. (X, average of less than 10 fish; 0, average of 10 or more fish.)

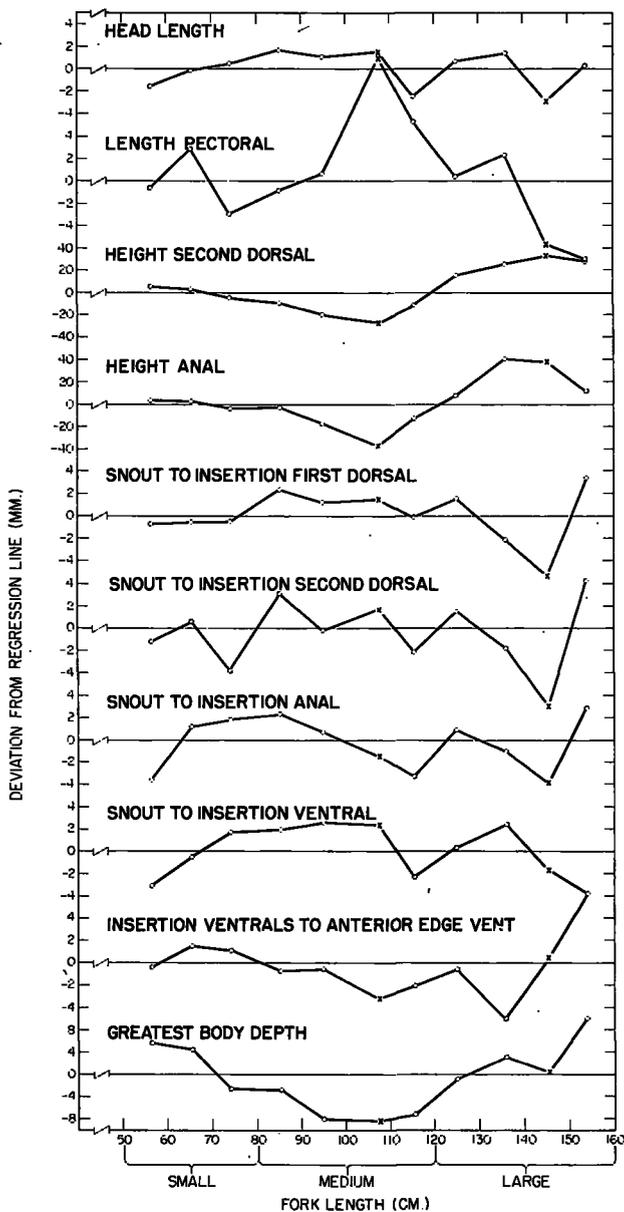


FIGURE 6.—Sample of yellowfin tuna from eastern Caroline Islands area. Deviations of 10-cm.-group means from regression. (X, average of less than 10 fish; 0, average of 10 or more fish.)

that also are well distributed over a wide range of lengths. They were the samples from the eastern Caroline Islands and the central Caroline Islands, which contained 171 and 211 sets of measurements, respectively. Similar plots of deviations of 10-cm.-group means from the rectangular regression lines (figs. 5 and 6) indicated

again that the lines cross less than the expected number of times for most characters.

When compared, the deviations from regressions of all three areas indicate that they tend to form a curve concave upwards for height of second dorsal fin, height of anal fin, and greatest body depth. Other characters, especially head length, snout to insertion of first dorsal fin, and snout to insertion of ventral fin, appear sinuous with some tendency for the line connecting means to start below the regression, then go above, then below, and then upward again. The line appears to be curved for length of the pectoral fin, but in a different way in each sample.

I conclude that for most characters in these large samples some curvilinearity remains that is not associated with sampling, but is rather an expression of the allometric growth of the fish. Furthermore, it is an irregular allometry which is not readily expressed by any linear or simple curvilinear formulation.

Such curvilinearity would not be troublesome if all samples had similarly distributed lengths, in which case it would probably be satisfactory to use the regression techniques proposed by Schaefer (1948). The rather small amount of curvilinearity would result in some bias in mean, variance, and regression constants, but if such bias were similar among samples it would not matter. However, it has not been possible to obtain samples covering a uniform range of lengths. In numerous areas, particularly along the Pacific Equator, where we have fished only with longline gear, we have obtained only very large fish, and in other areas, where fishing has been done only by trolling, we took mostly small fish.

The compromise solution has been to split the samples into three size groups and compare them at three different standard lengths, each very close to the grand mean of its size group. The following groups have been used:

Small (S)—fish less than 80 cm., most of which are more than 50 cm. and which have been compared at a length of 65 cm. (about 12 lb.); medium (M)—fish from 80 to 120 cm., compared at a length of 100 cm. (about 43 lb.); large (L)—fish more than 120 cm., most of which are less than 170 cm. and which have been compared at a length of 140 cm. (about 118 lb.).

Further restrictions were adopted: first, to avoid uncertainties due to the small samples it was

required that there be more than 20 specimens in each size group, and second, to minimize the effect of any curvilinearity remaining within a size group, it was required that more than 10 percent of the sample be above and more than 10 percent below the comparison size. For example, in Godsil's sample from Panama and Costa Rica there were 23 fish between 120 and 140 cm. and none above 140 cm. This part of his sample was not considered in the large group, whereas his sample from Cocos Island including 23 fish ranging from 120 to 160 cm., with 9 above 140 cm., was considered. One sample remains that is not well distributed in fork length—the one from northeast Africa. It has been used, but the comparisons are made with reservations.

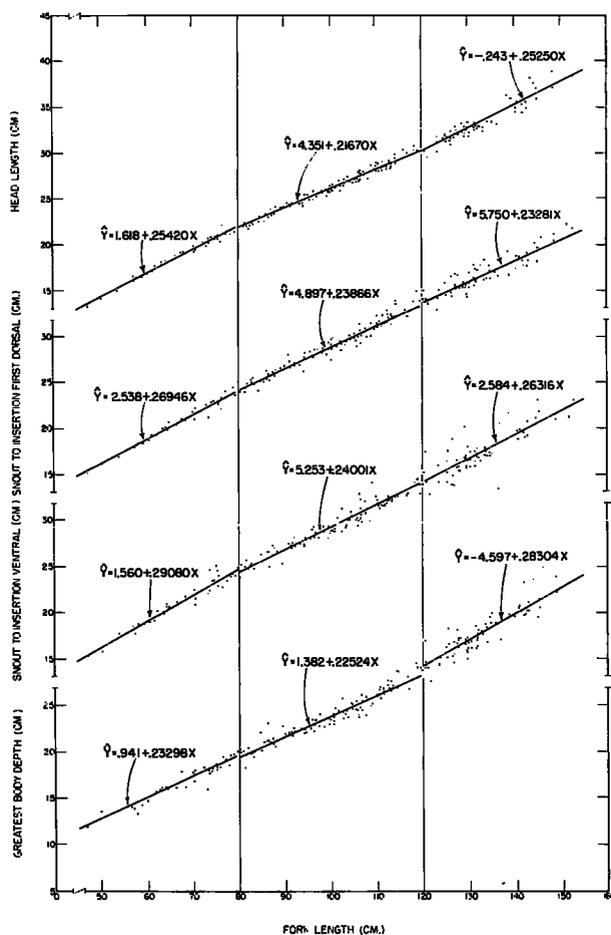


FIGURE 7A.—Regressions of head length, distances from snout to insertions of first dorsal and ventral fins, and greatest body depth in yellowfin tuna from central Caroline Islands area.

The fit of the lines to the three size groups may be judged from the plots of the data from the central Carolines area (figs. 7A, 7B, and 7C). Each of the three separate lines appears to be a

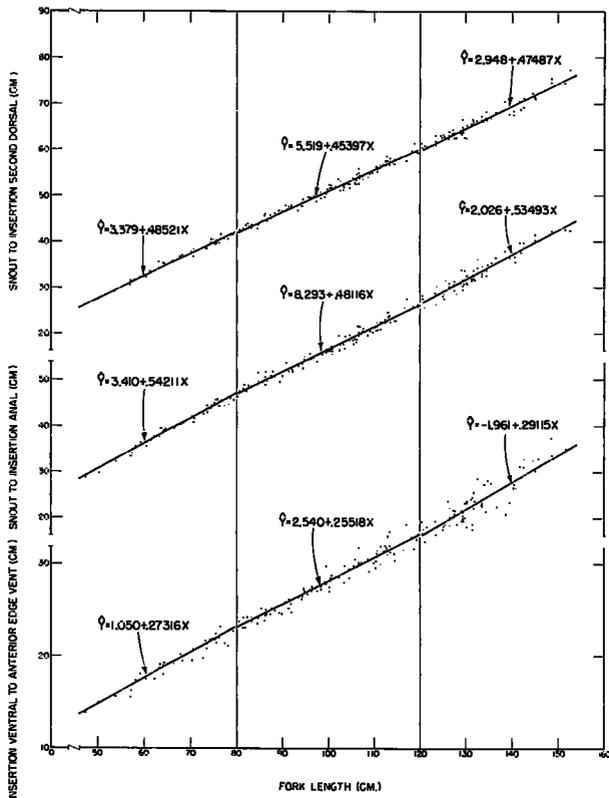


FIGURE 7B.—Regressions of distances from snout to insertion of second dorsal and anal fins and distance from insertion of ventral fin to anterior edge of vent, in yellowfin tuna from central Caroline Islands area.

good fit in its limited range, but when projected beyond the range it may rapidly diverge from the plotted points. The tendency that has been noted toward a sinuous line in certain characters is again evidenced in the plots and in the changing regression constants. I judge, however, that any remaining curvilinearity within each size group is much less than the dispersion of points about the line and that samples within each size group may be compared with little fear of erratic results due to curvilinear regression.

RELIABILITY OF SAMPLE STATISTICS

In addition to determining methods of regression analysis that will give reliable estimates of mean and variance the reliability of the raw data must be assessed. Two matters may be

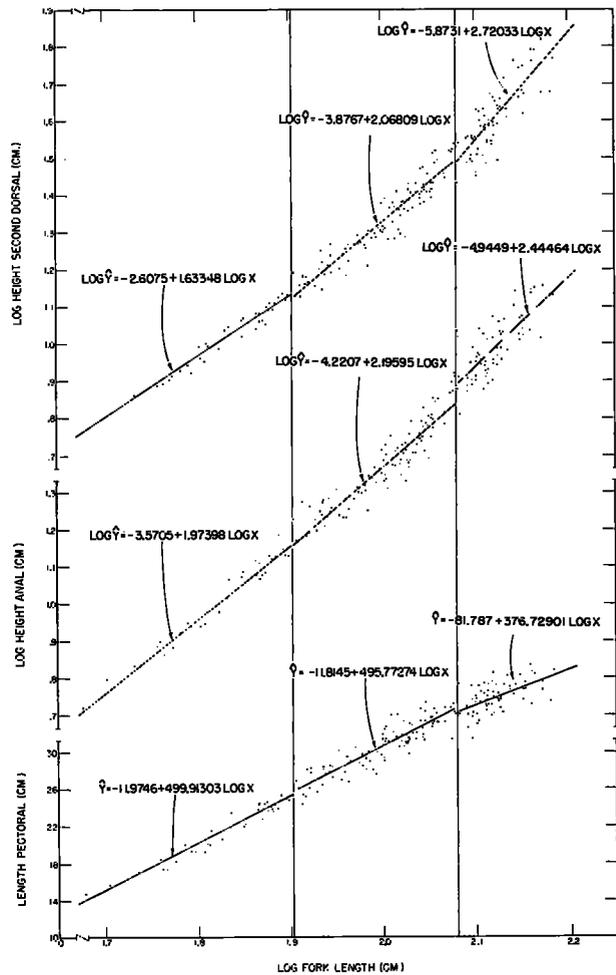


FIGURE 7C.—Regressions of log heights of second dorsal and anal fins and length of pectoral fin, in yellowfin tuna from central Caroline Islands area.

examined: first, the adequacy of the sampling, and second, the accuracy of the measurements.

An ideal sample of yellowfin tuna for a morphometric study would be representative of all sizes of tuna in the specified area during the period of study. Such a sample would contain a distribution of sizes proportionate to the numbers of each size in the ocean and would be randomized over the time and area covered. This ideal is far out of reach because it is not possible to catch all of the sizes, as each fishing gear selects certain size groups, and it has not been possible to fish any area at randomly selected locations or times.

Consideration of the habits of the yellowfin suggests, however, that satisfactory samples may be obtained from a relatively limited coverage.

The yellowfin is a schooling species (Murphy and Elliott, 1954), and I have suggested that schools in a limited area may vary slightly in their morphometric characteristics (p. 406). The yellowfin are fast swimmers, however, and it seems probable that they could cover hundreds of miles in a few days. Furthermore, the larger yellowfin at least are entirely independent of coastal regions. The ocean in which they are found is relatively uniform, with no absolute barriers to migration, although the yellowfin do prefer certain areas, presumably where they find the most food. So it is possible that a sample made up of subsamples from numerous, different schools may be adequately representative of an area even though the area is not randomly covered. The schools may be assumed to have been randomly swimming in the area. A similar assumption with regard to time is less safe because many species migrate annually, and even if yellowfin are present in an area throughout the year, they might be different spawning groups.

Even though the ideal sample cannot be obtained, samples with widely varying coverage in area and time (table 2) may be compared. As the samples were extended in space and time, however, they were taken by an increasing number of people, who may have varied in their techniques of measurement. Therefore, the problems of sampling and precision in measuring the fish must be considered simultaneously, and here I digress briefly to consider the problem of obtaining consistent measurements of yellowfin.

Fortunately, all tunas are easy to measure consistently. The body is stiff, and even when not in rigor mortis has almost no tendency to bend when the fish is laid on a flat deck on its side. The parts to be measured were accurately defined by Marr and Schaefer (1949). The numerous measurers from POFI have compared their methods—almost no one measured tuna without first working with someone who had measured them before—and most differing interpretations of the definitions have been quickly settled. Nevertheless, I consider that minor differences of technique must have occurred both among POFI and other measurers, and the problem is to assess how great the differences have been.

One approach to this problem might be to have different people repeat measurements on the same fish and then analyze the differences. We

have made repeat measurements to standardize our methods but have not analyzed the differences, because our concern is with what people have done independently and routinely and not what they could do under experimental conditions.

It will not be possible to separate the differences in technique from differences of time and area, but the combined problem can be approached by examining the variance in relation to coverage of the sample and number of measurers. Also mean values and overlap of closely related samples obtained by different measurers can be compared. The latter comparison must be left until I have introduced the method of comparing means and overlap.

The variance itself is not suitable for our comparison. Better is the standard deviation from regression $S_{y,x}$, which is directly indicative of the spread of points about the line, but it obviously is related to the size of the character, even when the characters have been transformed to logarithms. So I have used a kind of coefficient of variation,

$$C = \frac{100 S_{y,x}}{\bar{x}}$$

to eliminate the effect of size of character \bar{x} and so obtain a better mean value for all characters in a sample.

These coefficients of variation have been computed for each character in each sample and are shown in table 4 (except the samples of Godsil (1948) from Panama and Costa Rica and from Cocos Island, in which his curvilinear regressions were used and in which the range spreads extensively over two or more of our size groups).

Several samples contained measurements for only five characters, and hence the sample means and the grand means were computed from these five characters only.

This table shows close agreement among grand means of the coefficients of size groups for the five characters, which indicates that the standard deviation from regression is almost exactly related to size of the fish. Further, there is some difference among characters: length of pectoral fin and greatest body depth have a high coefficient; log heights of second dorsal and anal fins show coefficients that increase with size of fish; distances from snout to insertion of second dorsal and anal fins have the lowest values.

TABLE 4.—Coefficients of variation of yellowfin morphometrics

Area and size ¹	Length of head	Length of pectoral fin	Weight of second dorsal fin	Weight of anal fin	Snout to insertion of—				Great-est body depth	Insertion ventral to anterior edge vent	Means ²
					First dorsal fin	Second dorsal fin	Anal fin	Ventral fin			
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	
Mexico: ³ S	1.38				1.70	1.05	1.04	1.60			1.35
Guatemala: ³ S	1.32				1.64	1.06	.96	1.76			1.85
Costa Rica: ⁴ M	1.75	3.13	1.67	1.85	1.76	1.38	.95		3.14		1.46
Galapagos Island: ³ S	1.42				1.61	.92	.99	1.71			1.33
Clipperton Island: ³ S	1.33				1.36	1.18	.85	1.83			1.31
109°-119° W.: L	1.94	3.58	1.32	2.55	3.03	1.44	1.10	2.35	2.19	2.88	1.97
119°-129° W.: L	2.20	4.68	2.58	2.53	2.01	1.18	1.38	2.90	4.29	2.80	1.93
129°-139° W.: L	1.16	4.17	2.66	2.58	2.07	1.33	1.24	2.04	4.09	2.61	1.73
139°-149° W.: L	1.81	3.50	2.47	2.60	2.23	1.28	1.33	2.14	2.96	2.72	1.76
East Line Islands:											
M	1.57	3.03	2.50	2.34	2.02	1.34	1.63	1.84	3.24	2.27	1.68
L	1.82	4.05	2.57	2.71	2.44	1.62	1.33	2.55	2.51	2.54	1.95
West Line Islands:											
S	2.28	3.77	1.66	1.55	2.63	1.34	1.63	2.53	3.43	2.65	2.08
M	2.16	4.40	2.15	2.84	2.27	1.48	1.55	2.70	4.19	2.23	2.03
L	1.96	2.88	2.44	2.26	1.76	1.29	1.11	1.94	3.19	2.64	1.61
Palmyra Island: ³											
S	2.02				2.64	1.38	1.24	1.58			1.77
M	1.57				1.86	1.36	1.50	1.72			1.62
Phoenix Islands:											
S	2.33	4.09	1.63	1.80	1.85	2.20	1.50	2.53	2.59	2.15	2.08
M	2.30	4.45	2.02	2.59	2.00	2.49	1.70	2.57	4.10	1.99	2.21
L	1.93	3.22	2.22	1.97	2.09	1.37	1.32	2.80	3.73	2.53	1.90
East Marshall Islands: L	1.45	3.78	3.08	1.97	1.41	1.03	1.04	1.58	2.54	2.57	1.30
Bikini Island: S	1.51	3.30	1.28	1.58	1.78	.84	1.10	2.41	2.18		1.53
East Caroline Islands:											
S	1.34	4.04	1.25	1.49	2.04	1.21	1.19	1.75	2.83	2.50	1.51
M	1.25	3.79	1.34	1.49	1.66	.93	.87	1.78	2.68	2.28	1.30
L	1.60	3.27	1.98	1.66	2.22	1.10	1.11	1.90	3.23	2.04	1.59
Central Caroline Islands:											
S	1.64	3.01	.90	1.50	1.61	1.37	1.74	3.14	3.32	2.93	1.90
M	1.31	3.91	1.52	1.56	2.05	1.41	1.52	2.48	2.93	2.51	1.75
L	1.97	3.63	2.46	2.07	2.23	1.48	1.52	3.13	3.72	3.13	2.07
Philippines:											
S	2.14				2.82	2.49	2.02	2.50			2.39
M	2.37				2.31	1.62	1.55	2.30			2.03
L	2.74				3.11	1.87	2.25	3.62			2.72
Japan: S	1.78	3.65	1.32	1.49	2.01	1.34	1.11	2.16	2.91		1.68
Hawaii:											
S	1.77	4.87	1.75	1.79	2.17	1.51	1.56	2.77	3.70		1.96
M	2.19	5.04	1.95	2.55	2.65	1.37	1.49	2.72	3.42		2.08
L	1.74	3.84	2.20	2.13	2.01	1.41	1.26	2.04	3.36		1.69
Hawaii: ⁵											
S	1.52				1.70	1.01	1.05	1.98			1.45
L	1.32				2.03	1.20	1.05	1.51			1.42
Society Islands: S	1.49	4.12	1.60	1.97	2.42	1.43					1.78
Northeast Africa: S	2.19	3.90	1.53	2.08	2.92	1.93	1.87	2.98	2.52		2.38
Angola, Africa: ⁶											
M	1.88	3.98	1.33	1.47	2.29	1.39	1.46	1.62			1.73
L	1.90	3.58	1.86	2.36	2.24	1.19	1.46	1.72			1.70
Means:											
S	1.72	3.86	1.42	1.60	2.06	1.39	1.32	2.22	2.94	2.56	1.74
M	1.84	3.97	1.82	2.09	2.09	1.43	1.43	2.19	3.39	2.26	1.81
L	1.88	3.68	2.24	2.28	2.21	1.34	1.32	2.30	3.26	2.65	1.81

¹ S, fish less than 80 cm., and compared at a length of 65 cm.; M, fish from 80 to 120 cm., and compared at a length of 100 cm.; L, fish more than 120 cm., and compared at a length of 140 cm.

² Mean of columns (1), (5), (6), (7), and (8). ³ Godsil (1948) and in correspondence. ⁴ Schaefer (1952). ⁵ Godsil and Greenwood (1951). ⁶ Schaefer and Walford (1950).

Of most interest, however, is the rather small amount of variation in the mean *C* values for the different samples. These values range from a low of 1.30, equal in the eastern Marshalls group L and the eastern Carolines group M, to a high of 2.72 in the Philippines group L. The Philippines group S and the northeast Africa group S are next highest. (I have no information on how these samples were collected and the factors that may have caused the higher values.) Among the POFI samples the highest (2.21) value is found in the Phoenix Islands group M.

When I tried to relate the mean *C* to the number of measurers and to the coverage of the sample in

figure 8, I found little relation. The grand mean for one to three examiners is 1.62; for four to six examiners, 1.88; and seven or more, 1.92. The relation to length of sampling period is similar: for 1 to 9 days the mean is 1.64; for 10 to 19 days, 1.91; and for 20 or more days, 1.80.

None of this evidence is conclusive, but there appears to be a slight increase in the value of *C*, which is associated with increased time, greater number of measurers, or greater area sampled. I cannot segregate these factors, but because curvilinearity appears in some of Godsil's (1948) samples which were collected during only a few days, the samples taken on fewer than 10 different

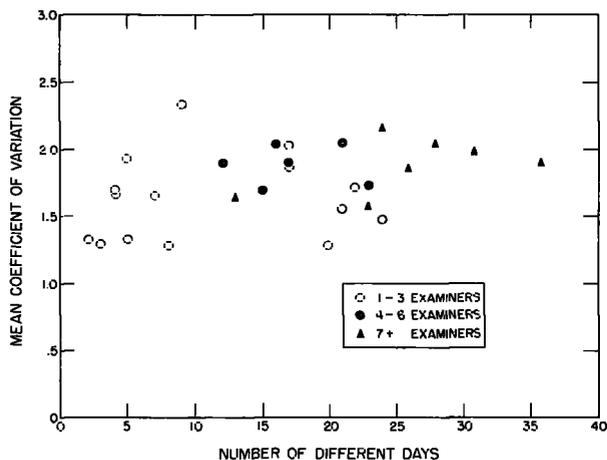


FIGURE 8.—Relation of the mean coefficient of variation of five selected characters to number of examiners and number of days on which parts of the sample were taken.

days may be less representative. Therefore, I conclude that important bias was not introduced by different techniques among measurers, at least not in the central and eastern Pacific area, where all of the measurers worked closely with one another.

CHARACTER-BY-CHARACTER COMPARISON OF SAMPLES

One of the most direct and useful ways of comparing morphological data is simply to compare the mean values estimated for certain fixed lengths. These values are particularly useful because they may be associated readily with geographic features and show directly the presence of character gradients or clines. Unlike tests of significance or amounts of overlap, an examination of the means shows directly the differences in number of parts or in body form. Of course, with all characters associated with body size it is necessary to control body size by the use of appropriate regressions.

A first comparison of samples is logically among the considerable series available from the equatorial Pacific. Areas from which these samples came extend from the American coast westward about 8,400 miles to the central Carolines area, which is bounded on the west by longitude 140° E. (fig. 2). This area of comparison is limited to the region between latitude 10° N. and latitude 10° S., although some of the samples are more

restricted than this in latitudinal coverage. In the southern and extreme northern parts of this zone are the westerly flowing South Equatorial and North Equatorial Currents. Between these two currents (5° N. to 10° N.) is the easterly flowing Countercurrent. Throughout this area⁶ yellowfin tuna have been taken near the Equator and have been found to be especially abundant between the Equator and the Countercurrent. They also have been found to be rather consistently scarce north of the Countercurrent and south of the Equator. They do, however, occur well to the north and south of this equatorial region, and no known barriers to their horizontal migration exist in any direction until water too cold for their liking is reached in the vicinity of latitude 40° N. or S.

So we know that the distribution of yellowfin is continuous from east to west in this equatorial band and that the tuna prefer a band about 300 miles wide in a north-south direction. Here is a situation where character gradients may be expected if the tuna are not freely intermingling across the whole equatorial Pacific.

In order to seek gradients I have adopted a slightly modified form of the method proposed by Hubbs and Hubbs (1953). There is a graphical method in which the mean is plotted, a measure of dispersion is indicated by one standard deviation plotted on either side of the mean as a hollow bar, and a measure of reliability is indicated by two standard errors of the mean plotted as a solid bar on either side of the mean. The range is indicated by a base line. I have used comparable regression statistics, except for the range. First, the mean part size \hat{Y} was calculated directly from the regression equation

$$\hat{Y} = a + bX.$$

Second, the dispersion around the regression line is indicated by one standard deviation from regression

$$S_{y \cdot x} = \sqrt{\frac{\sum y^2 - (\sum xy)^2 / \sum x^2}{n - 2}}$$

plotted as a hollow bar on either side of the mean. The reliability of the mean is indicated by two

⁶ In the gap between longitude 109° W. and the American coast (fig. 2), yellowfin have been taken by commercial vessels and research ships sponsored by the Inter-American Tropical Tuna Commission.

standard errors of the mean estimated from regression

$$2S_{\hat{y} \cdot x} = 2S_{y \cdot x} \sqrt{1/n + x^2/\Sigma x^2}$$

plotted as a solid bar on either side of the mean.

These statistics were computed separately for each size group in each sample. For the small (S) group they were computed at a fork length of 65 cm., for the medium (M) group at 100 cm., and for the large (L) group at 140 cm. The three size groups are shown separately for all samples in figures 9 to 18. In each graph the equatorial Pacific samples are arranged in order from east to west and the other samples are added at the bottom.

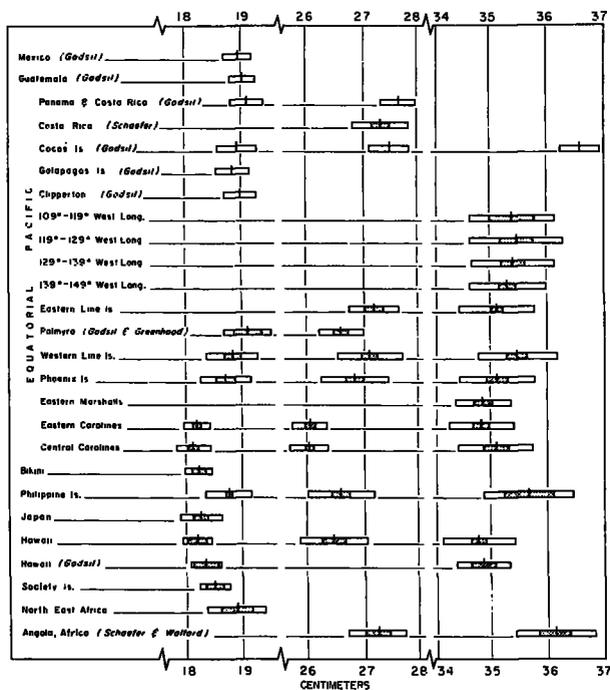


FIGURE 9.—Head length of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, solid bar \pm two standard errors of the mean, hollow bar \pm one standard deviation from regression.)

Almost all of the characters show gradients—sometimes stepped, sometimes continuous, and sometimes confused, perhaps because differences are small and sampling variation has its effect. The gradients, however, in most cases are unmistakable.

There is a distinct tendency toward shorter heads (fig. 9) in all three size groups from the western Pacific. The gradient is not smooth,

because fish of the large group from longitude 109° W. to the western Line Islands area have much the same size head, and head size in the samples from the medium and small groups is much the same near the ends of the range.

The length of the pectoral fin (fig. 10) is distinctly greater in fish from the Caroline Islands area than in those from the eastern Pacific. Again similar tendencies occur in all size groups except

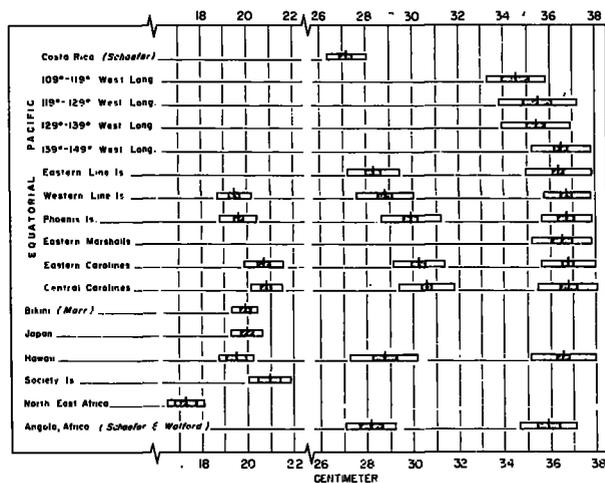


FIGURE 10.—Length of pectoral fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, solid bar \pm two standard errors of the mean, hollow bar \pm one standard deviation from regression.)

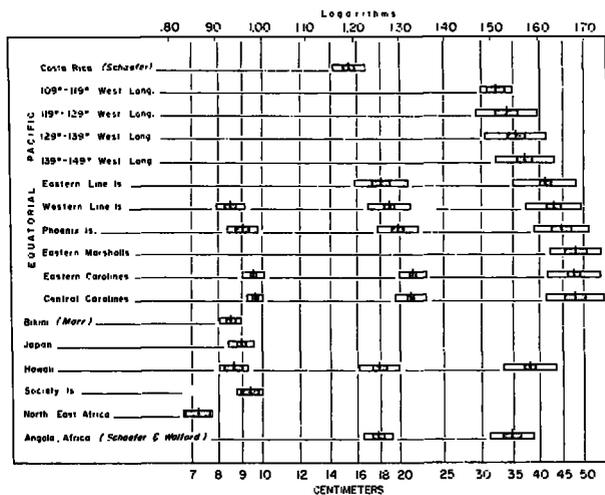


FIGURE 11.—Height of second dorsal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm one standard deviation from regression.)

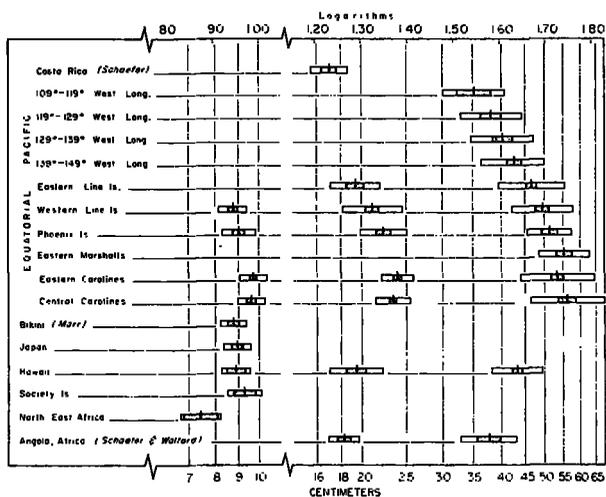


FIGURE 12.—Height of anal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

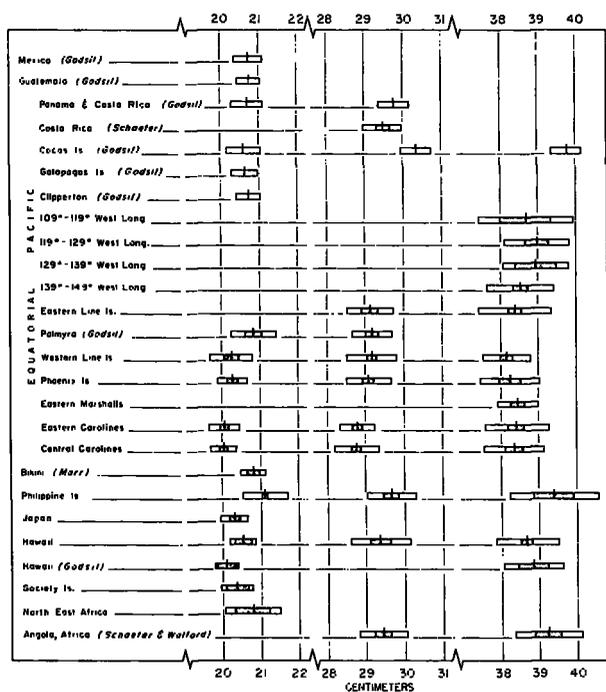


FIGURE 13.—Distance from snout to insertion of first dorsal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

that both the small and medium groups suggest a rather smooth cline, whereas the large group shows a rather similar fin length from longitude 139° W. to the Caroline Islands.

The differences in the height of the anal fin (fig. 12) and the height of the second dorsal fin (fig. 11) are even more marked, with clear and almost uniform gradients from the vicinity of Costa Rica to the eastern Marshalls and then about the same length fins on through the Caroline Islands area. Here the difference among samples of the large size group is about 16 cm. for height of second dorsal fin and 20 cm. for height of anal fin from longitude 109° W. to the Caroline Islands.

The distance between the snout and the insertion of the first dorsal fin (fig. 13) shows a distinct but somewhat irregular trend in the opposite direction, with the fish in the eastern Pacific having the greater measurement between these two points. In all size groups, insofar as samples are available, clearer trends in the same direction are to be noted in the measurements between the snout and the insertion of the second

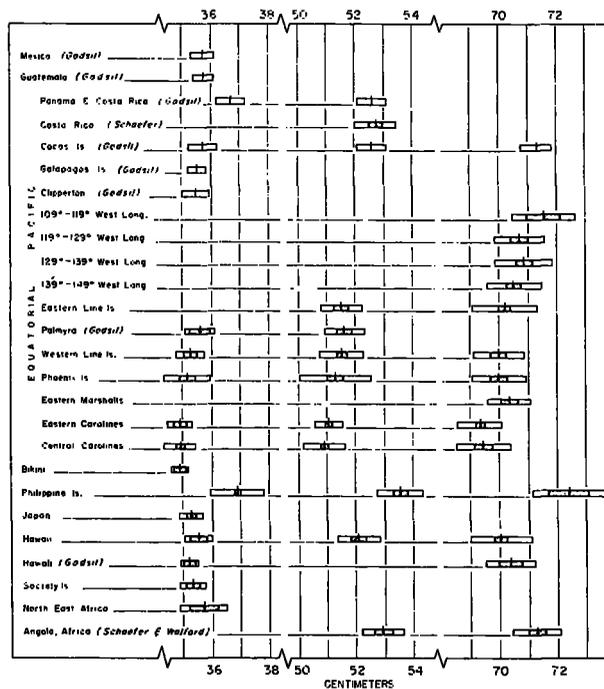


FIGURE 14.—Distance from snout to insertion of second dorsal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

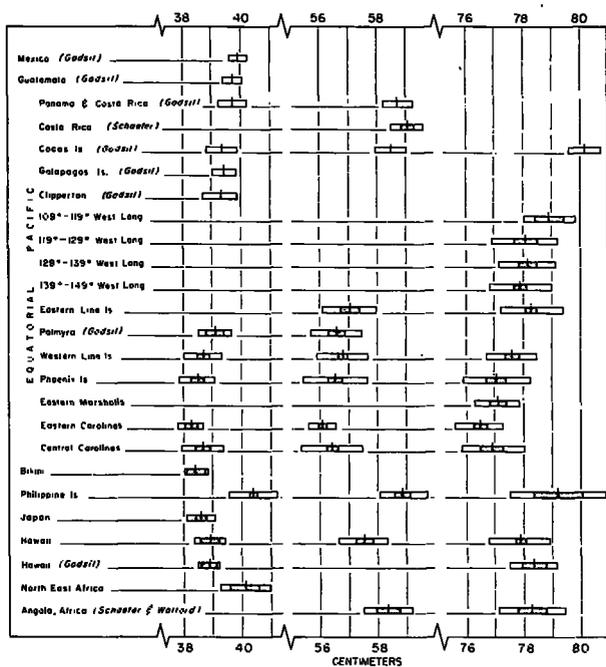


FIGURE 15.—Distance from snout to insertion of anal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

dorsal fin (fig. 14) and between the snout and the insertion of the anal fin. In the large fish the trend is especially clearcut for the snout to insertion of anal fin (fig. 15). The snout to insertion of ventral fins (fig. 16) shows a somewhat similar tendency, but again the differences are smaller and sampling variation causes some confusion. The remaining characters, distance from the insertion of the ventral fins to the anterior edge of the vent (fig. 17) and greatest body depth (fig. 18), present a more confused picture. In the medium-sized fish there is a tendency for the fish from the eastern Pacific to have a greater body depth, but this tendency is not so noticeable among the larger specimens. The distance from the ventral insertion to the anterior edge of the vent divides the samples into two groups. The distance is about 40 cm. in the large size group among all samples from between longitudes 109° W. and 149° W. and about 39 cm. in the samples from the eastern Line Islands to the central Caroline Islands area.

Clearly, then, a more or less steady cline from the eastern to the west-central Pacific exists,

YELLOWFIN TUNA

with the average yellowfin in the eastern Pacific having the larger head, shorter pectoral, second dorsal, and anal fins, and greater distances from the snout to the insertions of first dorsal and ventral fins. It also has considerably the greater distances from the snout to the insertion of the second dorsal and anal fins, a greater body depth, and greater length from the ventral fins to the vent. Evidently, these greater distances to the insertions of the second dorsal and anal fins mean a correspondingly shorter caudal peduncle.

When this series of samples from the equatorial Pacific is compared with other samples from the more temperate waters some surprising differences are found. In the Bikini Island sample, which came from just outside the equatorial area at latitude 12° N., the fish would be expected to resemble those from the nearby Caroline Islands to the southwest, but they had especially short second dorsal and anal fins and a greater distance from the snout to the insertion of the first dorsal fin. The Bikini fish were small and were taken by trolling close to the island. In many regions of the Pacific these small yellowfin appear to be

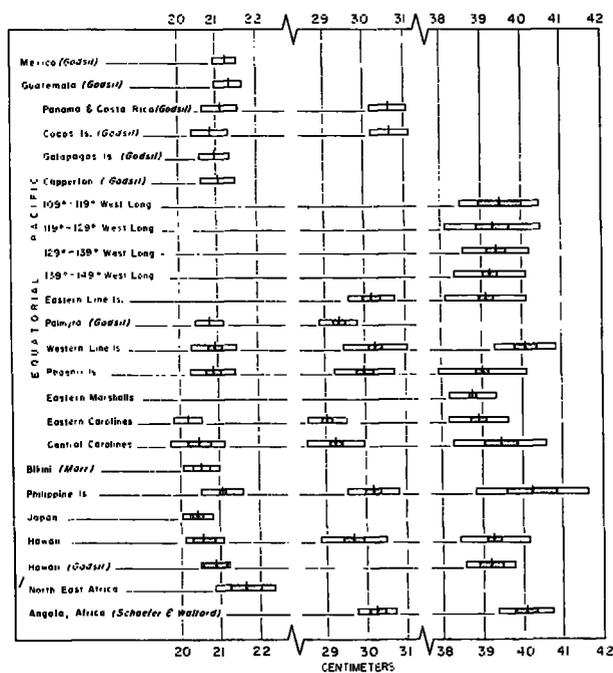


FIGURE 16.—Distance from snout to insertion of ventral fins of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

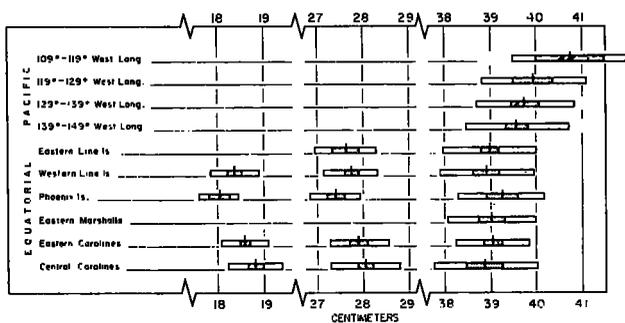


FIGURE 17.—Distance from insertion of ventral fin to anterior edge of vent of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

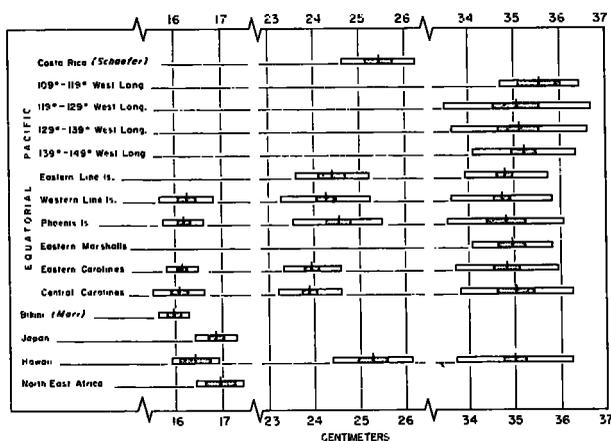


FIGURE 18.—Greatest body depth of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar \pm two standard errors of the mean, the hollow bar \pm one standard deviation from regression.)

common in the vicinity of islands and are very rarely taken on longlines. So this group of small fish near Bikini may be a relatively isolated one.

Characteristics of the sample from the Philippines are particularly surprising, because in all of the characters examined the fish are much more like those of the eastern Pacific than those of the nearby Caroline Islands area. This is consistently true for all size groups in all characters. Further, in the distance from the snout to the insertion of the first dorsal fin and also to the second dorsal, the means for the Philippine sample are distinctly larger than for any other samples.

The sample from Japan consisted only of small fish and in all respects is remarkably like the groups sampled from Hawaii. In not a single character is the difference of the means great enough to separate the dark bars that represent twice the standard error of the mean and, hence, indicate a statistically significant difference between the means.

The samples from Hawaii show somewhat mixed relationships with those from the equatorial area. In head length they are similar to those from the Caroline Islands, whereas in length of fins and in the distances from snout to insertion of the second dorsal and anal fins they are much more like the yellowfin of the equatorial area southeast of Hawaii between longitudes 129° and 159° W.

The sample of small yellowfin from the Society Islands was measured after being landed and thawed in Honolulu. Such handling may have changed the dimensions and this sample may not be directly comparable to the others. For this reason this is not a satisfactory sample. It is, however, near the Phoenix Islands sample in head length, height of the anal fin and distances from snout to first and second dorsal fins, but it has a very short second dorsal fin and much longer pectoral and anal fins than any other sample.

The sample from off Somaliland in northeast Africa is the most diverse of the group. It is similar to one or more central Pacific equatorial samples in head length and distances from snout to insertion of first and second dorsal fins, but it has very short pectoral, second dorsal, and anal fins. Somaliland fish also have a very long distance from the snout to the insertion of the anal fin, an especially deep body, and a long distance from the snout to the insertion of the ventral fins. This sample is very different from the sample from the west coast of Africa taken near Angola, where the fish are remarkably similar to those of the eastern Pacific in most dimensions. The yellowfin from Angola differ from those from Costa Rica principally in having slightly longer fins (as was pointed out by Schaefer and Walford, 1950).

In summary, yellowfin from the Pacific show a continuous cline morphologically along the Equator, whereas the samples taken in areas distant from the Equator differ erratically from the equatorial cline. The dimensions, however, are within the range of characters in the equatorial cline or

are so close to one of the ends of the cline that there appears to be no evidence of genetically isolated stocks in the Pacific. This evidence will be considered further after data on overlap have been discussed.

COMPARISON OF SAMPLES FROM THE SAME AREA

Samples by Godsil (1948) and Godsil and Greenhood (1951) were obtained from areas also sampled by Schaefer and Walford (1950) or by POFI, and it is useful to look for evidence that different methods of measurement may have been used. Godsil's sample from Panama and Costa Rica came from an area close to that of Schaefer and Walford's from Costa Rica, and agreement among the four characters available for comparison is generally good even though Godsil's fish have slightly longer heads and a slightly longer distance from the snout to first dorsal fin. In addition, Godsil's sample from Hawaii may be compared with that of POFI, for it was obtained from rather limited areas: the small fish came from near Johnston Island and off islands between Kauai and French Frigate Shoals and the large fish from the Honolulu fish market. The POFI sample was obtained from a much wider area, although again most of the large fish were measured in the Honolulu market. Five measurements in two size groups are available to compare, and in not a single instance is the difference between means great enough to separate the black bars (and indicate a statistically significant difference).

Not as close statistically are Godsil and Greenhood's samples from Palmyra Island and the POFI samples from the eastern and western Line Islands, but the differences are complicated. Samples are available for comparison of small and medium size yellowfin taken by Godsil and Greenhood with similar sizes taken by POFI from the western Line Islands and a sample of medium size yellowfin from the eastern Line Islands. Godsil and Greenhood's data from Palmyra Island were obtained from frozen fish in a catch made during about 12 days of fishing in the vicinity of Fanning and Palmyra Islands. These days were nearly consecutive during February 1949. The POFI samples of small and medium fish were obtained from these islands as well as in the vicinity of the neighboring Washington and Christmas Islands, Kingman Reef, and a few from farther offshore.

(All of these islands are near the borderline between our eastern and western Line Islands areas.) They were, however, taken over a much longer period (table 2) so they should be much more representative of the areas than Godsil and Greenhood's samples.

When a comparison of the mean character sizes of group M fish is made between our eastern and western Line Islands samples, not a single character differs by more than the length of the black bars, except height of the anal fin, and here the difference is in line with the general trend along the Equator. But when these two samples and the sample of small yellowfin from the western Line Islands are compared with Godsil and Greenhood's sample, I find that in head length their group M runs smaller and their group S somewhat larger; in distance from snout to insertion of first dorsal fin, their group M is about the same, and their group S considerably larger. Their distances from snout to insertions of second dorsal and anal fins show fairly good agreement with POFI samples. In the last character—distance from snout to insertion of the ventral fins—there is fairly good agreement between Godsil and Greenhood's sample and the POFI sample from the western Line Islands for group S; but then for group M the distance is markedly shorter than in either of the other two samples. Such erratic results suggest either that Godsil and Greenhood may have been sampling too few schools of fish to obtain a thoroughly representative sample or that freezing and thawing may have changed the proportions of the fish.

Despite these differences, I conclude that the techniques of measurement used by POFI were sufficiently close to those used by Godsil and Greenhood to arrive at about the same conclusions with regard to morphological differences among yellowfin from different areas of the Pacific.

MULTIPLE CHARACTER COMPARISON

After having examined the data for the mean differences in body shape, I shall consider next the overlap of the frequency distributions not merely of one character but of all characters considered simultaneously.

The measure of overlap that I shall use is similar to the measures of overlap used by taxonomists in many fields (Mayr et al., 1953: 146). The measures have all arisen from the concept of

two overlapping frequency distributions and are expressed either as the percent of the actual frequency classes in the area of overlap or as a proportion of the observations estimated to be in the area of overlap of two normal distributions. The amount of overlap can be indicated as the distance between the means in units of the standard deviation or as an area under the curves. I prefer a measure of the overlapping area under two normal curves, which I have described fully (Royce, 1957) and which I have called Ω . The overlap (Ω) is expressed as a percent and varies from 0 to 100 as the means of the distributions approach one another.

This concept of overlap is especially useful because it answers the question, "What parts of population *A* possess characters that are within the range of population *B*?" I shall construe the answer to this question as a maximum for the proportion of population *A* which might have migrated from the area of population *B*.

In the computational procedure I shall follow closely the method outlined by Rao (1952, chapters 8 and 9). His method starts with pooled estimates of the correlations and standard deviations which are applied to the normalized mean values in order to transform them to values that are uncorrelated and that have unit standard deviations. In this method of analysis the amount of work increases approximately as the square of the number of characters used. To reduce the number, we have dropped from further consideration the greatest body depth, the distance from insertion of ventral fin to anterior edge of vent, and the distance from snout to insertion of ventral fins. This procedure seemed justifiable because (1) in some of our samples one or more of these characters were not measured, (2) none of them revealed as large differences between areas as other characters, (3) the distance from snout to insertion of ventral fins is highly correlated with head length and distance from snout to insertion of anal fin, and (4) it will be shown subsequently that seven characters are probably more than are necessary.

Because the statistics have arisen from regression analysis, it will be necessary to substitute for Rao's statistics comparable statistics determined from regression. Instead of the intragroup standard deviations from the mean, I use the intragroup standard deviations from regres-

sion. Instead of the intragroup correlations of the several characters, I use the intragroup partial correlations independent of total length. Instead of the actual mean values of the characters, I use the mean values estimated for certain given fork lengths. Therefore, in all of the statistics the effect of any changes with fork length is removed.

It has been impossible to assume that the regression lines were satisfactory beyond limited length groups, so we have broken down all of our statistics (except for partial correlations) into the length groups which were used in the previous section for character-by-character comparisons. They are group *S*, composed of fish less than 80-cm. fork length, which are compared at a length of 65 cm. (about 12 lb.); group *M*, from 80 to 120 cm., compared at a length of 100 cm. (43 lb.); and group *L*, more than 120 cm., compared at a length of 140 cm. (118 lb.). The basic regression constants, means, et cetera are in the appendix.

Because adequacy of the sampling varied widely, I have sought to obtain estimates of standard deviations from samples that I consider to be more representative. I have chosen the three areas most widely represented in time and among all three length groups; namely, Hawaii, western Line Islands, and eastern Caroline Islands. From these samples for each character in each size group I have obtained the standard deviation from regressions squared, $S_{y,x}^2$, averaged it for the three areas, and ended with an estimate of a pooled standard deviation from regression (within groups) which gives equal weight to the three areas (table 5).

TABLE 5.—Pooled mean standard deviations from regression for each body character for the three size groups

Size group (cm.)	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Small, <80.....	0.3981	0.7822	0.03163	0.03283	0.4470	0.5990	0.5897
Medium, 80-120 -	.5903	1.2891	.04626	.06141	.6776	.9426	.8943
Large, >120.....	.6596	1.2280	.06011	.05680	.7376	.9581	.9614

These standard deviations are the basic units of morphological distance, and it is desirable to examine them to determine how representative they are of all samples. Two matters are pertinent: first, I have used the actual standard

deviation from regression without adjusting for the difference of the mean \bar{x} from the X used for comparisons, so I need to know how close the means are to the comparison values; and second I need to consider whether the average dispersion about the lines is close to the grand average of all samples. The mean lengths of the three areas (giving equal weight to each) are 62.10, 99.32, and 142.04 cm. The means chosen for comparison are 65, 100, and 140 cm. If we consider that the standard deviation is directly proportional to the length of fish, then I have tended to underestimate slightly the standard deviation for the small and the medium groups and have slightly overestimated it for the large group.

In addition, the standard deviation of \hat{Y} increases with distance from \bar{y} . For this reason I have tended to slightly underestimate the $S_{y,x}$ for the small and large groups.

Finally, the average coefficients of variation (table 4) of the three selected areas (for five characters) for the three size groups are 1.85, 1.80, and 1.63. These coefficients are close to the grand means of all samples, which are 1.74, 1.81, and 1.81 for small, medium, and large groups, respectively. With these partly compensating and in all cases small differences, I have chosen to make no adjustments but used the standard deviations from regression directly with confidence that they are very close to the grand average.

For the partial correlations of the several characters independent of fork length I have used a selected sample of 30 fish each from Hawaii, Costa Rica, eastern Line Islands, western Line Islands, and central Carolines. The 30 fish were selected from each area in the size range from 80 to 130 cm. and were chosen at random within the size group. From these, the intragroup correlations (table 6) and partial correlations were calculated (table 7).⁷

From the means and the pooled standard deviations the normalized mean values of each character have been obtained. The means were simply averaged to obtain a grand average, and then the deviations of each mean from the grand

⁷ This table of partial correlations is one of the more laborious parts of the entire computation. The particular data were chosen during preliminary computations as a test of the method on rather widely dispersed groups, all with good sample coverage. The size group corresponds nearly but not exactly to size group M. I have assumed that the partial correlations of these body parts for what is essentially the medium-size group for five samples with wide coverage are the same for all areas and also for the small and large size groups.

average in units of the average standard deviation were found (table 8).

Using the notation of Rao (1952), the normalized mean values $x_1 \dots x_p$ were then transformed to values $Y_1 \dots Y_p$, which are uncorrelated, and subsequently to other values $y_1 \dots y_p$, which have unit standard deviation. The general formulas as given by Rao are—

$$Y_p = x_p - a_{pp-1} - \dots - a_{p1}Y_1$$

$$a_{ij} = \frac{b_{ij}}{\sqrt{V(Y_j)}} \text{ when } j < i - 1$$

$$b_{ij} = \lambda_{ij} - \sum_{t=j-1}^1 a_{it}b_{it}$$

$$V(Y_i) = \lambda_{ii} - \sum_{j=1}^{i-1} a_{ij}b_{ij}$$

$$y_i = \frac{Y_i}{\sqrt{V(Y_i)}}$$

The a and b values (tables 9 and 10) are convenient intermediate values in the computations. $V(Y_i)$ (table 11) is the variance of Y_i and y_i and is the final transformed value of the normalized mean (table 12). From these transformed means which have unit standard deviation and which are uncorrelated with one another, I obtained the distance in units of the standard deviation squared (D^2) for each possible area comparison in each size group (table 13). The total D^2 , obtained by adding the D^2 values for each of the seven characters, is subject to a small bias due to the number of characters and the size of the samples. This bias (which is largest in the smallest samples and most troublesome in the samples most closely related) is removed by subtracting the value

$$p \frac{n_1 + n_2}{n_1 n_2}$$

in which p is the number of characters and n_1 and n_2 the number of observations in each sample (Rao, 1952: 364).⁸

From the adjusted sum of D^2 the value of the overlap (Ω) is determined by finding D , then $\frac{D}{2}$,

which is used as an argument to enter the tables of the area under a normal curve to find the area of one tail and then multiplying by 200 to express the area of two tails as a percentage Ω .

⁸ I have ignored the slight variation in value of n among different characters within the samples.

TABLE 6.—Intragroup correlations of body characters

[See text for explanations]

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Fork length.....	0.98422	0.92124	0.93830	0.92534	0.97846	0.99448	0.99210
Head length.....		.90009	.92767	.91515	.98329	.98667	.98618
Length of pectoral fin.....			.92373	.89801	.89439	.90894	.90865
Height of—							
Second dorsal fin.....				.96177	.91393	.92877	.92584
Anal fin.....					.90770	.91479	.90931
Snout to insertion of—							
First dorsal fin.....						.98647	.97739
Second dorsal fin.....							.99074

TABLE 7.—Partial correlations of body characters, independent of fork length

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Head length.....	1.0000						
Length of pectoral fin.....		-0.0960	0.0683	0.0657	0.5549	0.4243	0.4387
Height of—		1.0000					
Second dorsal fin.....			1.0000	.7133	-.0583	-.1199	-.1164
Anal fin.....				1.0000	.0292	-.1367	-.1833
Snout to insertion of—							
First dorsal fin.....					1.0000	.6191	.2571
Second dorsal fin.....						1.0000	.3131
Anal fin.....							1.0000

TABLE 8.—Normalized mean values x_1 of body characters

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
SMALL-SIZE GROUP							
West Line Islands.....	0.9797	-0.3068	-0.2308	-0.1889	-0.2461	0.0334	-0.1187
Phoenix Islands.....	.6782	-.0511	.5185	.2315	-.2287	-.0334	-.5257
Bikini Island.....	-.5024	.2813	-.2940	-.1614	.9843	-.4841	-.5935
East Caroline Islands.....	-.5777	1.3424	1.2235	1.2489	-.7383	-.5175	-.8818
Central Caroline Islands.....	-.7284	1.3468	1.3468	1.0448	-.7393	-.4674	-.2035
Japan.....	-.3266	.3963	.3351	.1340	-.2013	.1669	-.2713
Hawaii.....	-.5526	-.1790	-.1676	-.0061	.3803	.5342	.2544
Northeast Africa.....	1.1304	-3.0043	-2.7347	-2.3089	.8725	.7846	2.3402
MEDIUM-SIZE GROUP							
Costa Rica.....	.8809	-1.4274	-1.7034	-1.3109	.4870	1.0397	2.0463
East Line Islands.....	.6776	-.5740	-.2810	-.3843	-.0443	-.2228	-.1565
West Line Islands.....	.5590	-.1164	.0843	.2215	0	-.2228	-.4137
Phoenix Islands.....	.1016	.7214	.5275	.6009	-.1033	-.5092	-.7045
East Caroline Islands.....	-1.2197	.9619	1.1911	1.0780	-.5313	-.7532	-1.3083
Central Caroline Islands.....	-1.2367	1.2411	1.1176	.9168	-.5756	-.8805	-.8722
Hawaii.....	-.5252	-.1551	-.4172	-.3713	.3542	.3395	.3406
Angola, Africa.....	.7623	-.6283	-.5275	.7572	.4280	1.2306	1.0846
LARGE-SIZE GROUP							
109°-119° W.....	.2122	-1.3029	-1.5339	-1.9894	.1320	1.2420	1.2690
119°-129° W.....	.3335	-.5130	-1.1429	-1.2993	.5280	.4175	.364
129°-139° W.....	.2436	-.5782	-.8265	-.8838	.4884	.5219	.4473
139°-149° W.....	.0910	.2524	-.5107	-.4806	-.0528	.1774	.2288
East Line Islands.....	-.2122	.1629	.2196	.2289	-.2640	-.1566	.5409
West Line Islands.....	.3487	.3502	.5523	.6954	-.5412	-.3862	-.1144
Phoenix Islands.....	-.2122	.3339	.7969	1.0000	-.4488	-.3549	-.6969
East Marshall Islands.....	-.5761	.2769	1.2610	1.4754	-.1584	-.0417	-.6553
East Caroline Islands.....	-.6216	.5375	1.3026	1.5933	-.2376	-1.0437	-1.3106
Central Caroline Islands.....	-.2274	.4805	1.3159	1.5827	-.3300	-.9498	-.8217
Hawaii.....	-.6822	.3013	-.3876	-.4947	.1188	-.2818	.1768
Angola, Africa.....	1.3190	-.2606	-1.0497	-1.4261	.8316	.9185	.5721

The results of these computations expressed as the percentage of overlap between areas appear in table 14. Here the equatorial series has been arranged in order from Costa Rica on the east to

the central Carolines on the west. The other samples from Bikini Island, Japan, Hawaii, Angola, and northeast Africa are added in no special order.

TABLE 9.—Table of a

[See text for explanation]

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Head length.....	1.0000	—0.0960	0.0633	0.6507	0.5549	0.4243	0.4387
Length of pectoral fin.....		1.0000	.45162	.31804	— .03435	— .13713	— .06731
Height of—							
Second dorsal fin.....			1.0000	.71415	— .10190	— .11033	— .14654
Anal fin.....				1.0000	— .12486	— .11991	— .21979
Snout to insertion of—							
First dorsal fin.....					1.0000	.56912	.01926
Second dorsal fin.....						1.0000	.14781
Anal fin.....							1.0000

TABLE 10.—Table of b

[See text for explanation]

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Head length.....	1.0000	—0.0960	0.0683	0.0657	0.5549	0.4243	0.4387
Length of pectoral fin.....		1.0000	.44746	.31511	— .03403	— .13587	— .06668
Height of—							
second dorsal fin.....			1.0000	.56650	— .08083	— .08752	— .11625
Anal fin.....				1.0000	— .06129	— .05886	— .10790
Snout to insertion of—							
First dorsal fin.....					1.0000	.37742	.01300
Second dorsal fin.....						1.0000	.08478
Anal fin.....							1.0000

NOTE.—These values are recorded in 5 significant figures; however, 8 significant figures were carried in the computations leading to *a*-values. The first row was obtained by preceding computations to 4 significant figures.

TABLE 11.—Variances and square roots of variances for various body measurements

[See text for explanation]

Variate	Variance ¹ $V(Y_i)$	$D\sqrt{V(Y_i)}$	Variate	Variance ¹ $V(Y_i)$	$D\sqrt{V(Y_i)}$
$V(Y_1)$	1.00000	1.00000	$V(Y_6)$57360	.75736
$V(Y_2)$99078	.99538	$V(Y_7)$74952	.86575
$V(Y_3)$79325	.89065	$V(Y_8)$76599	.87521
$V(Y_4)$49090	.70064	$V(Y_9)$40215	.63415
$V(Y_5)$67503	.82160	$V(Y_{10})$33024	.57466

¹ Values are recorded in 5 significant figures; however, 8 significant figures were carried in the computations leading to *a*-values (in table 9).

In the equatorial series there is a clear tendency for more closely located samples to have greater overlap. The overlap varies from a maximum of 82 percent and 81 percent in medium and large size groups for the comparison between eastern Carolines and central Carolines to a low of 3 percent for the comparison of Costa Rica with eastern Carolines and central Carolines. The relation of the average overlap to the separation of the samples in miles (fig. 19) is clear cut and much the same in all size groups. This graph has been made with the assumption that each population was located in the center of each 10° block of longitude and that the centers of these blocks were separated by units of 600 miles.

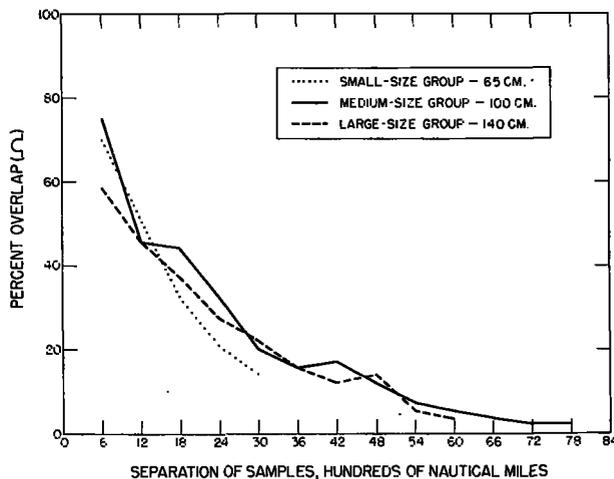


FIGURE 19.—Average percent of overlap of samples of yellowfin from the equatorial Pacific.

(This assumption disregards the small variations in location within the sample areas and the fact that one sample area was 11° of longitude in width instead of 10°.)

From this graph it appears that, on the average, samples of yellowfin tuna from along the Equator separated by 1,500 miles overlap less than 50

TABLE 12.—Transformed normalized mean values y_i of characters

[See text for explanation]

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
SMALL-SIZE GROUP							
West Line Islands.....	0. 9797	-0. 2137	-0. 2209	-0. 0644	-0. 9877	0. 0200	-0. 6794
Phoenix Islands.....	. 6782	. 0141	-. 5269	-. 2178	-. 6433	. 0159	-. 8993
Bikini Island.....	-. 5024	. 3342	-. 4126	. 0855	1. 4924	-1. 2648	-. 3296
East Caroline Islands.....	-. 5777	1. 2929	. 7622	. 5606	-. 4301	. 2953	-. 4415
Central Caroline Islands.....	-. 7284	1. 4967	. 8085	. 1493	-. 2710	. 3465	-. 5855
Japan.....	-. 3266	. 3666	. 2144	-. 1384	. 0293	. 5073	-. 1779
Hawaii.....	-. 5526	-. 2331	-1. 0979	. 2481	-. 7879	. 5083	. 5033
Northeast Africa.....	1. 1304	-2. 9092	-. 1. 6824	-. 5596	. 5116	-. 4330	1. 6070
MEDIUM-SIZE GROUP							
Costa Rica.....	. 8809	-1. 3491	-1. 2942	-. 1691	-. 1833	. 5806	1. 5185
East Line Islands.....	. 6776	-. 5113	-. 1056	-. 2852	-. 5141	-. 4994	-. 5564
West Line Islands.....	. 5590	-. 0630	. 0867	. 2135	-. 3933	-. 3452	-. 6631
Phoenix Islands.....	. 1016	. 7346	. 2143	. 3217	-. 1744	-. 4276	-. 6604
East Caroline Islands.....	-1. 2197	. 8487	. 9957	. 3656	. 2835	-. 1604	-. 5967
Central Caroline Islands.....	-1. 2367	1. 1276	. 7736	. 2127	. 2444	-. 2908	-. 1059
Hawaii.....	-. 5252	-. 2065	-. 3269	-. 0907	. 7508	. 1975	. 5458
Angola, Africa.....	. 7623	-. 5577	-. 3650	-. 5689	. 0031	. 9849	. 5397
LARGE-SIZE GROUP							
109°-119° W.....	. 2122	-1. 2885	-1. 0870	-1. 2908	-. 0190	1. 0161	. 7226
119°-129° W.....	. 3335	-. 4832	-1. 0630	-. 7023	. 3547	-. 1536	-. 5763
129°-139° W.....	. 2426	-. 5575	-. 6661	-. 4276	. 3794	. 0388	-. 1557
139°-149° W.....	. 0910	. 2448	-. 7034	-. 1065	-. 1755	. 2241	. 0757
East Line Islands.....	-. 2122	. 1432	. 1894	. 1100	-. 1623	. 0735	. 7850
West Line Islands.....	. 3487	. 3855	. 4008	. 4218	-. 3788	-. 0040	-. 1270
Phoenix Islands.....	-. 2122	. 3150	. 7508	. 6232	-. 3732	. 1000	-. 4551
East Marshall Islands.....	-. 5761	. 2226	1. 3444	. 8387	. 2648	. 4147	-. 1544
East Caroline Islands.....	-. 6216	. 4800	1. 2644	. 9676	. 1873	-. 7855	-. 7008
Central Caroline Islands.....	-. 2274	. 4608	1. 2610	. 9273	-. 1833	-. 6629	-. 3540
Hawaii.....	-. 6322	. 2369	-. 5063	-. 2895	. 5901	-. 4029	. 4817
Angola, Africa.....	1. 3190	-. 1346	-1. 2044	-1. 0049	. 0897	. 1274	-. 3964

percent in the seven characters considered; those separated by 3,000 miles overlap less than 25 percent; and those separated by 6,000 miles overlap less than 6 percent.

The graph also shows that the average overlap varies little with the size group of fish, although the data in table 14 indicate a slight tendency for the small and medium size groups to have less overlap than the large. This tendency appears to be most marked in the comparisons of samples from the western Line and Phoenix Islands areas with those from the eastern and central Caroline Islands areas. In all of these comparisons the large size group shows the most overlap and the small size group the least. In the comparisons of the Hawaiian samples with those from the equatorial area, the small size group shows the least overlap, but the medium size group generally shows slightly greater overlap than the large. The data are too scant to establish the significance of this tendency, but it may be associated with more wandering by the larger fish.

The overlap of the other samples with those from the equatorial Pacific area follows, in general, the relations that were deduced from consideration of single characters. The Bikini Island

sample shows rather little overlap with any of the equatorial samples—even the sample from the nearby Caroline Islands area—but a considerable overlap with samples from Japan and Hawaii. The Japanese sample, on the other hand, is apparently intermediate in structure between the Bikini Island and equatorial samples, for it shows a considerable overlap with all other samples where a comparison is possible. The samples from Hawaii, likewise, show a fairly large amount of overlap with most of the equatorial samples, but the largest size group is most similar to the equatorial yellowfin from between longitudes 129° and 159° W. This area is generally southeast of Hawaii rather than directly south. The Angola, Africa, fish show a large amount of overlap with the large fish from longitudes 119° to 149° W. They are as similar to these fish as are many of the samples from adjoining areas along the Pacific Equator. Moreover, in all comparisons of Angola samples with samples from 119° to 149° W. there is a marked tendency for the overlap to be less among the larger size group than the medium size group. This finding conforms with the observation made by Schaefer and Walford (1950) that the principal characters differentiating

TABLE 13.—Value of D^2 computed from transformed means and adjusted for sample size to determine percentage of overlap (Ω)

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—			D^2	Bias	Adjusted J^2	Ω
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin				
SMALL-SIZE GROUP											
West Line-Phoenix Islands	0.0909	0.0519	0.5592	0.0235	0.1152	0.0000+	0.0484	0.8891	0.3482	0.5409	71
-Bikini Island	2.1966	2.006	.0367	.0225	6.1509	1.6507	.1266	10.3846	.3949	9.9997	11
-East Caroline Islands	2.4255	2.2698	.9665	.3906	.3109	.0758	.0566	6.4957	.2758	6.2199	21
-Central Caroline Islands	2.9276	2.9255	1.0597	.0457	.5137	.1066	1.0772	8.6460	.3482	8.2978	15
-Japan	1.7064	.3367	.1895	.0055	1.0343	.2375	.2515	3.7614	.3949	3.3765	36
-Hawaii	2.3479	.0004	.7691	.0977	3.1528	.2384	1.3988	8.0051	.3535	7.6516	17
-Northeast Africa	.0227	7.2657	2.1360	.2462	2.2479	.2052	5.2276	17.3503	.3049	17.0454	4
Phoenix-Bikini Islands	1.3938	.0484	.8827	.0920	4.5826	1.6402	.3314	8.9711	.4150	8.5561	14
-East Caroline Islands	1.5773	1.6353	.0554	.6059	.0476	.0731	.2096	4.2092	.3059	3.9033	32
-Central Caroline Islands	1.9785	1.0811	.0793	1.348	.1424	.1093	1.5821	6.2245	.3784	5.8461	23
-Japan	1.0096	.1243	.0977	.0063	.4591	.2415	.6204	2.4589	.4150	2.0439	47
-Hawaii	1.5149	.0611	2.6400	.2171	2.0627	.2748	1.9673	8.7379	.3836	8.3543	15
-Northeast Africa	.2045	8.5457	4.8810	1.198	1.3454	.2015	6.2315	21.5764	.3350	21.2414	2
Bikini-East Caroline Islands	.0057	1.1208	1.3802	.2257	3.6960	.2439	.0139	8.8762	.3425	8.5337	14
-Central Caroline Islands	.0511	1.5939	1.4911	.0041	3.1096	2.5963	.4653	9.3114	.4150	8.8964	14
-Japan	.0309	.0175	.3931	.0501	2.1407	3.1403	.0212	5.7938	.4516	5.3422	25
-Hawaii	.0025	.2184	.4966	.0264	.4963	3.1439	.6833	5.0409	.4203	4.6206	28
-Northeast Africa	2.6660	9.8810	1.6124	.4162	.9620	.6919	3.7272	19.9567	.3716	19.5851	3
East Caroline-Central Caroline Islands	.0227	.0415	.0021	.1692	.0253	.0026	.6400	.9034	.3059	.5975	70
-Japan	.0631	.8580	.3001	.4856	.2110	.0449	.0695	2.0362	.3425	1.6927	51
-Hawaii	.0006	2.3287	3.4600	.0977	1.4835	.0454	.8926	8.3085	.3111	7.9974	16
-Northeast Africa	2.9176	17.6576	5.9761	1.2548	.8868	.5304	4.1964	33.4197	.2625	33.1572	4
Central Caroline Islands-Japan	.1614	1.2771	3.6340	.0628	.0902	.0259	.2877	2.2781	.4150	1.8631	49
-Hawaii	.0309	2.9922	3.6344	.0098	1.1213	.0262	.0210	7.8358	.3836	7.4522	17
-Northeast Africa	3.4551	19.4120	6.2046	.5025	.6125	.6076	1.5588	32.3531	.3350	32.0181	4
Japan-Hawaii	.0511	.3596	1.7221	.1494	.5755	.0000+	.4640	3.3217	.4203	2.9014	39
-Northeast Africa	2.1228	10.7309	3.5979	.1774	.2826	.8842	3.1359	20.9317	.3716	20.5601	2
Hawaii-Northeast Africa	2.5325	7.1615	.3416	.6524	.0763	.8860	1.2182	13.1685	.3403	12.8282	7
ΣD^2	33.8002	101.3132	45.2911	6.8107	37.8848	20.1191	36.5245	-----	-----	-----	-----
Mean	1.2072	3.6183	1.6175	.2254	1.3530	.7185	1.3044	-----	-----	-----	-----
Σ means	1.2072	4.8255	6.4430	6.6684	8.0214	8.7399	10.0443	-----	-----	-----	-----
Ω	58	27	20	20	16	14	11	-----	-----	-----	-----
MEDIUM-SIZE GROUP											
Costa Rica-East Line Islands	0.0413	0.7019	1.4128	0.0135	0.1094	1.1236	4.3052	7.7077	0.4535	7.2542	18
-West Line Islands	.1036	1.6541	1.9069	.1494	.0441	.8205	4.7594	9.4350	.3218	9.1132	13
-Phoenix Islands	.6073	4.3418	2.2756	.2409	.0001	.9765	4.7476	13.1898	.3600	12.8298	7
-East Caroline Islands	4.4125	4.8303	5.2436	.2859	.2179	.5198	4.4741	19.9641	.3086	19.6155	3
-Central Caroline Islands	4.4842	6.1340	4.2758	.1458	.1829	.7249	2.6387	18.6863	.3100	18.2763	3
-Hawaii	1.9771	1.3055	.9557	.0061	.8725	.1318	.9461	6.1748	.4473	5.7275	23
-Angola, Africa	.0141	.6263	.8634	.1598	.0347	.1800	.9580	2.8363	.5747	2.2616	45
East Line-West Line Islands	.0141	.2010	.0370	.2487	.0146	.0288	.0114	.5506	.2926	.2580	80
-Phoenix Islands	.3318	1.5523	1.023	.3663	.1154	.0052	.0108	2.4961	.3908	2.1553	46
-East Caroline Islands	3.5997	1.8496	1.2129	.4235	.6362	.1149	.0016	7.8384	.3394	7.4990	17
-Central Caroline Islands	3.6645	2.6860	.7730	.2479	.5753	.0435	.2030	8.1922	.2807	7.9125	16
-Hawaii	1.4467	.0929	.0490	.0378	1.6000	.4857	1.2148	4.9269	.4180	4.5089	19
-Angola, Africa	.0072	.0022	.0673	.0805	.2675	2.2031	1.2014	3.8292	.5454	3.2838	36
West Line-Phoenix Islands	.2062	.0362	.0163	.0117	.0479	.0068	.0000+	.9281	.1991	.7290	67
-East Caroline Islands	3.1638	.8312	.8203	.0231	.4581	.0342	.0044	5.3411	.2077	5.1334	26
-Central Caroline Islands	3.2245	1.4175	.4718	.0000+	.4067	.0030	.3105	5.8340	.1491	5.6849	23
-Hawaii	1.1755	.0206	.1711	.0925	1.3090	.2945	1.4614	4.5246	.2983	4.2383	30
-Angola, Africa	.0413	.2447	.2040	.6121	.1571	1.7892	1.4467	4.4751	.4138	4.0613	31
Phoenix-East Caroline Islands	1.7458	.0130	.6106	.0019	.2097	.0714	.0041	2.6565	.2459	2.4106	44
-Central Caroline Islands	1.7910	.1544	.3128	.0119	.1754	.0187	.3075	2.7717	.1873	2.5844	42
-Hawaii	.3929	.8857	.2929	.1701	.8560	.3908	1.4549	4.4433	.3245	4.1188	31
-Angola, Africa	.4365	1.6700	.3356	.7932	.0315	1.9952	1.4402	6.7022	.4520	6.2502	21
East Caroline-Central Caroline Islands	.0003	.0778	.0493	.0234	.0015	.0170	.2409	.4102	.1959	.2143	82
-Hawaii	.4823	1.1134	1.7493	.2082	.2184	.1281	1.3053	5.2050	.3332	4.8718	27
-Angola, Africa	3.9283	1.9780	1.8515	.8733	.0786	1.3117	1.2914	11.3128	.4606	10.8522	10
Central Caroline Islands-Hawaii	.5062	1.7798	1.2111	.0921	.2564	.2384	.4247	4.5087	.2745	4.2342	30
-Angola, Africa	3.9960	2.8402	1.2964	.6109	.0582	1.6274	.4168	10.8459	.4019	10.4440	11
Hawaii-Angola, Africa	1.6577	1.233	.0015	.2287	.5591	.6200	.0000+	3.1903	.5392	2.6511	41
ΣD^2	43.4554	39.7637	28.5558	6.1582	9.4942	15.8797	35.5809	-----	-----	-----	-----
Mean	1.5520	1.4201	1.0199	.2199	.3391	.5671	1.2707	-----	-----	-----	-----
Σ means	1.5520	2.9721	3.9920	4.2119	4.5510	5.1181	6.3888	-----	-----	-----	-----
Ω	53	39	32	30	29	26	21	-----	-----	-----	-----
LARGE-SIZE GROUP											
109°-119° West-119°-129° W	.0147	.6485	.0006	.3457	.1397	1.3682	4.2045	.4823	3.7222	3.7222	33
-129°-139° W	.0009	.5344	.1772	.7443	.1587	.8599	.3214	2.7968	.4823	2.3145	45
-139°-149° W	.1469	2.3510	1.471	1.2629	.0245	.6273	.4185	4.9782	.3953	4.5829	28
-East Line Islands	.1801	2.0498	1.6292	1.9608	.0207	.8885	.0089	6.7330	.3779	6.3551	21
-West Line Islands	.0186	2.8023	2.2135	2.9313	.7393	1.0406	.7218	10.4674	.4540	10.0134	11
-Phoenix Islands	.1801	2.5712	3.3775	3.6615	.1245	.8392	1.3870	12.1420	.4855	11.6565	9
-East Marshall Islands	.6214	2.2834	5.9117	4.5326	.0805	.3617	.7891	14.5604	.5083	14.0521	6
-East Caroline Islands	.6982	3.1276	5.5291	5.0981	.0426	3.2458	2.0261	19.7845	.4583	19.3062	3
-Central Caroline Islands	.1932	3.0601	5.5131	4.9177	.0287	2.8130	1.1591	17.6909	.4306	17.2603	4
-Hawaii	.8000	2.3268	.3372	1.0016	.3710	2.0136	.0580	6.9082	.3880	6.5222	20
-Angola, Africa	1.2250	1.3315	.0138	.0815	.0118	.7898	1.2522	4.7056	.5926	4.1130	31

TABLE 13.—Value of D^2 computed from transformed means and adjusted for sample size to determine percentage of overlap (Ω)—Continued

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—			D^2	Bias	Adjusted D^2	Ω
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin				
LARGE-SIZE GROUP—continued											
119°-129° West-129°-139° W.....	0.0083	0.0055	0.1575	0.0755	0.0006	0.0588	0.5358	0.8420	0.2979	0.5441	71
-139°-149° W.....	.0588	.5300	.1213	.2871	.2811	.1427	.4251	1.8541	.2109	1.6432	82
-East Line Islands.....	.2978	.3924	1.5685	.6598	.2678	.0516	1.8531	5.0910	.1935	4.8975	27
-West Line Islands.....	.0002	.7546	2.1427	1.2636	1.8215	.0224	.2019	5.9069	.2896	5.6373	24
-Phoenix Islands.....	.2678	.6371	3.2899	1.7570	.6298	.0643	.0147	6.5906	.3011	6.2895	21
-East Marshall Islands.....	.8274	.4982	5.7956	2.3747	.0081	.3230	.1780	10.0050	.3239	9.6811	12
-East Caroline Islands.....	.9122	.9278	5.4168	2.7894	.0280	.3993	.0155	10.4882	.2739	10.2143	11
-Central Caroline Islands.....	.3146	.8911	5.4010	2.6556	.2943	.2594	.0494	9.8659	.2462	9.6197	12
-Hawaii.....	1.0316	.5185	.3099	.1704	.0554	.0622	1.1194	3.2674	.2016	3.0658	38
-Angola, Africa.....	.9712	.1215	.0200	.0916	.0702	.0790	.0324	1.3359	.4082	.9777	62
129°-139° West-139°-149° W.....	.0230	.6437	.0014	.0682	.3079	.0133	.0064	1.0689	.2109	.8580	64
-East Line Islands.....	.2088	.4910	.7319	.2890	.2940	.0002	.3960	2.4089	.1935	2.2154	46
-West Line Islands.....	.0113	.8892	1.1393	.7215	1.5831	.0086	.0709	4.4319	.2696	4.1623	31
-Phoenix Islands.....	.2068	.7613	2.0076	1.1042	.5064	.0001	.3731	5.0195	.3011	4.7184	28
-East Marshall Islands.....	.6703	.6086	4.0421	1.6035	.1062	.0131	.0962	7.1400	.3239	6.8161	19
-East Caroline Islands.....	.7468	1.0764	3.7268	1.9406	.0369	.7644	.7336	9.0315	.2739	8.7576	14
-Central Caroline Islands.....	.2209	1.0369	3.7137	1.8358	.3223	.5651	.2598	7.9545	.2462	7.7083	16
-Hawaii.....	.8563	.6311	.0255	.0101	.0444	.2418	.1063	1.9235	.2016	1.7219	51
-Angola, Africa.....	1.1586	.1788	.2898	.3333	.0839	.0015	.3048	2.3507	.4082	1.9425	49
139°-149° West-East Line Islands.....	.0919	.0103	.7971	.0765	.0002	.0227	.5091	1.5018	.1065	1.3953	55
-West Line Islands.....	.0664	.0198	1.2193	.3461	.4946	.0520	.0411	2.2393	.1826	2.0567	47
-Phoenix Islands.....	.0919	.0049	2.1147	.0236	.0391	.0154	.2817	3.1713	.2141	2.9572	39
-East Marshall Islands.....	.4450	.0005	4.1935	1.0104	.1939	.0363	.0529	5.9325	.2369	5.6956	23
-East Caroline Islands.....	.5078	.0563	3.8722	1.2861	.1316	1.0193	.6030	7.4753	.1869	7.2884	18
-Central Caroline Islands.....	.1014	.0467	3.8589	1.1964	.0002	.7868	.1846	6.1750	.1592	6.0158	23
-Hawaii.....	.5978	.0001	.0388	.0151	.5861	.3931	.1648	1.7958	.1146	1.6812	52
-Angola, Africa.....	1.5080	.1439	.2510	.7029	.0703	.0094	.2229	2.9084	.3212	2.5872	42
East Line-West Line Islands.....	.3146	.0587	.0447	.0972	.5127	.0060	.8317	1.8656	.1653	1.7003	51
-Phoenix Islands.....	.0000+	.0295	.3152	.2634	.0443	.0007	1.5378	2.1909	.1967	1.9942	48
-East Marshall Islands.....	.1324	.0063	1.3340	.5310	.1823	.1104	.8225	3.1854	.2196	2.9658	39
-East Caroline Islands.....	.1676	.1135	1.1556	.7355	.1226	.7379	2.2076	5.2403	.1696	5.0707	26
-Central Caroline Islands.....	.0002	.1009	1.1483	.0670	.0007	.5423	1.2973	3.7667	.1418	3.6149	34
-Hawaii.....	.2209	.0088	.4840	.1896	.5669	.2270	.0920	1.7592	.0872	1.6620	82
-Angola, Africa.....	2.3446	.0772	1.9427	1.2430	.0638	.0029	1.3957	7.0999	.3038	6.7661	19
West Line-Phoenix Islands.....	.3146	.0050	.1225	.0406	.2556	.0108	.1076	.8567	.2729	.5838	70
-East Marshall Islands.....	.8563	.0265	.8904	.1738	1.3078	.1753	.0751	3.5042	.2957	3.2085	37
-East Caroline Islands.....	.9415	.0889	.7458	.2979	1.1366	.0107	.3292	4.0706	.2457	3.8249	33
-Central Caroline Islands.....	.3319	.0057	.7399	.2555	.4768	.4341	.0515	2.2954	.2179	2.0775	47
-Hawaii.....	1.0625	.0221	.8228	.5059	2.1577	.1591	.3705	5.1009	.2476	4.8533	27
-Angola, Africa.....	.9415	.2705	2.3797	2.0355	.9380	.0173	.0720	6.8521	.3799	6.4722	20
Phoenix-East Marshall Islands.....	.1324	.0085	.3524	.0464	.4070	.0996	.0604	1.1361	.3272	.9089	65
-East Caroline Islands.....	.1676	.0272	.2638	.1180	.3142	.7841	.0604	1.7359	.2772	1.4587	55
-Central Caroline Islands.....	.0002	.0213	.2603	.0925	.0342	.5836	.6540	1.6451	.2494	1.3657	55
-Hawaii.....	.2209	.0061	1.5803	.8390	.9276	.2529	.8770	4.6987	.2048	4.4939	29
-Angola, Africa.....	2.3446	.2021	3.8228	2.6507	.2143	.0008	.0034	9.2387	.4114	8.8278	11
East Marshall-East Caroline Islands.....	.0021	.0663	.0064	.0166	.0060	1.4405	.2986	1.8365	.3000	1.5365	53
-Central Caroline Islands.....	.1216	.0567	.0070	.0073	.2053	1.1612	.0398	1.5994	.2722	1.3272	56
-Hawaii.....	.0113	.0002	3.4251	1.2728	1.058	.0685	.4046	5.9883	.2276	5.6607	23
-Angola, Africa.....	3.5914	.1276	6.4904	3.3989	.0307	.0825	.0586	13.7861	.4343	13.3518	7
East Caroline-Central Caroline Islands.....	.1554	.0004	.0000+	.0016	.1411	.0150	.1203	.4338	.2222	.2116	81
-Hawaii.....	.0037	.0501	3.1354	1.5503	.1622	.1404	1.3683	6.4854	.1776	6.3078	21
-Angola, Africa.....	3.7650	.3777	6.0950	3.8908	.0095	.8394	.0627	15.0650	.3843	14.6807	6
Central Caroline Islands-Hawaii.....	.2068	.0501	3.1233	1.4806	.6059	.0676	.6954	6.2927	.1498	6.0829	22
-Angola, Africa.....	2.3914	.3545	6.0782	3.7334	.0773	.6246	.0018	13.2612	.3565	12.9047	7
Hawaii-Angola, Africa.....	4.0048	.1380	.4873	.5118	.2504	.2812	.7711	6.4446	.3119	6.1327	22
ΣD^2	41.0543	37.1912	128.5601	78.4819	20.8264	29.4377	33.4614				
Mean.....	.6220	.5635	1.9479	1.1891	.3156	.4460	.5070				
Σ means.....	.6220	1.1855	3.1334	4.3225	4.6931	5.0841	5.5911				
Ω	69	59	38	30	28	26	24				

the Angola and Costa Rica samples—length of the pectoral fin and heights of the second dorsal fin and the anal fins—all have significantly higher regression coefficients in the Angola samples and diverge more from the Costa Rica sample in the larger size groups.

Lastly, the sample from northeast Africa shows little overlap with any other sample. Such is to

be expected because of the marked differences in fin lengths and distance from the snout to the insertion of the anal fin, which have already been pointed out. However, it has also been mentioned that this sample from northeast Africa was not composed of yellowfin of a size strictly comparable to any of our size groups. Thus, much of these differences may have arisen because of the effects

TABLE 14.—Percent of overlap (Ω) between areas, using seven characters

Area and size group	109°-119° W.	119°-129° W.	129°-139° W.	139°-149° W.	East Line Islands	West Line Islands	Phoenix Islands	East Marshall Islands	East Caroline Islands	Central Caroline Islands	Bikini Island	Japan	Hawaii	Angola, Africa	North-east Africa
Costa Rica: M					18	13	7		3	3			23	45	
109°-119° W.: L		33	45	28	21	11	9	6	3	4			20	31	
119°-129° W.: L			71	52	27	24	21	12	11	12			38	52	
129°-139° W.: L				64	46	31	28	19	14	16			51	49	
139°-149° W.: L					55	47	39	23	18	29			52	42	
East Line Islands:															
M						80	48		17	16			19	36	
L						51	48	39	26	34			52	19	
West Line Islands:															
S							71		21	15	11	36	17		4
M							67		26	23			30	31	
L							70	37	33	47			27	20	
Phoenix Islands:															
S									32	23	14	47	15		2
M									44	42			31	21	
L								65	55	55			29	14	
East Marshall Islands: L									53	56			23	7	
East Caroline Islands:															
S										70	14	51	16		4
M										82			27	10	
L										81			21	6	
Central Caroline Islands:															
S											14	49	17		4
M													30	11	
L													22	7	
Bikini Island: S												25	28		3
Japan: S													39		2
Hawaii:															
S														41	7
M														22	
L															

of curvilinear regressions, and I cannot say with confidence that this size group is as different as the data indicate.

EVALUATION OF MULTIVARIATE ANALYSIS

A full evaluation of the merits of the multivariate analysis which I have used here is beyond the scope of this article.⁹ But the procedure is so laborious that some discussion of the value of considering extra characters is warranted. The labor increases approximately in relation to the square of the number of characters, but Mahalanobis, Majumdar, and Rao (1949) refer to Mahalanobis, Bose, and Roy (1937),¹⁰ in which it is shown that D^2 approaches a limit as additional characters are considered. On an intuitive basis this would be expected to happen rather quickly, because as additional characters are considered they would have an increased chance of being correlated with previously considered characters. The extra amount of work involved in making the D^2 analysis is approximately related to the square of the number of characters considered, so the problem is how many characters must be con-

sidered to arrive at a reasonably stable estimate of overlap.

It can be shown readily that more than one character must be considered. To demonstrate this, I have taken 10 comparisons at random out of the total of 122 and calculated the overlap of the single characters showing the greatest difference between samples. These, I compared with the overlap computed from seven characters (table 15). In all but one¹¹ there is a substantial reduction in the overlap due to the extra characters. In fact, the single character comparison with the least overlap, that between eastern Marshalls and Angola with respect to height of the anal fin, still shows an overlap of 40 percent. This is reduced to 7 percent when six more characters are added.

The average effect of adding characters one by one may be obtained from the grand average, D^2 , for each size group. These averages have been obtained from table 13 for each character and the overlap computed, first for one character, then two characters, and so on until the seven are considered. It may be seen (fig. 20) that most

⁹ A detailed evaluation of the application of D^2 to an anthropometric survey may be found in Mahalanobis, Bose, and Roy (1937).

¹⁰ Not available to me.

¹¹ In this instance the seven characters show an overlap of 83 percent and the single character with the greatest difference shows an overlap of only 75 percent. This anomaly occurs because the other six characters when combined show less difference than the correction for small samples.

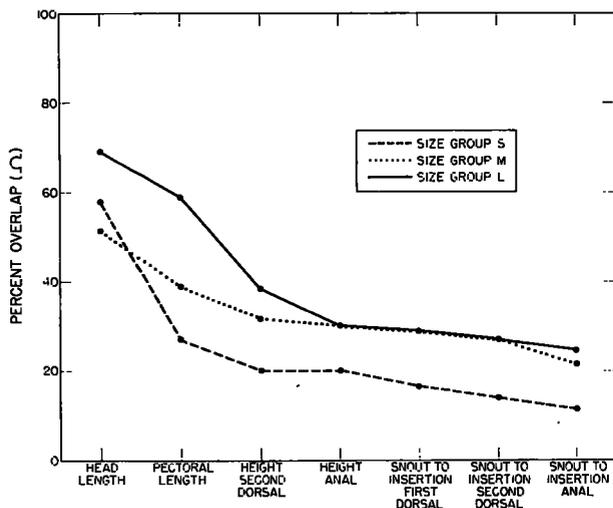


FIGURE 20.—Effect of adding characters on average overlap of all sample comparisons.

of the reduction (if any) in D^2 occurs in the first three or four characters, but that there is a continuing gradual reduction to the seventh character.

TABLE 15.—Comparison of overlap of one character with overlap of seven characters considered simultaneously

Sources of samples compared	Size group	Character showing greatest difference	Overlap (Ω)	
			1 character	7 characters
West Line Islands-Northeast Africa.	Small	Length of pectoral fin.	41	4
Bikini Island-Central Caroline Islands.	do.	Height of second dorsal fin.	56	14
East Line Islands-Hawaii	Medium	Head length.	59	19
East Caroline-Central Caroline Islands.	do.	Snout to insertion of anal fin.	75	82
119°-129° West-East Line Islands.	Large	Height of anal fin.	54	27
129°-139° West-Phoenix Islands.	do.	do.	50	28
139°-149° West-Phoenix Islands.	do.	do.	55	39
Phoenix Islands-Hawaii	do.	do.	54	29
East Marshall Islands-Angola, Africa.	do.	do.	40	7
Hawaii-Angola, Africa	do.	Head length.	48	22

Another approach has been made in an examination of the character-by-character overlap of our most different, most similar, and moderately different equatorial samples (fig. 21). Here again it may be seen that in each case most of the reduction in overlap (if any) occurs in the first three or four characters.

It would also have been possible to improve the order in which I have considered the characters. The most useful characters are those that show the greatest difference among samples and the least

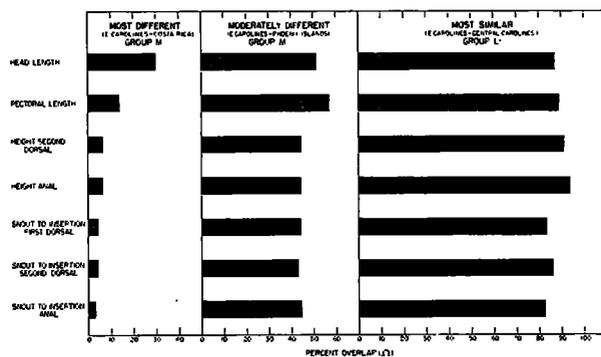


FIGURE 21.—Effect of adding characters on overlap of selected comparisons.

correlation with other characters. Thus, a consideration of our character-by-character comparisons and the partial correlations of table 7 indicates that it would be desirable to consider height of the anal fin, which is one of the characters showing the greatest difference among samples, but not height of second dorsal fin, which is closely correlated with the height of the anal fin. For a similar reason I could have omitted the distance from the snout to insertion of the second dorsal fin after considering that of the snout to insertion of the first dorsal fin, with which it is highly correlated. Another rather high correlation exists between head length and distance from snout to insertion of first dorsal fin.

Thus, it would appear that had I considered only the best four characters, I would have found substantially the same overlap that I did in considering seven. This would have reduced the work of computation to about one-third of that for the seven characters. Rao (1952: 256) notes also that it is profitable to use samples of equal size.

EXTENT OF INTERMINGLING

As I have previously argued, the percentage of overlap of two samples may be considered to represent the maximum proportion of one sample that might belong to the other. When this concept is extended to two populations separated geographically, the overlap may be assumed to be the proportion of one which might have come from the other. There is, of course, no evidence that any part of the population did come from another, but the overlap may be used, together with other data, to estimate how much intermingling might be occurring.

Such use requires an assumption that the characters selected to estimate the overlap are fixed. If the characters are genotypic and fixed at time of fertilization, then the overlap would indicate a maximum amount of genetic mixing (gene flow). Many characters, however, are fixed during early development and vary according to environment, especially temperature. Even so, the amount of overlap would still indicate a maximum possible amount of intermingling.

Clearly, between the two ends of the Pacific Equator the overlap is so small (3 percent) that there can be practically no intermingling. Along this long belt where the yellowfin distribution is continuous, I have previously noted that the average overlap is less than 50 percent in samples separated by 1,500 miles and less than 25 percent in samples separated by 3,000 miles. Consequently, it seems probable that east-west migration must be relatively limited and that most yellowfin tuna probably remain within a few hundred miles of where they occur as postlarvae. The eggs and larvae drift passively with the currents, but development is rapid and it seems unlikely that they could drift more than 300 or 400 miles before becoming active swimmers.

I have noted previously that the average overlap among samples was about the same for the different size groups. This clearly indicates that after they reach a weight of about 5 pounds (50 cm.) there is no tendency for samples of the larger fish to become more diverse. Such evidence indicates that the morphological differences arise very early in life and considering the similar environment in the surface layers along the Equator it seems probable that the differences are genotypic.

The samples from farther away from the Equator—Bikini Island, Japan, and Hawaii—are separated from the Equator by a zone where yellowfin are relatively scarce. The Bikini sample shows little overlap with samples from the adjoining equatorial areas, much less in fact than with the Japanese sample. The Hawaiian sample shows little overlap with the smaller sizes from the equatorial areas, but the larger sizes are quite like those from the Equator southeast of Hawaii. There is also considerable similarity between the Japanese sample and the Hawaiian sample.

The sample from Angola, Africa, has so much overlap with some of the equatorial Pacific samples that the maximum amount of intermingling

might be large, but of course the geographic separation makes absurd the suggestion of any intermingling. In the case of the northeast Africa sample, both the markedly low overlap with all other samples and the geographic separation make the possibility of intermingling very small.

GEOGRAPHIC DISTRIBUTION OF YELLOWFIN

One kind or another of yellowfin tuna, genus *Neothunnus*, has been described from each of the warm seas of the world except the Mediterranean. Rosa (1950) has reviewed the extensive literature and noted that the distribution extends from Point Conception, California, to San Antonio, Chile, in the eastern Pacific; from Hokkaido, Japan, south through the Indonesian Archipelago to Cape Naturaliste, southwest Australia; around the shores of the Indian Ocean to the tip of South Africa; from French Equatorial Africa north to the coast of Portugal in the eastern Atlantic, and from Maryland in the United States south to the coast of Brazil in the western Atlantic. He also reported that yellowfin occur in the Red Sea, which is the warmest sea in the world, so the distribution extends from the warmest waters to those in the vicinity of latitudes 40° N. and 40° S.

To these coastwise records must be added the records of capture in the open Pacific far from land, as reported by Yōichi Yabuta in the Japanese atlas "Average Year's Fishing Condition of Tuna Longline Fisheries," from the exploratory fishing of POFI along the central and eastern Pacific Equator, in offshore records from the eastern Atlantic by Mather and Day (1954), and in the more recent unpublished records of the capture of yellowfin tuna in the open parts of the Gulf of Mexico and Caribbean Sea by exploratory fishing vessels. The Japanese atlas records the capture of yellowfin tuna along the Equator from longitude 170° W. to the Philippines, thence northward at various places to as far as latitude 43° N. along the coast of Japan, in all of the major seas of the southwest Pacific, and in the Indian Ocean in the vicinity of Sumatra and the Nicobar Islands.

This distribution corresponds quite closely to that of waters warmer than the 65° F. isotherm (line of equal warming) shown by Hutchins and Scharff (1947). Along the coast of Chile the limit is between the 65° F. and the 60° F. isotherms,

and in other areas the most poleward record is not quite to the 65° F. isotherm. Further, no temperature barrier exists between any of the populations of yellowfin, for there is a broad band of summer temperatures between 65° F. and 70° F. around the Cape of Good Hope between the Atlantic and Indian Oceans.

Within the broad range of this species, however, there are widely varying concentrations. Already mentioned is the concentration along the Pacific Equator, where the yellowfin occur in an east-west band, and the scarcity in the open ocean north and south of this band. They do, however, occur in concentrations in the vicinity of many islands, in the Coral Sea off Australia, and possibly in other places separated from this equatorial belt by a region of yellowfin scarcity. The small yellowfin, in particular, seem to be concentrated fairly close to the islands, because they are rarely seen or caught on the high seas. The persistence of groups of these yellowfin along the reefs of certain islands has led to commercial fishing for them by trolling, and many fishermen feel that such yellowfin populations are relatively static. Thus, concentrations of yellowfin may vary enormously in extent from the clearly continuous distribution along many thousands of miles of the Pacific Equator to perhaps a relatively isolated group around a coral atoll.

Despite the variations in abundance, their widespread occurrence in all tropical oceans, near land and far from land, indicates that yellowfin tuna belong to the pelagic fauna of the warm seas and not merely to local faunal areas.

NOMENCLATURE

A great variety of scientific names has been assigned to yellowfin tuna in various parts of the world, and there has been no general agreement on the correct names to be assigned to the various species or subspecies. Rosa (1950) recognized three species: *Neothunnus albacora* (Lowe) 1839 of the eastern Atlantic Ocean, *N. argentivittatus* (Cuvier and Valenciennes) 1831 from the western Atlantic Ocean, and *N. macropterus* (Temminck and Schlegel) 1842 from the Pacific and Indian Oceans. Schaefer and Walford (1950) considered the Atlantic form to be *N. albacora* and the Pacific form to be *N. macropterus*. They designated a specimen from the Malabar coast of India as the lectotype of *N. argentivittatus*, and thus this

name clearly applies to the Indian Ocean form unless it is decided that the Indian Ocean form should be the same species as one with a prior name from another ocean. Later Ginsburg (1953) considered that the name *Thunnus albacares* (Bonnaterre) 1788 was appropriate for the eastern Atlantic yellowfin, *T. subulatus* (Poey) 1875 for the western Atlantic yellowfin, *T. catalinae* (Jordan and Evermann) 1926 for the eastern Pacific yellowfin, and *T. macropterus* (Temminck and Schlegel) 1842 for the western Pacific yellowfin.

Rivas (1954: 316) referred in a footnote to Ginsburg's usage of *T. albacares* and accepted it as a valid name for all Atlantic yellowfin. Rivas (1961) reviewed the status of *T. albacares* again and opined that the various yellowfin populations from the Atlantic and the Pacific were not worthy of separate nomenclatural recognition. He noted the widespread distribution in tropical waters and stated, ". . . it would seem therefore, that the yellowfin tuna represents a single pantropical species"

The characters that almost all authors have used to distinguish the species have been length of the pectoral fin and height of the second dorsal and anal fins. Ginsburg (1953) admits that the differences between the tuna of the eastern Atlantic and Hawaii (which he calls western Pacific) are only of racial magnitude and do not warrant separate names. He retained the separate names because he considered that (1) specimens of the two populations had not been directly compared, (2) not all promising phases of the morphology had been studied, (3) the tuna inhabit totally different faunal areas, and (4) most authors have treated the populations as distinct species. He, therefore, considered it desirable to avoid the confusion of shifting names in and out of synonymy.

Schaefer and Walford (1950) considered the differences between the eastern Pacific and eastern Atlantic forms sufficient to warrant separate species pending more information on the variability within oceans as compared with the variability between oceans. This information is now at hand from our studies and it shows clearly that the entire range of variation which has heretofore been used to describe the species of yellowfin occurs within one continuous distribution of yellowfin along the Pacific Equator. In fact,

the differences between yellowfin from Costa Rica and from Angola (which Schaefer and Walford consider to be sufficient for a separate species) are much less than the differences between yellowfin from Costa Rica and the eastern Carolines. This difference between the Costa Rican and Caroline Islands yellowfin is far beyond the conventional level of a subspecific difference, but because of the clear evidence of continuous distribution and morphological gradients between these two areas the yellowfin from the two areas must be considered conspecific.

There also may be a similar cline across the tropical Atlantic. Ginsburg (1953) reviewed the scanty evidence which indicates that the western Atlantic form has longer second dorsal and anal fins than the eastern Atlantic form. If the cline is present, then the Atlantic forms, also, are conspecific.

If we add to this evidence the fact that the yellowfin is clearly a fish of the high seas and not restricted to any coastal faunal areas and the strong probability that the distribution is continuous in the oceans from the Pacific through the Indian to the Atlantic, all of the forms should be

considered conspecific. The confusion can best be settled by reducing them to one species.

There will remain, of course, the possibility that certain yellowfin populations may be distinct enough to warrant a separate specific or subspecific name. This must be considered for the sample from northeast Africa off Somaliland, in which the fins are shorter than any we have found in the Pacific. However, our sample is not good, and with the evidence of continuous distribution through the Indian Ocean it seems most probable that this group is not completely separated from other yellowfin populations. Furthermore, it occurs in one of the warmest parts of the ocean, where the yellowfin would be expected to be the most different in structure.

Settling the matter of the proper specific name is only part of the problem. The generic name is also in dispute. Fraser-Brunner (1950) and Ginsburg (1953) used *Thunnus* rather than the long established generic name of *Neothunnus*. Godsil (1954) did not follow Fraser-Brunner but separated *Thunnus*, *Neothunnus*, and *Parathunnus*, principally on the basis of markings on the liver; however, he gives this problem of generic separation

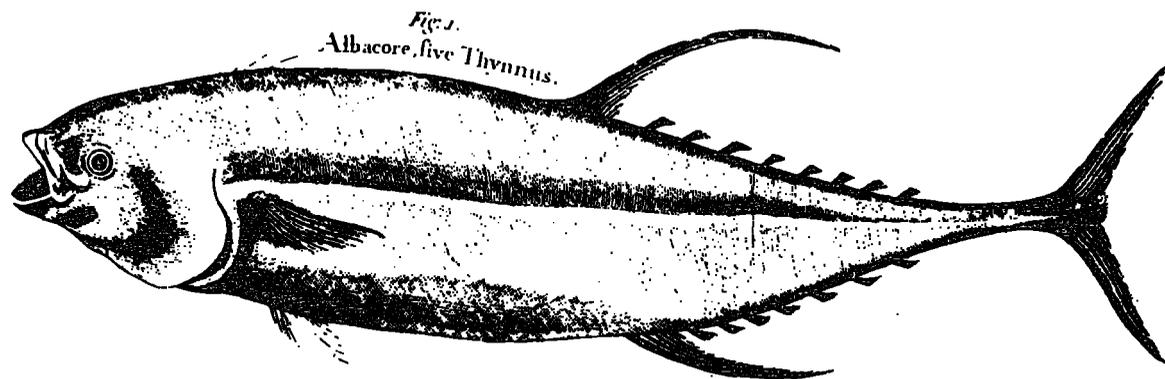


FIGURE 22.—Figure of tuna from Sloane (1707) on which Bonnaterre's description (1788) was based.

little consideration. Fraser-Brunner reduced *Parathunnus* and *Neothunnus* to subgeneric status on the principle that a generic name is intended to express relationship. It is not desirable to have a group of monotypic genera. There is now no evidence to indicate that these genera should be separate, and so I follow Fraser-Brunner and Ginsburg, who use *Thunnus* for the bluefin, yellowfin, bigeye, and albacore group.

The final question is which specific name is correct. Schaefer and Walford (1950) considered that *T. argentivittatus* (Cuvier and Valenciennes) 1831 would have priority if only one species of yellowfin was recognized, but they did not discuss the merits of *T. albacares* (Bonnaterre) 1788. Ginsburg (1953) reviewed the question and concluded that the original figure of *albacares*, which shows the distinctive long second dorsal and anal fins of the yellowfin, must be considered a yellowfin even though the pectoral fin is too short. Bonnaterre's description of the yellowfin was based on a description and figure by Sloane (1707) which I reproduce here in full (fig. 22).

The Sea hereabout is very well provided with *Albacores*, or *Thynni*, whose Description follows:

ALBACORES DESCRIBED

This Fish was Five Foot long from the end of the Chaps to that of the Tail, the Body was of the make and shape of a Mackerel, being roundish or torose, covered all over with small Scales, White in some places, and Darker colour'd in others, there was a Line run along each side. The coverings of the Gills of each side were made of two large and broad Bones covered with a shining Skin, the Jaws were about Six Inches long, having a single row of short strong sharp Teeth in them, and were pointed. The Eyes were large, and the Gills very numerous, behind which were a small pair of Fins. *Post anum* was a Foot long Fin, about Three Inches broad at bottom, and Tapering to the end. It had another on its Back answering that on the Belly, and from these were small *Pinnula* at every Two Inches distance to the forked Tail, which was like a New Moon falcated, before which on the Line of the two sides was a membranous thick horny Substance, made up of the Fishes Skin, stood out about three quarters of an Inch where it was highest, something like a Fin. It was about Three Foot Circumference a little beyond the Head, where it was thickest. The Eye was about an Inch and a half Diameter. The Figure of this Fish is here added, *Tab. I. Fig. I.* taken from a dried Fish, where every thing was perfect save the first Fin on the Back, which I suppose was accidentally rub'd off.

It is frequently taken by Sailors with Fisgigs or White Cloath, made like Flying-Fish, and put to a Hook and Line for a Bait; The Flesh is coloured, and Tasts as the *Tunny* of the Mediterranean, from whence I am apt to

believe it the same Fish. It is to be found not only about *Spain*, and in the way to the *West-Indies*; but in the South-Seas about *Guayaquil*, and between *Japan* and *New-Spain* every where.

This is called *Tunnys* of *Oviedo fum.* p. 214. *Albicores* of *Terry*, p. 9. *Albicores* of *Mandefsto*, p. 196. *Dolphin* or *Tunin* of *Marten*, *Orcynus Rondelet*, p. 249. *Thunnus Gesner*. 1158. *Aldrovand.* p. 307. *Mus. srammerd. Raii. Hist.* p. 176. *Tab. M. I. Corett. Thynni Species ejusd. app.* p. 5. & 24. *Tab. 9. No. I.* where the Figure seems not good. *Thynnus Bellon.* p. 106. *Salvian.* p. 124. *An palamite of Oviedo Sum.* p. 211? *Guarapucu Brasiliensibus, an Cavala Lusitanis, nostratibus Coninghvisch. Marcgr.* p. 178? *Pif. Ed.* 1658. p. 59? *vel an Curvata pinima ejusd.* p. 150? *Ed.* 1650. p. 51? *Tons of Escarbot Nova Francia,* p. 35. *du Raveneau de Lussan,* p. 171. *An Albacoretta Pis. Ed.* 1658. p. 73? *Toni di Fernan Colon vita di Christof. f.* 29. *An Ox-Eye of Anonymus Portugal. ap. Purchas,* p. 1313? *vel Toninas Ejusd. ib.* p. 1314? *Tunnies of Francis Gualle. Purchas,* 806. *Albacoras Ejusd.* p. 446. *Hakl. of Smith New-England,* p. 227. *of Galvanos Purchas,* in 42°. *North Lat. South-Seas,* p. 1685. *Ton ou tasard de Cauche,* p. 138. *An tonine Ejusd.* p. 142? *Ulasso a Tuny Fish of Duddleley.* p. 576. *Albacore of Ligon.* p. 6. *Abbeville.* p. 30. *An a Spanish Macquerel of Ligon? Albachores Pyrard. de Laval.* p. 6. 137.

A tuna of the size of Sloane's specimen almost certainly must have been one of either the yellowfin or the bluefin group. A comparison of measurements of Atlantic bluefin, Angola yellowfin, and Sloane's figure (table 16) indicates that Sloane's figure is closer to the yellowfin than to the bluefin in all characters except length of the pectoral fin. Further, Sloane's figure was taken from a dried fish from which the first fin on the back was missing and his figure is a dorsolateral view instead of a lateral one. These facts explain most of the differences from an accurate sketch of a yellowfin, which include the shorter pectoral fin, shorter anal

TABLE 16.—Comparison of body proportions calculated from Sloane's figure of *Albacore*, yellowfin from *Angola*, *Africa*, and bluefin tuna from *Cape Cod*, *Mass.*

[Expressed as thousands of fork length]

Character	Sloane's figure ¹	Yellowfin ²	Atlantic bluefin ³
	cm.	cm.	cm.
Fork length.....	152	140	125.7-131.4
Head length.....	212	258	284-294
Length of pectoral fin.....	135	256	197-216
Height of second dorsal fin.....	276	249	132-145
Height of anal fin.....	197	268	129-144
Snout to insertion of—			
First dorsal fin.....	190	280	306-318
Second dorsal fin.....	489	509	541-559
Anal fin.....	580	559	606-621
Ventral fins.....	276	286	315-339

¹ From Sloane (1707) fig. 1, table 1.

² From Schaefer and Walford (1950³), using the regressions for our large size group and assuming a fork length of 140 cm.

³ From Godsil and Holmberg (1950), page 7, converted from their ratios of part size to body length.

fin, more slender body, and first dorsal fin too far forward.

Therefore, I concur with Ginsburg and conclude that *T. albacares* (Bonnaterre) 1788 is a valid name for yellowfin tuna. It has priority and hence the appropriate name for a single worldwide species of yellowfin tuna is *Thunnus albacares* (Bonnaterre) 1788.

SUMMARY AND CONCLUSIONS

The study was undertaken in order to understand better the intermingling of the populations of yellowfin tuna and to distinguish the species.

Twenty-four samples of yellowfin tuna from the Pacific Ocean, one from the Atlantic off Angola, Africa, and one from the Indian off Somaliland are compared.

Regression statistics are used to control effect of size of fish in order to compare samples by each of ten characters. Seven of the characters are further used in a multiple character measure of overlap.

The regression equations used by Schaefer (1948) are used. These require log of fork length with log height of second dorsal fin and log height of anal fin, and log fork length with length of pectoral fin. All other characters approximate a linear relationship.

Neither linear, transformed linear, nor simple curvilinear regression equations are completely satisfactory for the full range of the data. Therefore, samples are divided into small fish, less than 80 cm.; medium, 80 to 120 cm.; and large, more than 120 cm. in fork length. Comparisons are made at 65 cm., 100 cm., and 140 cm., respectively.

A cline, or character gradient, exists along the Pacific Equator from the eastern Pacific to the Caroline Islands. The yellowfin in the eastern Pacific have larger heads, slightly shorter pectoral fins, much shorter second dorsal and anal fins, and greater distances from snout to the insertion of first dorsal, second dorsal, ventral, and anal fins. They also have a greater body depth and a greater distance from the insertion of the ventral fins to the vent.

Most other samples were like some part of the cline. The sample from Angola, Africa, closely resembled the samples taken between Costa Rica and the Line Islands. The samples from Hawaii were quite like those taken between longitude 129° W. and the Line Islands. The sample from

Japan was like the one from the Caroline Islands. The Bikini Island sample, however, was rather unlike the others but most similar to those from Japan and Hawaii. The Philippine sample was most like samples from the eastern Pacific and very different from the nearby Caroline Islands samples. Most diverse was the sample from Somaliland, which had especially short fins, deep body, and a long distance from the snout to the insertion of the ventrals.

The overlap of samples from along the Pacific Equator is inversely related to distance between samples. The average between samples taken 1,500 miles apart is less than 50 percent; 3,000 miles apart, less than 25 percent; and 6,000 miles apart, less than 6 percent. It is concluded that east-west migration is limited and that most yellowfin remain within a few hundred miles of where they occur as juveniles.

The multivariate analysis is evaluated. It is shown that overlap is greatly reduced by considering more than one character but that it is not worthwhile to use more than four characters.

The distribution of the yellowfin indicates that it belongs to the pelagic faunal group and not to coastal faunal groups. It occurs in all oceans, except the Mediterranean, in waters warmer than 65° F. at the surface. No temperature barrier to movement of the yellowfin exists between the Atlantic and Indian or Indian and Pacific Oceans. The distribution is probably continuous although not uniform.

It is considered desirable to place all yellowfin tunas of the world in a single species because of the continuous distribution and because the full range of characters which have been used to distinguish species occurs in the series of samples from the Pacific Equator. The name should then be *Thunnus albacares* (Bonnaterre) 1788.

ACKNOWLEDGMENTS

My debt to the many people who have carefully measured thousands of tuna is detailed in a previous paper (Dung and Royce, 1953). The formidable task of analyzing the data has been accomplished almost entirely by Mrs. Dorothy D. Stewart, nee Dung. Joseph J. Graham, Garth I. Murphy, O. E. Sette, and A. L. Tester critically reviewed the manuscript.

LITERATURE CITED

- BLUNT, C. E., JR.
1954. Two mid-Pacific recoveries of California-tagged albacore. California Fish and Game, vol. 40, No. 3, p. 339.
- BONNATERRE, JOSEPH P.
1788. Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature . . . Ichthyologie. . . . Published in Paris, by Panckoucke, 1788. 215 pp., 102 plates.
- DUNG, DOROTHY I. Y., and WILLIAM F. ROYCE.
1953. Morphometric measurements of Pacific scombrids. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 95, pp. 1-170.
- FRASER-BRUNNER, A.
1950. The fishes of the family Scombridae. The Annals and Magazine of Natural History, vol. 3, No. 26, Series 12, pp., 131-163.
- GANSSELE, DAVID, and H. B. CLEMENS.
1953. California-tagged albacore recovered off Japan. California Fish and Game, vol. 39, No. 4, p. 443.
- GINSBURG, ISAAC.
1953. The taxonomic status and nomenclature of some Atlantic and Pacific populations of yellowfin and bluefin tunas. Copeia, 1953, No. 1, pp. 1-10.
- GODSIL, H. C.
1948. A preliminary population study of the yellowfin tuna and the albacore. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 70, 90 pp.
1954. A descriptive study of certain tuna-like fishes. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 97, 185 pp.
- GODSIL, H. C., and E. C. GREENHOOD.
1951. A comparison of the populations of yellowfin tuna, *Neothunnus macropterus*, from the eastern and central Pacific. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 82, 33 pp.
- GODSIL, H. C., and EDWIN K. HOLMBERG.
1950. A comparison of the bluefin tunas, genus *Thunnus*, from New England, Australia, and California. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 77, 55 pp.
- HUBBS, CARL L., and CLARK HUBBS.
1953. An improved graphical analysis and comparison of samples. Systematic Zoology, vol. 2, No. 2, pp. 49-56, 92.
- HUTCHINS, L. W., and MARGARET SCHARFF.
1947. Maximum and minimum monthly means sea surface temperatures charted from the "World Atlas of Sea Surface Temperatures." Journal of Marine Research, vol. 6, No. 3, pp. 264-268.
- IVERSEN, EDWIN S., and HOWARD O. YOSHIDA.
1957. Longline and troll fishing for tuna in the central equatorial Pacific, January 1955 to February 1956. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 203, 38 pp.
- LEGALL, JEAN.
1951. Ichthyométrie des thonidés. De l'emploi d'une technique internationale. Journal du Conseil, vol. 17, No. 3, pp. 267-273.
- MAHALANOBIS, P. C.
1936. On the generalized distance in statistics. Proceedings of the National Institute of Sciences (India), vol. 2, No. 1, pp. 49-55.
- MAHALANOBIS, P. C., R. C. BOSE, and S. N. ROY.
1937. Normalization of statistical variates and the use of rectangular coordinates in the theory of sampling distributions. Appendix, Sankhyā, vol. 3, p. 35.
- MAHALANOBIS, P. C., D. N. MAJUMDAR, and C. R. RAO.
1949. Anthropometric survey of the United Provinces, 1941: a statistical study. Sankhyā, vol. 9, nos. 2, 3, pp. 89-266+.
- MARR, JOHN C., and MILNER B. SCHAEFER.
1949. Definitions of body dimensions used in describing tunas. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 51, No. 47, pp. 241-244.
- MATHER, FRANK J., III, and C. G. DAY.
1954. Observations of pelagic fishes of the tropical Atlantic. Copeia, 1954, No. 3, pp. 179-188.
- MAYR, ERNST, E. G. LINSLEY, and R. L. USINGER.
1953. Methods and principles of systematic zoology. McGraw-Hill, New York. 328 pp.
- MURPHY, GARTH I., and KEITH C. ELLIOTT.
1954. Variability of longline catches of yellowfin tuna. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 119, pp. 1-30, March.
- MURPHY, GARTH I., and RICHARD S. SHOMURA.
1953a. Longline fishing for deep-swimming tunas in the central Pacific, 1950-51. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 98, 47 pp.
1953b. Longline fishing for deep-swimming tunas in the central Pacific, January-June 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 108, 32 pp.
1955. Longline fishing for deep-swimming tunas in the central Pacific, August-November 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 137, 42 pp.
- PEARSON, KARL.
1948. Tables for statisticians and biometricians. 3rd ed. Cambridge University Press. 143 pp.
- RAO, C. R.
1947. The problem of classification and distance between two populations. Nature, vol. 159, No. 4027, pp. 30-31.
1952. Advanced statistical methods in biometric research. Wiley, New York. 390 pp.
- RIVAS, LUIS RENE.
1954. A preliminary report on the spawning of the western North Atlantic bluefin tuna (*Thunnus thynnus*) in the Straits of Florida. Bulletin of Marine Science of the Gulf and Caribbean, vol. 4, No. 4, pp. 302-322.

RIVAS, LUIS RENE—Continued

1961. A review of the tuna fishes of the subgenera *Parathunnus* and *Neothunnus* (genus *Thunnus*). *Annali del Museo Civico di storia Naturale di Genova*, vol. 72, pp. 126-148.

ROSA, HORACIO, JR.

1950. Scientific and common names applied to tunas, mackerels and spearfishes of the world with notes on their geographic distribution. Food and Agriculture Organization of the United Nations, Washington. 235 pp.

ROYCE, WILLIAM F.

1953. Preliminary report on a comparison of the stocks of yellowfin tuna. *Proceedings Indo-Pacific Fisheries Council*, vol. 4 (Section II), pp. 130-145.

1957. Contributions to the study of subpopulations of fishes (co-ordinated by J. C. Marr). [Statistical comparison of morphological data.] U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 208, pp. 7-28.

SCHAEFER, MILNER B.

1948. Morphometric characteristics and relative growth of yellowfin tunas (*Neothunnus macropterus*) from Central America. *Pacific Science*, vol. 2, No. 2, pp. 114-120.

1952. Comparison of yellowfin tuna of Hawaiian waters and of the American west coast. U.S. Fish and Wildlife Service, *Fishery Bulletin*, vol. 52, No. 72, pp. 353-373.

1955. Morphometric comparison of yellowfin tuna from southeast Polynesia, Central America, and Hawaii. *Inter-American Tropical Tuna Commission, Bulletin*, vol. 1, No. 4, pp. 91-136.

SCHAEFER, MILNER B., and LIONEL A. WALFORD.

1950. Biometric comparison between yellowfin tunas, (*Neothunnus*) of Angola and of the Pacific coast of Central America. U.S. Fish and Wildlife Service, *Fishery Bulletin*, vol. 51, No. 56, pp. 425-443.

SETTE, OSCAR E., and POFI.

1954. Progress in Pacific Oceanic Fishery Investigations 1950-53. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 116, 75 pp.

SHOMURA, RICHARD S., and GARTH I. MURPHY.

1955. Longline fishing for deep-swimming tunas in the central Pacific, 1953. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 157, 70 pp.

SLOANE, HANS.

1707. A voyage to the islands Madera, Barbados, Nieves, S. Christophers and Jamaica with the natural history of the herbs and trees, four footed beasts, fishes, birds, insects, reptiles, etc., of the last of those islands. Vol. I. Printed by B. M. for the author. London, 1707. 16 folio plates, CLIV, 264 pp.

TSURUTA, SABURO.

1954. Morphometric comparison of yellowfin tuna of southwestern Pacific, off southwest of Gilbert Islands and of Hawaiian waters. *Journal of the Shimonoseki College of Fisheries*, vol. 3, No. 3, pp. 217-228.

WILSON, ROBERT C.

1953. Tuna marking, a progress report. *California Fish and Game*, vol. 39, No. 4, pp. 429-442.

APPENDIX

TABLE A-1.—Morphometric measurements of yellowfin tuna (mm.), from longline catches near the Equator and longitude 110° W., March 1954

Fork length	Weight (lb.)	Head length	Snout to insertion of—				Insertion of ventral fin to anterior edge of vent	Greatest body depth	Length of pectoral fin	Height of—		Diameter of iris	Sex	Examiner
			First dorsal fin	Second dorsal fin	Anal fin	Ventral fin				Second dorsal fin	Anal fin			
764		217	243	416	454	238		188	207	98	99	33	F	William F. Royce.
800	23½	223	242	430	479	243	242	214	225	113	113	30	M	Do.
823		228	247	435	487	252	235	202	242	119	119	31	F	Do.
1051		288	310	582	605	319		278	284	180	186	38	M	Do.
1175		310	342	616	678	350	343	306	309	222	205	36	F	Do.
1180		309	334	605	678	333		300	310	229	246	40	F	Do.
1206		308	341	627	689	344	353	293	322	218	213	34	F	Do.
1232		314	339	623	692	353	346	303	308	216	234	35	F	Do.
1283		325	359	661	733	365	377	311	330	276	269	36	F	Do.
1412		350	387	722	791	391		348	336	363	434	40	F	H. S. H. Yuen.
1446		367	417	735	819	411		375	341	368	465	41	M	Do.
1449		360	400	732	816	399	428	380	356	378	416	41	M	William F. Royce.
1465		367	394	779	819	404	421	362	380	396	381	44	F	Do.
1466		366	383	737	817	400	448	388	343	366	319	38	M	Do.
1476		379	416	765	844	420	441	391	369	379	404	40	F	H. S. H. Yuen.
1480		369	391	756	840	419	427	379	358	363	393	38	F	Do.
1507		388	417	767	851	431	445	382	347	362	443	42	F	Do.
1525		385	425	764	853	430	433	398	378	391	465	40	M	Do.
1531		404	445	781	858	454		417	371	446	512	42	M	Do.
1537		379	420	777	846	417		400	379	417	434	45	M	William F. Royce.
1567	165	387	429	791	880	428	461	411	361		592	42	F	H. S. H. Yuen.
1603		408	437	813	893	459	452	420	367	506	10	41	M	Do.
1608		408	430	808	913	466	457	417	358	458	543	40	M	Do.
1649		415	450	828	906	454	470	429	391	420	502	41	M	Do.
1650		435	457	828	908	472	453	427	375	477	362	40	M	Do.
1680	200	429	438	841	937	471	478	445	404	493	543	42	M	W. F. Royce.
1680	220	427	483	871	957	471	508	454	406	640	716	46	M	Do.

† Frayed.

TABLE A-2.—Morphometric measurements (cm.) of yellowfin tuna taken near Bender Cassim, Somaliland, Africa

[Measured by A. Fraser-Brunner]

Fork length	Weight (kg.)	Head length	Snout to insertion of—				Insertion of ventral fin to anterior edge of vent	Greatest body depth	Length of pectoral fin	Height of—		Diameter of iris	Number of gill rakers	Sex	Months of 1953
			First dorsal fin	Second dorsal fin	Anal fin	Ventral fin				Second dorsal fin	Anal fin				
62.5	5.25	18.5	20.5	34	39	23	16.5	16.5	7	6.5	2.5	9+18	M	March.	
65	6.3	18.75	20	35.5	40	21.5	17	18	7.25	7.5	3	8+20	M	February.	
65	6.4	19	21	36	40	21.5	17	18	8.5	8	3.5	9+18	F	January.	
65	6.4	19	21.5	36.5	39.5	21	17	17.5	9	9	3.5	9+18	F	February.	
67.5	6	19.5	21.5	37.5	42	22	17	18.5	8.5	9	3	10+10	F	Do.	
68	6	19.5	22.5	38	42	22	17.5	18.5	8.5	9	3	10+10	F	January.	
69.5	6.4	20	21.5	38	42	22	18.5	19	9.5	10	3.25	10+21	M	February.	
70	5.6	20	22	41	44	23	20	19.5	8.5	8	3	8+20	M	January.	
70	5.5	20	22	40	43	22	17.5	18	8.5	8	3.5	10+18	F	March.	
70	7	20	22	39	43	22	17.5	18	8	8.8	3.5	9+19	F	Do.	
70.5	5	20	23	39	42.5	23	18.5	19	8.5	8	3	9+20	F	January.	
70.5	5.4	20.5	22	38	42.5	23.5	18.5	18.5	8.5	8	3	9+20	M	February.	
70.5	5.8	20	22.5	39	43	23	19	20	9	8	3.5	9+20	F	January.	
70.5	7.8	20.5	22.5	39	43	23.5	19	18.5	8.25	9	3.5	9+20	F	March.	
71.5	7	20.5	22.5	39.5	43	23.5	19	20	8	8.5	3.5	10+20	M	Do.	
72	7.8	20.5	22.5	38	46	24	19	19.5	10	10	3.25	9+20	M	Do.	
73	8	20.5	22.5	37.5	45	24	19	19.5	9.5	10	3.5	9+20	M	Do.	
73	8	20.5	23	39	44	23.5	19	19.5	8.5	8.5	3	9+20	F	Do.	
73.5	7.3	20.5	25	42	45	24	20	20	9	11	3.5	9+20	F?	February.	
74	8	21	24	41	45.5	25	20	20	9	10	3.5	9+20	M	March.	
74	7.7	21.5	23	41.5	46	24	19.5	20	9.5	10	3.5	9+19	F	Do.	
75	5.5	18.5	21	36	40	21	16.5	19	8	8.25	3.5	9+21	M	Do.	
76	6	18.5	21	35	40	21.5	16.5	13	8.5	8.25	3.5	9+21	M	Do.	
76	9	22	24.5	42	46	25	20.5	21.5	10	11.5	3.5	9+22	F	Do.	
77	5.5	21.5	23.5	36.5	40.5	22	17	19	8	8.5	3.5	9+20	M	Do.	
80	10	23	24	42.5	49.5	26	22	20	11.25	12	3.5	9+20	F	Do.	
80	10	23	24	42.5	49	25	22	20	11	11.5	3.75	10+20	F	Do.	
80	11	23	26	44	48.5	26	22	21.5	11	12	4	9+20	F	Do.	
80	11	23	26	44	48	26	22	21.5	11	12	4	9+21	F	Do.	
80.5	10	22.5	25	44	48	26	21	20.5	9.5	10	4	9+21	F	Do.	
80.5	10	22.5	25	44	48	26	21	20	9.5	10	4	9+22	F	Do.	
81	10	23	25.5	44	47	25.5	21	21	9	11	3.5	8+20	M	Do.	
81	10	23	24	43	50	26	22.25	20	11.5	12	3.75	9+20	F	Do.	
81.5	10.7	23	25.5	44	47	25.5	21	21	9	11	3.5	9+20	M	Do.	
81.5	10	23	25	43.25	44	27	20.5	22.5	9.5	10	4	10+22	F	Do.	
81.5	10	24	26.5	44	49	25	22	20.5	9.5	12	3.5	10+21	F	Do.	
82	11.6	24	27	45.5	49	26	21.5	23.5	10.5	12.5	4	10+22	M	Do.	
82.5	10.5	22.5	24	43.5	46.5	24	22	22.5	12	14	3.5	9+20	M	Do.	
83	11.5	23	25.5	44.5	50	26.5	22	21.5	11	12	3.5	9+20	F	Do.	
83	11.7	23.5	25.5	44.5	50.5	26.5	21.5	21.5	11	11.5	3.5	9+20	F	Do.	
84	11	22.5	26	45	50	26.5	22.5	22	11	13	3.5	9+20	F	Do.	
84	11.8	23.5	25.5	44.5	50.5	26.5	21.5	21.5	11	11	3.5	10+20	F	Do.	
84	12	24	26.5	45	50	27	23	21	11	12	4	10+20	M	Do.	
84	12	24.5	26	46	50	27	22.5	21	10.5	11.5	4	9+20	M	Do.	
84	12.6	24	27	45	50.5	27	22.5	21	11	12.5	4.25	9+21	M	Do.	
84.5	12	24.5	26	47	52	28.5	23	23	12.5	16.5	3.5	8+20	F	Do.	
84.5	12	23	26	45.5	50.5	26.5	22	21.5	11.5	11.5	4	9+21	M	Do.	
84.5	12.7	23	26	46.5	50.5	26.5	22	23	11.5	11.5	4	8+21	M	Do.	
85.5	12	23.5	26.5	45	51	26	22.5	22	11	14	4	10+20	F	Do.	
86	12	23.5	27	45	49	26	23	22	11.5	10.5	4	8+21	F	Do.	
86	13	24	27.5	46.5	52.5	27.5	23	24	12.5	14	3.5	9+20	M	Do.	
86	13	24	27	46.5	51	27.5	23	23	12	13	4	10+20	F	Do.	
87	13	24.5	26.5	45.5	50.5	26.5	23.5	22	12	12	4	9+22	F	Do.	
87	13.3	24.5	27	46	52	27.5	23	24.5	13	14.5	3.75	9+20	F	Do.	
89	14	26	28	48	52	29	24	23	13.5	15	4	8+20	F	Do.	
105.5	22	28	31.5	56	61	31.5	27	26	16	18	4	9+20	M	Do.	

NOTE.—Data furnished through the courtesy of G. L. Kesteven, Fisheries Division, U.N. Food and Agriculture Organization. Measurements were recorded in half or quarter centimeter units identified by the upper limit of each unit; thus are $\frac{1}{8}$ to $\frac{1}{4}$ cm. too great.

TABLE A-3.—Regression statistics of yellowfin tuna samples

[N=number used in sample; S=summation; X=fork length (mm.) or log. (mm.); Y=other characters as listed; r=deviations from mean \bar{x} ; y=deviation from mean \bar{y} ; b=regression coefficient; a=constant in regression equation; s=standard deviation from regression (cm.); \hat{Y} =estimated character size (cm.) at standard comparison length of size group (cm. except for logarithms which have characteristics for mm.)]

Character and size group ¹	N	SX	SY	SX ²	SY ²	SXY	Sr ²
X=fork length; Y=head length:							
Costa Rica: M	29	2,596.5	789.9	292,493.79	21,688.87	79,625.98	3,193.3676
106°-119° W.: L	21	3,146.2	797.0	475,009.34	30,504.64	120,353.68	3,648.6524
119°-129° W.: L	47	6,895.9	1,739.1	1,016,781.01	64,638.71	256,300.39	5,005.7588
129°-139° W.: L	46	6,667.6	1,680.6	988,059.18	62,520.78	248,469.53	21,605.0543
139°-149° W.: L	111	16,507.1	4,150.5	2,468,795.29	156,032.57	620,546.47	13,961.3223
East Line Islands:							
M	33	3,382.8	913.8	349,710.50	25,445.64	94,305.02	2,942.7473
L	155	22,524.5	5,631.8	3,288,056.75	205,463.66	821,786.66	14,810.9420
West Line Islands:							
S	43	2,954.4	849.3	205,448.86	16,939.55	58,973.52	2,460.9680
M	86	8,407.2	2,286.3	832,615.32	61,334.71	225,881.30	10,743.0894
L	57	7,876.2	1,998.8	1,094,133.62	70,433.44	277,547.24	5,808.5948
Palmyra Island: ³							
S	35	2,587.2	730.7	184,770.90	15,308.81	53,170.94	845.6475
M	57	5,379.7	1,446.6	511,867.03	36,886.28	137,303.18	3,627.1688
Phoenix Islands:							
S	37	2,503.6	715.2	171,117.96	13,927.34	48,793.54	1,712.2044
M	59	5,795.3	1,559.6	576,982.99	41,586.04	154,811.32	7,737.1913
L	46	6,142.5	1,639.6	836,866.39	52,653.16	209,836.18	16,642.8411
East Marshall Islands: L	40	5,453.4	1,359.8	746,253.02	46,398.12	186,058.50	2,763.7310
Bikini Island: S	31	1,829.9	520.9	109,843.77	8,859.57	31,185.95	1,826.5439
East Caroline Islands:							
S	60	3,916.3	1,096.1	259,183.29	20,224.83	72,382.71	3,559.8619
M	55	5,404.4	1,411.5	539,532.20	36,002.69	140,475.74	8,486.0288
L	94	7,516.0	1,872.4	1,052,115.44	65,213.40	261,891.54	5,999.5852
Central Caroline Islands:							
S	37	2,513.9	698.9	173,346.55	13,369.39	48,132.23	2,544.0309
M	102	10,286.2	2,673.5	1,049,698.10	70,659.51	272,240.75	11,780.0938
L	69	9,125.8	2,287.5	1,211,069.54	76,126.13	303,577.84	4,109.7482
Philippines (SW. Panay):							
S	242	15,776.4	4,550.2	1,040,719.56	86,405.94	296,780.77	12,228.6635
M	81	7,349.8	1,943.6	674,621.22	49,439.00	182,526.07	7,713.0714
L	32	4,234.2	1,085.1	36,933.97	144,065.00	2,089.5488	2,089.5488
Japan: S	31	1,789.5	508.7	108,296.33	8,686.13	30,690.85	4,995.9994
Hawaii: ²							
S	36	1,884.6	534.2	100,518.50	8,061.62	28,461.45	1,859.6900
M	34	3,404.4	913.2	356,040.12	24,662.30	93,673.95	2,630.4448
L	133	19,955.4	4,923.5	3,028,042.30	184,479.19	747,296.96	33,922.0808
Hawaii: ³							
S	47	2,679.3	762.9	153,111.13	12,412.53	43,589.67	373.9281
L	20	2,859.2	714.2	409,803.42	25,588.64	102,383.11	1,082.1880
Society Islands: S	17	988.5	284.4	58,503.31	4,827.06	16,801.56	1,024.8424
Northeast Africa: S	48	3,805.0	1,077.3	304,447.00	24,356.69	86,085.00	2,821.4782
Angola, Africa: ⁴							
M	21	2,050.5	560.5	206,377.69	15,248.01	56,039.06	6,061.0115
L	27	3,717.0	961.3	515,125.62	34,411.43	133,110.49	3,418.6200
Y=pectoral fin length:							
Costa Rica: M	28	83,897	755.5	251,444377	20,519.41	2,266,4008	.061998
106°-119° W.: L	21	66,850	758.0	211,569398	27,490.42	2,407,5195	.031883
119°-129° W.: L	46	154,626	1,680.7	617,064214	61,652.59	5,322,9928	.043656
129°-139° W.: L	46	145,115	1,650.4	458,068769	60,123.18	5,322,2868	.308265
139°-149° W.: L	113	358,339	4,216.1	1,130,467083	157,636.55	13,374,0386	.123376
East Line Islands:							
M	124	391,907	4,570.7	1,238,755335	168,894.65	14,450,0028	.117459
L	32	96,266	917.8	289,652924	26,501.70	2,763,9444	.054713
West Line Islands:							
S	43	121,882	874.9	345,577724	18,022.45	2,484,4753	.107447
M	86	256,925	2,418.1	767,775975	68,804.05	7,236,1381	.212538
L	56	175,831	2,030.0	552,137153	73,803.70	6,376,8446	.056072
Phoenix Islands:							
S	37	104,643	751.9	296,022337	15,457.43	2,129,8423	.072136
M	58	173,201	1,696.1	517,898774	50,125.13	5,075,4469	.144105
L	46	143,943	1,643.0	450,460353	58,862.76	5,142,9820	.034544
East Marshall Islands: L	40	125,349	1,441.5	362,839243	52,058.77	4,518,2636	.029648
Bikini Island: S	31	85,798	558.8	237,546178	10,226.10	1,560,0649	.084901
East Caroline Islands:							
S	60	168,697	1,239.1	474,472711	25,954.71	3,491,1148	.161415
M	53	158,390	1,568.3	473,500596	46,927.19	4,695,2198	.153576
L	53	173,007	2,023.5	544,271157	74,624.13	6,367,6194	.083484
Central Caroline Islands:							
S	36	101,854	778.3	288,288240	17,128.15	2,207,7750	.114982
M	102	306,117	3,125.4	918,930709	96,471.08	9,391,1201	.228635
L	72	224,688	2,576.1	701,222332	92,351.33	8,040,8810	.054980
Japan: S	30	82,441	515.3	226,832298	9,385.21	1,428,2000	.281682
Hawaii: ²							
S	36	97,754	550.6	265,544952	8,636.70	1,499,6342	.104827
M	34	102,230	960.4	367,429448	29,046.90	2,980,3773	.047893
L	133	422,105	5,032.9	1,339,929670	191,379.69	15,986,6720	.286128
Society Islands: S	21	57,897	374.4	159,676581	6,854.34	1,035,2576	.054552
Northeast Africa: S	48	139,053	999.5	402,913285	20,984.25	289,8690	.085435
Angola, Africa: ⁴							
M	21	62,646	569.8	187,000176	15,924.06	1,707,0178	.118209
L	27	84,710	953.7	265,799772	33,830.51	2,993,9101	.029991

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	N	SX	SY	SX ²	SY ²	SXY	Sr ²
Y=height second dorsal fin:							
Costa Rica: ² M	28	83.896	61.318	251.435890	134.538996	183.841218	0.059504
109°-119° W.: L	20	63.455	51.701	301.355243	133.863361	164.117955	.031392
119°-129° W.: L	45	142.407	116.934	450.704783	304.507874	370.192937	.043591
129°-139° W.: L	45	141.932	115.801	447.967290	299.620879	305.902723	.307444
139°-149° W.: L	109	345.664	287.463	1,096.300848	739.324805	911.906839	.121033
East Line Islands:							
M	32	96.220	72.790	289.372416	165.827650	218.957612	.050903
L	155	489.958	412.957	1,548.906650	1,102.197991	1,305.785473	.139929
West Line Islands:							
S	42	119.137	83.006	338.044643	164.359096	235.620544	.101197
M	84	250.789	189.036	748.954439	426.449708	564.797120	.202581
L	57	178.935	149.275	561.771999	391.609033	468.772714	.057394
Phoenix Islands:							
S	36	101.821	71.606	288.058653	142.698836	202.657672	.072097
M	55	164.262	125.241	490.710168	285.685185	374.264864	.128266
L	44	137.612	114.589	430.427630	298.849489	358.489012	.039895
East Marshall Islands: L							
Bikini Island: S	38	119.107	100.708	373.357959	267.243844	315.739082	.028606
East Caroline Islands:	30	82.935	55.723	229.368553	103.721167	154.177996	.078159
S	60	168.697	118.869	474.472711	235.963849	334.477857	.161415
M	55	164.390	126.919	491.506908	368.639628	379.691965	.162543
L	54	169.785	144.745	533.898401	388.441770	455.251731	.069064
Central Caroline Islands:							
S	36	101.779	72.384	287.862165	145.852994	204.828458	.119142
M	102	306.117	237.642	918.930709	554.760656	713.871428	.228635
L	71	221.566	185.713	691.475448	486.391527	579.666959	.045979
Japan: S	31	85.299	57.732	234.830597	108.176324	159.229245	.283555
Hawaii: ³							
S	33	89.605	59.351	243.40909	161.30366	211.30366	.10436
M	34	102.231	77.106	307.43281	175.05126	231.91726	.04524
L	133	422.105	352.442	1,339.93162	936.08909	1,119.25091	.28778
Society Islands: S							
Northeast Africa: S	20	55.062	37.290	151.047056	69.692726	102.737708	.055864
Angola, Africa: ⁴	43	124.960	86.819	363.189526	175.472595	252.384244	.049954
M	20	59.739	44.580	178.549527	99.720328	133.352260	.112121
L	26	81.631	65.771	256.319531	166.546780	206.535552	.06448
Y=height anal fin:							
Costa Rica: ² M	28	83.898	62.249	251.448856	138.67823	186.641229	.060484
109°-119° W.: L	20	63.445	52.351	201.234243	137.390109	166.158030	.030842
119°-129° W.: L	45	145.618	121.359	461.013864	320.731273	384.301592	.044287
129°-139° W.: L	44	138.731	115.337	437.720969	304.022121	364.330992	.305279
139°-149° W.: L	110	348.752	295.097	1,106.828784	792.763031	985.861205	.120079
East Line Islands:							
M	33	99.292	76.066	298.809600	175.647828	228.981829	.055016
L	153	483.531	414.601	1,528.254051	1,125.407081	1,310.662739	.134914
West Line Islands:							
S	42	119.118	83.219	337.989288	165.233633	236.198792	.103624
M	87	259.891	199.596	776.573131	459.430550	596.750575	.212995
L	54	169.496	144.323	532.067676	386.427807	453.165245	.051121
Phoenix Islands:							
S	37	104.641	73.489	296.010719	146.301409	207.082031	.071831
M	58	173.326	134.937	518.112303	314.633461	403.515203	.148471
L	43	134.444	114.370	420.379512	304.506932	357.661681	.026277
East Marshall Islands: L							
Bikini Island: S	39	122.276	105.833	383.995914	287.459047	331.880495	.026166
East Caroline Islands:	31	85.907	57.758	238.182920	108.065174	160.283217	.117996
S	60	168.697	119.181	474.472711	237.383145	335.404648	.161415
M	55	164.390	126.428	491.506908	365.304016	387.196621	.162543
L	52	163.420	142.437	518.642164	390.578717	447.776963	.063388
Central Caroline Islands:							
S	35	99.042	70.543	280.380896	142.657533	199.846930	.114674
M	101	303.205	239.524	910.451025	569.235948	719.542699	.220609
L	70	218.412	187.800	681.527732	504.318944	586.077836	.044850
Japan: S	30	82.632	55.604	227.876798	103.864664	153.619860	.275217
Hawaii: ³							
S	34	92.360	60.270	250.99237	107.19607	163.90159	.09915
M	133	422.105	358.549	1,339.93164	968.75793	1,138.64039	.28780
L	84	102.239	78.230	307.43041	180.25731	235.32153	.04473
Society Islands: S							
Northeast Africa: S	19	52.360	35.319	144.346252	65.858589	97.429882	.053115
Angola, Africa: ⁴	43	124.960	86.273	363.189526	181.467413	256.620348	.049954
M	21	62.646	46.863	187.000176	105.043883	140.028416	.118209
L	27	84.710	69.103	265.801668	177.057928	216.862426	.031887
Y=snout to insertion first dorsal fin:							
Costa Rica: ² M	29	2.896.5	853.9	292.493.79	25.390.27	86.182.62	3.193.3676
109°-119° W.: L	21	3.146.2	865.8	475.009.34	35.969.34	130.656.84	3.648.6524
119°-129° W.: L	44	6.450.3	1,784.5	959.350.67	72.671.25	262.735.30	4.751.8498
129°-139° W.: L	46	6.067.6	1,848.3	988.059.18	75.600.75	273.216.64	21.605.0548
139°-149° W.: L	112	16.645.1	4,573.0	2,487.698.53	187.782.94	683.312.55	13.954.2978
East Line Islands:							
M	33	3,382.8	951.3	349,710.50	29,370.83	101,318.62	2,942.7473
L	155	22,538.9	6,152.4	3,262,495.07	245,222.02	898,248.44	15,062.7267
West Line Islands:							
S	44	3,022.1	935.9	210,032.15	20,100.84	64,948.35	2,461.9589
M	86	8,402.3	2,459.2	831,632.87	70,984.24	242,859.66	10,718.3899
L	55	7,576.8	2,068.7	1,049,124.22	78,177.79	286,342.03	5,344.2830
Palmyra Island: ³							
S	35	2,537.2	797.5	184,770.90	18,240.39	58,031.19	845.6475
M	57	5,379.7	1,586.9	511,367.03	44,399.43	150,634.50	3,627.1688
Phoenix Islands:							
S	35	2,384.8	740.5	164,052.42	15,795.21	50,893.98	1,558.9618
M	59	5,795.3	1,690.9	574,982.99	48,913.93	167,924.19	7,737.1919
L	45	6,069.5	1,670.0	822,105.79	62,171.45	22,601.378	3,465.1178

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	N	SX	SY	SX ²	SY ²	SXY	Sr ²
East Marshall Islands: L	39	5,310.9	1,461.4	725,946.77	54,957.40	199,720.51	2,724.7493
Bikini Island: S	31	1,829.9	580.6	109,848.77	10,254.82	33,547.13	1,826.5439
East Caroline Islands:							
S	59	3,861.4	1,189.4	256,180.28	24,203.44	78,707.02	3,450.4672
M	55	5,404.4	1,660.8	539,532.20	44,782.08	155,380.26	8,486.0298
L	56	7,837.2	2,150.0	1,103,798.16	83,008.82	302,614.71	6,982.0200
Central Caroline Islands:							
S	35	2,378.7	729.8	163,986.53	15,390.80	50,225.33	2,323.2818
M	102	10,289.2	2,955.1	1,049,698.10	86,320.21	300,905.71	11,780.0938
L	71	9,404.3	2,597.7	1,249,939.11	95,321.55	345,077.67	4,293.2158
Philippines (SW. Panay):							
S	242	15,776.4	5,121.5	1,040,719.56	109,406.73	337,258.66	12,228.6635
M	81	7,349.8	2,232.5	674,621.22	61,959.87	204,321.76	7,713.0714
L	33	4,388.7	1,243.0	586,223.85	47,014.72	165,933.26	2,566.6473
Japan: S	31	1,789.5	564.0	108,296.33	10,681.40	33,999.64	4,995.9994
Hawaii: ²							
S	36	1,884.6	601.8	100,518.50	10,234.96	32,067.13	1,859.6900
M	34	3,466.4	1,015.2	356,040.12	30,484.58	104,134.53	2,630.4448
L	131	19,610.4	5,379.7	2,963,469.30	222,997.89	813,401.91	32,837.3299
Hawaii: ³							
S	47	2,679.3	834.6	153,111.13	14,856.44	47,686.86	373.9281
L	20	2,859.2	794.0	409,803.42	31,624.14	113,819.11	1,052.1880
Society Islands: S	22	1,260.6	400.2	73,377.44	7,375.30	23,254.99	1,145.0090
Northeast Africa: S	48	3,805.0	1,189.5	304,447.00	29,713.75	95,067.25	2,821.4792
Angola, Africa: ⁴							
M	21	2,050.5	606.8	206,277.69	17,860.48	60,639.16	6,061.0115
L	27	3,717.0	1,042.7	515,125.62	40,514.29	144,427.97	3,418.6200
Y ² =snout to insertion second dorsal fin:							
Costa Rica: ² M	29	2,896.5	1,527.6	292,493.79	81,184.30	154,073.13	3,193.3676
109°-119° W.: L	21	3,146.2	1,600.1	475,009.34	122,765.07	241,457.31	3,648.6524
119°-129° W.: L	44	6,470.7	3,255.0	956,166.11	241,933.41	480,926.32	4,576.1444
129°-139° W.: L	46	6,667.6	3,364.6	988,059.18	250,829.34	497,756.66	21,605.0548
139°-149° W.: L	112	16,666.4	8,371.8	2,494,141.78	629,133.06	1,252,559.93	14,082.4142
East Line Islands:							
M	33	3,382.8	1,739.9	349,710.50	92,411.27	179,750.04	2,942.7473
L	155	22,517.0	11,248.8	3,268,363.68	819,667.82	1,641,017.17	15,142.9719
West Line Islands:							
S	43	2,947.9	1,588.1	204,526.51	59,288.00	110,045.93	2,430.8261
M	86	8,394.8	4,337.7	830,036.12	221,074.05	428,290.45	10,586.5083
L	56	7,732.7	3,868.1	1,073,541.37	268,490.83	536,827.26	5,779.7756
Palmyra Island: ³							
S	34	2,468.9	1,329.1	180,106.01	52,136.85	96,888.92	827.5627
M	57	5,379.7	2,796.1	511,367.03	137,936.41	265,548.40	3,627.1688
Phoenix Islands:							
S	37	2,503.6	1,347.5	171,117.96	49,464.81	91,972.04	1,712.2044
M	59	5,795.3	2,978.1	576,982.99	151,964.35	295,988.89	7,737.1919
L	46	6,207.1	3,110.9	841,039.65	211,181.35	421,398.64	3,473.3672
East Marshall Islands: L	39	5,321.7	2,675.8	728,908.13	184,225.62	366,426.68	2,741.6970
Bikini Island: S	31	1,829.9	993.7	109,848.77	32,271.29	59,529.17	1,826.5439
East Caroline Islands:							
S	59	3,844.2	2,063.0	253,984.88	72,921.12	136,067.49	3,512.4455
M	55	5,404.4	2,764.7	539,532.20	140,667.69	275,442.73	8,486.0298
L	56	7,837.2	3,881.4	1,103,798.16	270,556.54	546,441.18	6,982.0200
Central Caroline Islands:							
S	37	2,513.9	1,344.8	173,346.55	49,465.68	92,604.46	2,544.0309
M	101	10,183.7	5,180.5	1,038,567.85	268,193.53	527,681.15	11,758.4870
L	68	8,997.1	4,472.9	1,194,303.33	295,159.21	593,660.04	3,894.3828
Philippines (SW. Panay):							
S	241	15,711.8	8,908.0	1,086,546.40	332,391.36	586,730.54	12,228.3119
M	81	7,349.8	3,996.1	674,621.22	198,764.79	366,077.21	7,713.0714
L	28	3,713.5	1,925.6	494,392.59	132,923.10	256,315.20	1,889.6525
Japan: S	31	1,789.5	979.4	108,296.33	32,343.84	59,082.02	4,995.9994
Hawaii: ²							
S	36	1,884.6	1,041.4	100,518.50	30,637.02	55,486.52	1,859.6900
M	34	3,466.4	1,800.3	356,040.12	95,877.41	184,731.92	2,630.4448
L	132	19,777.4	9,852.0	2,996,358.30	742,617.26	1,491,512.29	33,134.4306
Hawaii: ³							
S	47	2,679.3	1,463.8	153,111.13	45,690.52	83,635.85	373.9281
L	20	2,859.2	1,437.6	409,803.42	103,634.86	206,068.57	1,052.1880
Society Islands: S	21	1,209.3	665.7	70,745.75	21,367.69	38,872.54	1,107.3458
Northeast Africa: S	46	3,665.0	1,978.2	294,647.00	85,750.74	158,920.80	2,642.1087
Angola, Africa: ⁴							
M	21	2,050.5	1,089.0	206,277.69	57,692.46	109,041.36	6,061.0115
L	27	3,717.0	1,892.8	515,125.62	133,489.44	282,208.21	3,418.6200
Y ² =snout to insertion anal fin:							
Costa Rica: ² M	29	2,896.5	1,709.6	292,493.79	101,635.80	172,442.86	3,193.3676
109°-119° W.: L	21	3,146.2	1,766.2	475,009.34	149,575.84	266,533.77	3,648.6524
119°-129° W.: L	47	6,895.9	3,825.4	1,016,781.01	312,644.10	563,751.14	5,005.7588
129°-139° W.: L	46	6,667.6	3,711.3	988,059.18	305,198.05	549,037.23	21,605.0548
139°-149° W.: L	113	16,807.0	9,330.2	2,513,910.14	774,456.74	1,395,190.05	14,129.1754
East Line Islands:							
M	32	3,285.0	1,869.7	340,145.66	110,060.09	193,454.86	2,919.8788
L	153	22,239.8	12,270.3	3,247,595.60	988,185.19	1,791,256.16	14,858.9724
West Line Islands:							
S	43	2,956.6	1,750.1	205,741.90	71,942.63	121,639.51	2,451.5847
M	86	8,405.2	4,786.3	832,220.21	269,255.43	473,284.60	10,738.9654
L	56	7,724.0	4,296.3	1,070,968.78	320,570.95	504,058.99	5,608.4943
Palmyra Island: ³							
S	35	2,537.0	1,503.1	184,770.90	64,785.69	109,397.75	845.6475
M	57	5,379.7	3,069.5	511,367.03	166,188.61	291,470.97	3,627.1688
Phoenix Islands:							
S	36	2,446.3	1,439.9	167,834.67	58,036.31	98,677.17	1,601.7898
M	58	5,697.8	3,229.9	567,476.74	181,796.19	321,112.35	7,736.6566
L	45	6,078.7	3,350.5	824,552.99	250,453.07	454,396.25	3,428.6858

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	N	SX	SY	SX ²	SY ²	SXY	Sr ²
East Marshall Islands: L	40	5,453.4	3,002.7	746,253.02	226,261.25	410,890.35	2,763.7310
Bikini Island: S	31	1,829.9	1,094.9	109,843.77	39,177.77	65,588.67	1,826.5489
East Caroline Islands:							
S	60	3,916.3	2,302.4	259,183.29	89,401.86	152,204.64	3,559.8619
M	54	5,312.8	2,982.3	531,141.64	166,751.45	297,557.13	8,440.8282
L	55	7,682.1	4,196.5	1,079,742.15	321,854.99	589,467.25	6,748.3244
Central Caroline Islands:							
S	37	2,513.9	1,489.0	173,346.55	60,687.04	102,546.64	2,544.0309
M	102	10,289.2	5,796.7	1,049,698.10	332,230.77	590,407.37	11,780.0938
L	68	8,977.3	4,940.0	1,189,017.29	360,056.26	654,229.69	3,842.0652
Philippines (SW. Panay):							
S	242	15,776.4	9,798.3	1,040,719.56	400,472.31	645,393.74	12,228.6635
M	81	7,349.8	4,391.4	674,621.22	240,101.84	402,365.09	7,713.0714
L	31	4,109.1	2,351.4	546,703.59	173,857.36	312,602.06	2,035.7575
Japan: S	31	1,789.5	1,071.4	108,296.33	38,681.78	64,628.88	4,995.9994
Hawaii: 2							
S	36	1,884.6	1,144.4	100,518.50	36,977.80	60,956.99	1,859.6900
M	34	3,466.4	1,988.6	356,040.12	117,014.20	204,081.16	2,630.4448
L	132	19,809.0	10,946.0	3,006,609.34	916,354.34	1,659,647.04	35,908.7264
Hawaii: 3							
S	47	2,679.3	1,613.8	153,111.13	55,536.18	92,207.49	373.9281
L	20	2,859.2	1,599.7	409,803.42	128,289.01	250,277.36	1,052.1880
Northeast Africa: S	47	3,723.5	2,236.5	297,804.75	107,216.25	178,643.00	2,316.4043
Angola, Africa: 4							
M	21	2,050.5	1,196.7	206,277.69	69,706.95	119,863.37	6,061.0115
L	26	3,559.3	1,994.1	490,256.33	153,727.69	274,493.04	3,001.8497
Y=smout to insertion ventral fin:							
109°-119° W.: L	21	3,146.2	885.9	475,009.34	37,666.19	133,726.71	3,648.6524
119°-129° W.: L	47	6,895.9	1,929.5	1,016,781.01	79,629.77	284,429.37	5,005.7588
129°-139° W.: L	46	6,667.6	1,867.5	988,059.18	77,173.33	276,043.60	21,605.0548
139°-149° W.: L	113	16,807.0	4,688.3	2,513,910.14	195,546.89	700,965.38	14,129.1754
East Line Islands:							
M	31	3,183.1	955.3	329,762.05	29,610.51	98,779.60	2,919.2884
L	153	22,222.4	6,212.5	3,242,746.86	253,634.17	906,612.53	15,066.7178
West Line Islands:							
S	42	2,889.5	923.4	201,158.85	20,499.36	64,190.27	2,268.1298
M	84	8,216.6	2,495.6	814,259.78	74,868.24	246,773.28	10,539.3567
L	56	7,735.2	2,317.1	1,074,252.62	85,196.69	307,744.22	5,800.4943
Palmyra Island: 3							
S	35	2,537.2	799.1	184,770.90	18,312.33	58,159.51	845.6475
M	57	5,379.7	1,598.4	511,307.03	45,029.14	151,696.73	3,627.1688
Phoenix Islands:							
S	35	2,383.6	757.8	163,903.38	16,512.26	51,994.83	1,578.4098
M	56	5,535.9	1,668.0	554,436.73	49,892.32	166,246.01	7,153.3584
L	46	6,207.1	1,738.5	841,039.55	65,956.63	295,434.15	3,472.2672
East Marshall Islands: L	38	5,180.2	1,434.9	708,865.88	54,390.23	196,334.36	2,715.5632
Bikini Island: S	31	1,829.9	587.3	109,843.77	11,263.09	35,156.10	1,826.5430
East Caroline Islands:							
S	60	3,916.3	1,218.9	259,183.29	24,959.13	90,411.50	3,559.8619
M	54	5,311.8	1,546.5	530,957.44	44,777.95	154,125.35	8,453.3800
L	55	7,685.0	2,136.2	1,080,693.32	83,369.80	300,077.18	6,829.2291
Central Caroline Islands:							
S	36	2,459.9	771.5	170,480.55	16,747.37	53,398.72	2,344.2164
M	101	10,204.4	2,979.7	1,042,507.06	88,623.57	303,814.74	11,519.1456
L	68	8,958.5	2,533.2	1,184,125.53	94,729.64	334,759.16	3,909.0294
Philippines (SW. Panay):							
S	241	15,702.8	5,088.9	1,035,302.60	108,524.29	335,066.42	12,157.6712
M	81	7,849.8	2,256.4	674,621.22	63,326.76	206,603.06	7,713.0714
L	32	4,257.3	1,293.6	841,039.55	47,760.94	164,733.11	2,564.0372
Japan: S	31	1,789.5	568.9	108,296.33	10,356.37	34,274.53	4,995.9994
Hawaii: 2							
S	36	1,884.6	606.9	100,518.50	10,369.99	32,318.81	1,859.6900
M	34	3,466.4	1,025.2	356,040.12	31,083.84	105,169.90	2,630.4448
L	132	19,855.4	5,551.6	3,028,042.30	233,905.70	841,363.67	33,922.0808
Hawaii: 3							
S	47	2,679.3	870.5	153,111.13	16,161.23	49,734.11	373.9281
L	20	2,859.2	800.9	409,803.42	32,168.53	114,804.21	1052.1880
Northeast Africa: S	48	3,805.0	1,217.0	304,447.00	31,064.50	97,190.25	2,821.4792
Angola, Africa: 4							
M	21	2,050.5	622.5	206,277.69	18,826.95	62,290.02	6,061.0115
L	27	3,717.0	1,065.6	215,125.62	42,276.26	147,542.99	3,418.6200
Y=greatest body depth:							
Costa Rica: 2 M	29	2,896.5	737.1	292,493.79	18,981.65	74,476.86	3,193.3676
109°-119° W.: L	21	3,146.2	813.0	475,009.34	31,865.56	122,976.02	3,648.6524
119°-129° W.: L	47	6,895.9	1,729.6	1,016,781.01	64,060.80	255,053.53	5,005.7588
129°-139° W.: L	46	6,667.6	1,673.6	988,059.18	62,388.60	248,086.74	21,605.0548
139°-149° W.: L	109	16,168.8	4,111.2	2,412,075.52	156,425.62	613,937.28	13,634.2958
East Line Islands:							
M	32	3,278.6	797.7	338,852.86	20,035.94	82,350.48	2,939.7988
L	154	22,339.4	5,590.4	3,255,028.66	203,481.16	813,560.86	14,452.0863
West Line Islands:							
S	43	2,947.9	736.8	204,526.51	12,786.92	51,111.30	2,430.8261
M	88	8,106.1	1,973.0	801,700.31	47,469.79	194,905.57	10,027.3316
L	57	7,876.2	1,949.6	1,094,133.62	67,274.94	271,142.41	5,808.5948
Phoenix Islands:							
S	36	2,428.3	602.8	165,447.87	10,182.66	41,030.24	1,652.2998
M	59	5,795.3	1,422.5	576,982.99	34,800.57	141,587.97	7,737.1918
L	44	5,943.0	1,478.5	806,235.34	49,956.87	200,558.37	3,525.1355
East Marshall Islands: L	39	5,314.9	1,318.7	727,070.77	44,873.79	130,554.56	2,758.9236
Bikini Island: S	31	1,829.9	453.4	109,843.77	6,729.06	27,179.80	1,826.5439
East Caroline Islands:							
S	60	3,916.3	974.8	259,183.29	15,994.84	64,346.21	3,559.8619
M	55	5,404.4	1,295.6	539,532.20	31,008.22	129,299.56	8,486.0298
L	56	7,837.2	1,949.7	1,103,798.16	68,456.67	274,743.15	6,982.0200

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	N	SX	SY	SX ²	SY ²	SXY	Sx ²
Central Caroline Islands:							
S.....	37	2,513.9	620.5	173,346.55	10,554.85	42,751.50	2,544.0309
M.....	102	10,289.2	2,458.5	1,049,698.10	59,904.61	250,653.30	11,780.0938
L.....	71	9,394.9	2,332.8	1,247,581.59	77,105.00	309,934.35	4,424.6040
Japan: S.....	30	1,728.2	450.4	104,538.64	7,083.56	27,201.25	4,983.7387
Hawaii: ²							
S.....	36	1,984.6	490.7	100,518.50	6,787.50	26,098.06	1,859.6900
M.....	34	3,466.4	874.9	356,040.12	22,676.15	89,801.62	2,630.4448
L.....	132	19,792.5	5,011.4	3,001,505.89	193,468.40	761,486.24	33,755.4639
Northeast Africa: S.....	48	3,805.0	1,006.2	304,447.00	21,317.84	80,536.95	2,821.4792
Y=insertion ventral fin to anterior edge vent:							
109°-119° W.: L.....	17	2,553.6	739.8	387,099.44	32,482.38	112,090.41	3,518.6777
119°-129° W.: L.....	47	6,896.9	1,954.4	1,016,781.01	81,621.42	287,958.30	5,005.7588
129°-139° W.: L.....	46	6,667.6	1,891.8	988,059.18	79,521.56	280,216.10	21,605.0548
139°-149° W.: L.....	112	16,636.5	4,704.8	2,484,839.89	198,883.76	702,735.61	13,651.2091
East Line Islands:							
M.....	33	3,382.8	934.7	349,710.50	26,706.59	96,615.03	2,942.7473
L.....	153	22,251.1	6,194.2	3,251,069.35	252,070.96	904,976.23	15,046.7831
West Line Islands:							
S.....	38	2,600.9	734.4	179,843.35	14,337.12	50,761.20	1,825.4340
M.....	83	8,070.3	2,240.3	794,878.69	61,207.59	220,517.27	10,183.0022
L.....	56	7,746.7	2,154.5	1,077,363.37	83,350.01	299,662.14	6,731.9256
Phoenix Islands:							
S.....	19	1,309.2	363.7	90,730.80	7,006.19	25,206.01	510.0295
M.....	49	4,762.2	1,305.9	469,014.30	35,244.71	128,644.55	6,186.7277
L.....	36	4,834.4	1,353.4	651,354.14	51,091.58	182,369.37	2,147.9356
East Marshall Islands: L.....	39	5,321.7	1,479.3	728,908.13	56,402.21	202,694.27	2,741.6970
East Caroline Islands:							
S.....	60	3,916.3	1,120.2	259,183.29	21,192.68	74,090.23	3,559.3619
M.....	54	5,319.5	1,487.0	532,324.19	41,555.98	148,692.69	8,304.1854
L.....	55	7,699.4	2,146.7	1,084,809.32	84,431.95	302,678.93	6,977.3135
Central Caroline Islands:							
S.....	36	2,438.9	704.0	167,721.55	13,964.26	48,374.98	2,492.8498
M.....	102	10,289.2	2,884.7	1,049,698.10	82,400.69	293,998.80	11,780.0938
L.....	71	9,404.8	2,598.8	1,249,939.11	95,578.08	345,473.82	4,293.2158

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	Sp ²	Sxy	\bar{x}	\bar{y}	b	a	s	r
X=fork length; Y=head length:								
Costa Rica: ² M.....	173.6283	731.3126	99.879	27.238	0.22901	4.365	0.477	27.266
109°-119° W.: L.....	256.5924	947.8990	149.819	37.952	.25679	.969	.738	35.402
119°-129° W.: L.....	288.8096	1,137.4179	146.721	37.002	.22723	3.664	.815	35.475
129°-139° W.: L.....	1,120.4244	4,870.2135	144.948	36.535	.22542	3.661	.716	35.420
139°-149° W.: L.....	837.5227	3,314.7714	148.713	37.392	.23760	2.959	.677	35.323
East Line Islands:								
M.....	141.6873	632.2127	102.509	27.691	.21484	5.668	.435	27.152
L.....	836.7488	3,377.1175	145.319	36.334	.22820	3.198	.660	35.121
West Line Islands:								
S.....	164.8874	620.6846	68.707	19.761	.25221	2.422	.451	18.816
M.....	553.6904	2,376.9556	97.758	26.585	.22125	4.956	.575	27.081
L.....	342.1867	1,355.1600	138.179	35.067	.23330	2.830	.688	35.492
Palmyra Island: ³								
S.....	53.8817	201.4531	72.491	20.877	.23822	3.608	.422	19.092
M.....	173.0948	772.0569	94.381	25.379	.21285	5.290	.399	26.575
Phoenix Islands:								
S.....	102.7173	404.6286	67.665	19.330	.23632	3.339	.450	18.700
M.....	369.7323	1,618.9492	98.225	26.434	.20924	5.881	.607	26.805
L.....	1,103.4174	4,249.3757	133.533	33.470	.25534	-.626	.646	35.122
East Marshall Islands: L.....	171.7190	670.2270	136.335	33.995	.24251	.932	.492	34.883
Bikini Island: S.....	106.7697	437.7271	59.029	16.803	.23965	2.657	.254	18.646
East Caroline Islands:								
S.....	200.9099	838.4362	65.372	18.268	.23552	2.895	.244	18.204
M.....	373.4673	1,779.1337	98.262	25.664	.20966	5.062	.320	26.028
L.....	289.6638	1,281.1993	139.185	34.674	.21355	4.951	.556	34.848
Central Caroline Islands:								
S.....	167.7357	646.6973	67.943	18.889	.25420	1.618	.309	18.141
M.....	664.9781	2,552.7481	100.875	26.211	.21670	4.351	.344	26.021
L.....	290.5322	1,037.7814	132.258	33.152	.25250	-.243	.652	35.107
Philippines (S.W. Panay):								
S.....	850.8985	3,151.3350	65.192	18.802	.25770	2.002	.402	18.753
M.....	371.8277	1,630.8518	90.738	24.612	.21144	5.426	.584	26.570
L.....	138.9072	485.9244	132.319	33.909	.23255	3.138	.929	35.695
Japan: S.....	338.6271	1,295.7323	57.726	16.410	.25935	1.439	.292	18.297
Hawaii: ²								
S.....	134.6856	496.0800	52.350	14.839	.26675	.875	.263	18.214
M.....	134.8224	570.5241	101.953	26.859	.21089	4.746	.588	26.435
L.....	1,772.6468	7,634.8149	150.041	37.064	.22507	3.294	.644	34.804
Hawaii: ³								
S.....	29.2021	99.5004	57.006	16.232	.26610	1.063	.246	18.360
L.....	54.5580	291.0780	142.960	35.710	.27664	-3.838	.473	34.892
Society Islands: S.....	69.2153	264.5365	58.147	16.729	.25810	1.721	.250	18.498
Northeast Africa: S.....	178.0382	686.5313	79.146	22.319	.24332	3.061	.489	18.877
Angola, Africa: ⁴								
M.....	287.9981	1,310.2386	97.643	26.690	.21617	5.563	.501	27.200
L.....	185.5896	771.5233	137.667	35.604	.22568	4.535	.677	36.130

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	Sy^2	Sxy	\bar{x}	\bar{y}	b	a	s	\hat{r}
Y=pectoral fin length:								
Costa Rica: ² M.....	134.4011	2.6800	2.9963	26.982	432.27201	-102.540	0.845	27.142
109°-119° W.: L.....	130.2295	1.7719	3.1378	36.095	556.09955	-140.400	1.292	34.554
119°-129° W.: L.....	244.9272	2.2620	3.1658	36.537	614.59869	-136.375	1.709	35.523
129°-139° W.: L.....	909.6683	15.8129	3.1647	35.875	612.96547	-125.947	1.497	35.437
139°-149° W.: L.....	331.2473	4.1855	3.1711	37.311	359.49066	-70.345	1.305	36.462
East Line Islands:								
M.....	416.4364	4.1211	3.1605	36.890	350.85434	-74.028	1.493	36.354
L.....	178.0487	2.9152	3.0083	28.681	532.81670	-131.606	.870	28.239
West Line Islands:								
S.....	221.2870	4.6013	2.8945	30.347	428.23557	-101.051	.768	19.421
M.....	813.2639	12.0643	2.9875	28.117	567.63026	-141.463	1.237	28.526
L.....	216.2000	2.9708	3.1398	36.250	529.81860	-130.108	1.044	36.568
Phoenix Islands:								
S.....	177.6027	3.3268	2.8282	30.322	461.18443	-110.110	.831	19.617
M.....	525.9023	7.8803	2.9678	29.243	546.83293	-134.140	1.3023	29.910
L.....	143.0861	1.7135	3.1292	35.717	496.03040	-119.502	1.149	36.555
East Marshall Islands: L.....								
110.7138	1.0590	3.1337	36.038	366.06941	-78.959	1.361	36.493	
Bikini Island: S.....								
153.2794	3.4868	2.7677	18.026	410.25620	-95.520	.594	19.881	
East Caroline Islands:								
S.....	365.2299	7.2406	2.8116	20.682	448.57046	-105.468	.835	20.710
M.....	520.3053	8.3698	2.9884	29.591	544.99401	-133.275	1.122	30.223
L.....	177.7255	2.5316	3.1456	36.791	398.77764	-88.648	1.204	36.311
Central Caroline Islands:								
S.....	301.7364	5.7481	2.8293	21.619	499.01303	-119.746	.650	20.875
M.....	705.1471	11.3351	3.0011	30.841	495.77274	-118.145	1.197	30.587
L.....	133.6188	1.7322	3.1207	35.779	376.72901	-81.787	1.300	36.736
Japan: S.....								
534.0737	12.1384	2.7480	17.177	430.92565	-101.241	.627	19.974	
Hawaii: ²								
S.....	215.5789	4.5411	2.7154	15.295	433.19946	-102.336	.745	19.519
M.....	197.1306	2.4781	3.0068	29.129	517.42426	-126.450	1.467	28.777
L.....	927.9426	13.6475	3.1737	37.841	476.97184	-113.536	1.454	36.524
Society Islands: S.....								
179.3229	3.0368	2.7570	17.829	556.67867	-135.648	.735	20.940	
Northeast Africa: S.....								
171.7448	3.4800	2.8962	20.698	407.32721	-97.272	.808	17.305	
Angola, Africa: ⁴								
M.....	463.4867	7.2230	2.9831	27.133	611.03638	-155.145	1.079	28.166
L.....	143.7067	1.7647	3.1374	35.322	588.40986	-149.286	1.268	35.834
Y=height second dorsal fin:								
Costa Rica: ² M.....	.256956	.114971	2.9963	2.1899	1.63216	-3.5994	.0366	2.1071
109°-119° W.: L.....	.243691	.083607	3.1728	2.5851	2.66332	-5.8651	.0342	2.5140
119°-129° W.: L.....	.650678	.143801	3.1646	2.5085	3.29428	-7.8266	.0670	2.5375
129°-139° W.: L.....	1.623733	.681222	3.1540	2.5734	2.15071	-4.2099	.0685	2.5594
139°-149° W.: L.....	1.205756	.297734	3.1712	2.6373	2.46014	-5.1043	.0651	2.5755
East Line Islands:								
M.....	.258147	.057181	3.0069	2.2747	1.71269	-2.8752	.0588	2.2629
L.....	1.981996	.420403	3.1610	2.6642	3.00440	-6.8327	.0686	2.6194
West Line Islands:								
S.....	.310571	.166120	2.8366	1.9763	1.64155	-2.6801	.0308	1.9374
M.....	1.037693	.414389	2.9856	2.2504	2.04132	-3.8448	.0484	2.2798
L.....	.738760	.171563	3.1392	2.6188	2.99234	-6.7748	.0640	2.6394
Phoenix Islands:								
S.....	.270524	.130046	2.8284	1.9891	1.80376	-3.1127	.0325	1.9611
M.....	.497765	.222371	2.9666	2.2771	1.73367	-2.9007	.0490	2.3003
L.....	.425878	.106706	3.1275	2.6043	2.67467	-5.7607	.0578	2.6541
East Marshall Islands: L.....								
327443	.080457	3.1344	2.6502	2.71759	-5.8678	.0550	2.6820	
Bikini Island: S.....								
219490	.126190	2.7646	1.8574	1.61455	-2.6062	.0237	1.9354	
East Caroline Islands:								
S.....	.466530	.263826	2.8116	1.9812	1.63446	-2.6142	.0247	1.9834
M.....	.773031	.342803	2.9889	2.3076	2.10777	-3.9623	.0310	2.3310
L.....	.442076	.139895	3.1442	2.6805	2.11757	-3.9770	.0530	2.6945
Central Caroline Islands:								
S.....	.312898	.184815	2.8272	2.0107	1.63348	-2.6075	.0180	1.9873
M.....	1.103133	.472837	3.0011	2.3298	2.06809	-3.8767	.0359	2.3276
L.....	.626480	.125078	3.1205	2.6157	2.72033	-6.8731	.0644	2.6853
Japan: S.....								
660717	.430861	2.7506	1.8623	1.49817	-2.2448	.0245	1.9553	
Hawaii: ²								
S.....	.24851	.15071	2.7153	1.7955	1.44414	-2.1228	.0315	1.9894
M.....	.16846	.07539	3.0068	2.2678	1.66645	-2.7427	.0443	2.2566
L.....	2.13799	.69605	3.1737	2.6499	2.42564	-5.0484	.0583	2.6829
Society Islands: S.....								
202806	.102140	2.7631	1.8640	1.82837	-3.1897	.0299	1.9733	
Northeast Africa: S.....								
180996	.084192	2.9054	2.0141	1.68539	-2.8826	.0309	1.8582	
Angola, Africa: ⁴								
M.....	.351508	.194019	2.9870	2.2290	1.73044	-2.9398	.0296	2.2515
L.....	.168917	.055379	3.1397	2.5397	2.06388	-4.0445	.0470	2.5431
Y=height anal fin:								
Costa Rica: ² M.....	.286182	.120993	2.9964	2.2232	2.00041	-3.7708	.0412	2.2304
109°-119° W.: L.....	.328749	.087570	3.1723	2.6176	2.83931	-6.3895	.0667	2.5455
119°-129° W.: L.....	.557211	.126487	3.1659	2.6382	2.85608	-6.4030	.0667	2.5625
129°-139° W.: L.....	1.689788	.676053	3.1530	2.6213	2.21454	-4.3611	.0677	2.6061
139°-149° W.: L.....	1.106309	.264215	3.1705	2.6827	2.200343	-4.2685	.0697	2.6290
East Line Islands:								
M.....	.313393	.110790	3.0085	2.3050	2.01323	-3.7524	.0540	2.2873
L.....	1.916966	.385379	3.1603	2.7098	2.85643	-6.3175	.0735	2.6693
West Line Islands:								
S.....	.343110	.177820	2.8361	1.9514	1.71601	-2.8854	.0308	1.9416
M.....	1.566031	.506654	2.9873	2.2942	2.37965	-4.8145	.0651	2.3245
L.....	.703209	.162075	3.1388	2.6726	3.17042	-7.2787	.0603	2.6958
Phoenix Islands:								
S.....	.333352	.145208	2.8281	1.9962	2.02152	-3.7309	.0358	1.9554
M.....	.702531	.272264	2.9884	2.3265	1.83379	-3.1536	.0602	2.3478
L.....	.309390	.071908	3.1266	2.6598	2.73654	-5.8963	.0524	2.7131
East Marshall Islands: L.....								
263593	.064190	3.1353	2.7137	2.45318	4.9778	.0535	2.7401	
Bikini Island: S.....								
452704	.224620	2.7712	1.8631	1.90363	-3.4122	.0294	1.9425	

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	Sy^2	Sxy	\bar{x}	\bar{y}	b	a	s	\hat{Y}
East Caroline Islands:								
<i>S</i>	0.647966	0.813363	2.8116	1.9863	1.94135	-3.4720	0.0261	1.9888
<i>M</i>	816340	.350096	2.9889	2.8532	2.15387	-4.0845	.0351	2.3771
<i>L</i>	419122	.141299	3.1427	2.7392	2.22911	-4.2662	.0456	2.7468
Central Caroline Islands:								
<i>S</i>	4.77109	.226364	2.8298	2.0155	1.97398	-3.5705	.0303	1.9821
<i>M</i>	1.198553	.484446	3.0020	2.3715	2.19595	-4.2307	.0369	2.3672
<i>L</i>	4.78073	.108642	3.1202	2.6829	2.44494	-4.9449	.0556	2.7462
Japan: <i>S</i>	804493	.464202	2.7544	1.8535	1.68668	-2.7923		1.9522
Hawaii: ²								
<i>S</i>	35863	.17991	2.7165	1.7726	1.81452	-3.1565	.0317	1.9476
<i>M</i>	25928	.08162	3.0070	2.3009	1.82473	-3.1861	.0587	2.2881
<i>L</i>	2.16105	.70561	3.1737	2.6959	2.45174	-5.0652	.0574	2.6282
Society Islands: <i>S</i>	304886	.088154	2.7533	1.8589	1.84785	-3.2337	.0367	1.9644
Northeast Africa: <i>S</i>	255261	.094904	2.9054	1.89933	1.89933	-2.0478	.0427	1.8720
Angola, Africa: ⁴								
<i>L</i>	465751	.229392	2.9631	2.2316	1.94056	-3.5573	.0329	2.2644
<i>M</i>	197737	.058162	3.1374	2.5594	1.82400	-3.1632	.0605	2.5753
<i>Y</i> =snout to insertion first dorsal fin:								
Costa Rica: ² <i>M</i>	247.2317	875.6769	99.879	29.445	.27422	2.056	.517	29.478
109°-119° W.: <i>L</i>	273.6429	943.5086	149.819	41.229	.25859	1.249	.690	38.690
119°-129° W.: <i>L</i>	297.0080	1,131.0557	140.598	40.557	.25818	5.641	.817	38.986
129°-139° W.: <i>L</i>	1,335.2524	5,309.5731	144.948	40.180	.24576	4.558	.831	38.964
139°-149° W.: <i>L</i>	1,065.7168	3,637.1724	148.617	40.830	.26423	1.561	.912	38.553
East Line Islands:								
<i>M</i>	190.5364	726.4491	102.509	29.736	.24686	4.431	.601	29.117
<i>L</i>	1,015.4022	3,624.0935	145.412	39.693	.24060	4.707	.968	39.391
West Line Islands:								
<i>S</i>	193.8216	666.9063	68.684	21.270	.27089	2.664	.560	20.272
<i>M</i>	662.5582	2,592.9605	87.701	28.595	2.41917	4.959	.648	29.151
<i>L</i>	368.3411	1,357.9180	137.760	37.613	.25409	2.610	.663	38.183
Palmyra Island: ³								
<i>S</i>	68.7829	219.2757	72.491	22.786	.25930	3.989	.601	20.844
<i>M</i>	219.5772	861.7644	94.381	27.840	.23758	5.417	.519	29.175
Phoenix Islands:								
<i>S</i>	128.3457	438.3757	68.137	21.157	.28120	1.997	.392	20.275
<i>M</i>	453.8824	1,834.8211	98.225	28.659	.23714	5.366	.574	29.050
<i>L</i>	195.9245	767.8912	134.878	37.111	.23161	7.221	.774	38.246
East Marshall Islands: <i>L</i>	186.1190	711.5547	136.177	37.472	.26114	1.911	.528	38.471
Bikini Island: <i>S</i>	117.0019	455.4545	59.029	19.331	.24955	4.612	.344	20.820
East Caroline Islands:								
<i>S</i>	225.9424	863.6139	65.445	20.159	.25035	3.775	.412	20.048
<i>M</i>	489.4139	2,013.2142	98.362	28.378	.23724	5.066	.472	28.790
<i>L</i>	464.1772	1,722.2100	139.950	38.393	.24666	3.873	.854	38.405
Central Caroline Islands:								
<i>S</i>	173.4274	626.0369	67.963	20.851	.26946	2.538	.336	20.053
<i>M</i>	706.3275	2,811.4481	100.875	28.972	.23866	4.397	.595	28.763
<i>L</i>	278.6586	999.4995	132.455	36.537	.23281	5.750	.816	38.343
Philippines (S.W. Panay):								
<i>S</i>	1,019.2827	3,379.1865	65.192	21.163	.27633	3.148	.597	21.109
<i>M</i>	428.3114	1,748.5687	90.738	27.562	.22670	6.992	.626	29.662
<i>L</i>	195.0534	625.5600	132.901	37.667	.24373	5.253	1.172	39.375
Japan: <i>S</i>	420.2387	1,442.2852	57.726	18.194	.28869	1.629	.365	20.294
Hawaii: ²								
<i>S</i>	174.8700	562.9000	52.350	16.717	.30268	3.872	.363	20.546
<i>M</i>	171.9026	631.9042	101.953	29.859	.24023	5.367	.792	29.390
<i>L</i>	2,072.9122	8,073.1400	149.698	41.066	.24585	4.263	.827	38.682
Hawaii: ³								
<i>S</i>	36.0749	109.3328	57.006	17.757	.29239	1.089	.302	20.094
<i>M</i>	102.3400	308.8700	142.960	39.700	.29355	-2.266	.805	38.831
<i>L</i>	95.2982	323.5300	57.300	18.191	.28254	2.001	.441	20.366
Society Islands: <i>S</i>	238.4532	774.5938	79.146	24.656	.27453	2.928	.719	20.772
Northeast Africa: <i>S</i>								
<i>M</i>	326.8495	1,389.4743	97.643	28.895	.22925	6.510	.661	29.435
<i>L</i>	246.7698	882.9367	137.687	38.619	.25827	3.064	.865	39.222
<i>Y</i> =snout to insertion second dorsal fin:								
Costa Rica: ² <i>M</i>	716.6532	1,497.4966	99.879	52.676	.46894	5.839	.731	52.733
109°-119° W.: <i>L</i>	845.0696	1,731.8520	149.819	76.195	.47466	5.082	1.101	71.534
119°-129° W.: <i>L</i>	1,004.2098	2,109.2262	147.061	73.989	.46092	6.215	.873	70.744
129°-139° W.: <i>L</i>	4,730.7931	10,065.2044	144.948	73.143	.46587	5.616	.973	70.838
139°-149° W.: <i>L</i>	3,362.0565	6,772.2915	148.807	74.748	.48159	3.084	.956	70.507
East Line Islands:								
<i>M</i>	676.3607	1,394.4728	102.509	52.724	.47387	4.148	.709	51.535
<i>L</i>	3,309.7462	6,849.5643	145.275	72.572	.45233	6.860	1.176	70.186
West Line Islands:								
<i>S</i>	575.4945	1,172.4419	68.556	36.933	.48232	3.867	.494	35.218
<i>M</i>	2,287.5234	4,870.4040	97.614	50.438	.46006	5.630	.747	51.536
<i>L</i>	1,308.7299	2,704.8159	138.084	69.073	.46798	4.452	.892	69.969
Palmyra Island: ³								
<i>S</i>	180.7674	376.7145	72.615	39.091	.45521	6.036	.539	35.625
<i>M</i>	775.4415	1,650.5199	94.381	49.054	.45504	6.107	.666	51.611
Phoenix Islands:								
<i>S</i>	390.3168	793.6346	67.665	36.419	.46352	5.054	.801	35.183
<i>M</i>	1,640.9688	3,463.7556	98.225	50.476	.44768	6.603	1.259	51.271
<i>L</i>	796.5933	1,623.2820	134.937	67.628	.46748	4.548	.926	69.995
East Marshall Islands: <i>L</i>	638.2959	1,303.4785	136.454	68.610	.47543	3.786	.709	70.296
Bikini Island: <i>S</i>	418.3968	872.0206	59.029	32.058	.47742	3.576	.268	34.908
East Caroline Islands:								
<i>S</i>	786.0523	1,650.8019	65.156	34.966	.46999	4.343	.423	34.892
<i>M</i>	1,693.7611	3,778.2813	98.282	50.267	.44524	5.617	.466	51.041
<i>L</i>	1,533.9336	3,239.2500	139.950	69.311	.46394	4.383	.759	69.335

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	Sy^2	Sxy	\bar{x}	\bar{y}	b	a	s	\bar{y}
Central Caroline Islands:								
S.....	007.6519	1,234.3865	67.943	36.346	0.48521	3.379	0.499	34.918
M.....	2,474.0187	5,338.0020	100.829	51.292	.45397	5.519	.722	50.916
L.....	941.0570	1,849.3255	132.310	65.778	.47487	2.948	.976	69.430
Philippines (SW. Panay):								
S.....	3,128.0239	5,980.6878	65.194	36.963	.48909	5.077	.921	36.868
M.....	1,618.9233	3,478.0029	90.738	49.335	.45092	8.419	.801	53.511
L.....	490.8372	932.5000	132.625	68.771	.49348	3.323	1.283	72.410
Japan: S.....	1,301.1187	2,546.3652	57.726	31.594	.50914	2.203	.422	35.297
Hawaii: 2								
S.....	511.6323	960.2300	52.350	28.928	.52118	1.644	.437	35.521
M.....	551.5250	1,186.0400	101.953	52.950	.45089	6.980	.724	52.060
L.....	7,299.8055	15,399.0719	149.829	74.636	.46475	5.003	1.049	70.068
Hawaii: 3								
S.....	100.9362	189.9066	57.006	31.145	.50787	2.193	.316	35.205
M.....	300.1720	549.2740	142.960	71.880	.52203	-2.749	.864	70.335
L.....	265.0000	537.7300	57.586	31.700	.48500	3.736	.452	35.300
Society Islands: S.....	679.5392	1,309.8653	79.549	42.879	.49576	3.442	.828	35.666
Northeast Africa: S.....								
Angola, Africa: 4								
M.....	1,220.0315	2,708.2886	97.643	51.857	.44084	8.226	.720	52.910
L.....	797.1497	1,632.7434	137.667	70.104	.47760	4.354	.833	71.218
Y = snout to insertion anal fin:								
Costa Rica: 2 M.....	901.9325	1,659.1911	99.879	58.952	.52897	6.119	.558	59.016
109°-119° W.: L.....	1,030.0096	1,923.3681	149.819	84.105	.52714	5.129	.921	78.929
119°-129° W.: L.....	1,289.0966	2,483.5686	146.721	81.891	.49614	8.597	1.124	78.057
129°-139° W.: L.....	5,738.7524	11,092.3631	144.948	80.680	.51342	6.261	.997	78.140
139°-149° W.: L.....	4,079.4653	7,467.2943	148.773	82.568	.52850	3.941	1.095	77.934
East Line Islands:								
M.....	817.0247	1,518.4694	102.656	58.428	.52005	5.042	.955	57.047
L.....	4,131.1894	7,667.8075	145.368	80.998	.51604	5.987	1.074	78.233
West Line Islands:								
S.....	713.5600	1,305.8900	68.758	40.700	.53267	4.075	.662	38.699
M.....	2,875.5732	5,496.1261	97.735	55.655	.51179	5.635	.864	56.814
L.....	1,492.9556	2,855.7543	137.929	76.541	.50918	6.311	.848	77.596
Palmyra Island: 3								
S.....	233.9869	435.8838	72.491	42.946	.51544	5.581	.531	39.085
M.....	903.3425	1,769.4060	94.381	53.851	.48782	7.810	.855	58.592
Phoenix Islands:								
S.....	444.3098	831.9653	67.953	39.997	.51940	4.702	.599	38.463
M.....	1,929.7416	3,813.6506	98.238	55.888	.49293	7.264	.944	56.557
L.....	889.7312	1,803.2645	135.082	74.456	.52593	3.412	.951	77.042
East Marshall Islands: L.....	856.0673	1,517.2455	136.335	75.088	.54898	.223	.780	77.080
Bikini Island: S.....	506.6084	957.7826	59.029	35.290	.52437	4.337	.388	38.421
East Caroline Islands:								
S.....	1,051.0974	1,923.1547	65.272	38.373	.54023	3.111	.468	38.226
M.....	2,045.6484	4,142.9923	98.385	55.228	.49083	6.938	.483	56.021
L.....	1,814.6219	3,462.6946	139.675	76.282	.51312	4.612	.845	76.449
Central Caroline Islands:								
S.....	764.8509	1,379.1509	67.943	40.243	.54211	3.410	.701	38.647
M.....	2,802.0358	5,668.0991	100.875	56.830	.48116	8.293	.865	56.409
L.....	1,179.7895	2,055.2489	132.019	72.647	.53498	2.026	1.104	76.916
Philippines (SW. Panay):								
S.....	3,750.4799	6,625.5577	65.192	40.489	.54181	5.167	.818	40.385
M.....	2,022.9023	3,895.0441	90.738	54.215	.50499	8.393	.842	58.892
L.....	500.3775	920.1875	132.582	75.852	.45201	15.937	1.706	79.218
Japan: S.....	1,552.8136	2,781.4510	57.726	34.861	.55674	2.423	.384	38.611
Hawaii: 2								
S.....	598.5956	1,047.6500	52.350	31.789	.56335	2.298	.497	38.916
M.....	704.4953	1,337.5412	101.953	58.488	.50848	6.647	.873	57.495
L.....	8,065.5324	17,000.7218	150.068	82.924	.50137	7.684	1.045	77.876
Hawaii: 3								
S.....	124.4687	210.5892	57.006	34.337	.56318	2.232	.361	38.839
M.....	337.0055	584.2480	142.960	79.965	.55527	6.604	.836	78.342
L.....	792.1596	1,459.8564	79.098	47.460	.51834	6.460	.888	40.152
Northeast Africa: S.....								
Angola, Africa: 4								
M.....	1,512.1458	3,014.1629	7.643	56.986	.49730	8.428	.834	58.158
L.....	737.8897	1,508.4197	136.893	76.696	.50250	7.907	1.116	78.237
Y = snout to insertion ventral fin:								
109°-119° W.: L.....	293.8657	1,002.0157	149.819	42.186	.27463	1.041	.992	39.489
119°-129° W.: L.....	417.6371	1,330.6669	146.721	41.053	.26583	2.051	1.192	39.267
129°-139° W.: L.....	1,356.8898	5,353.5948	144.948	40.598	.24779	4.681	.830	39.372
139°-149° W.: L.....	1,032.2273	3,653.3615	148.773	41.489	.25857	3.021	.888	39.221
East Line Islands:								
M.....	171.8619	688.7797	102.651	30.816	.23594	6.589	.568	30.133
L.....	1,378.2468	4,281.4189	145.244	40.605	.28416	-.668	1.035	39.114
West Line Islands:								
S.....	197.7514	662.5486	68.798	21.966	.27978	2.736	.556	20.924
M.....	725.1324	2,662.0067	97.817	29.710	.35258	5.003	.802	30.261
L.....	419.3256	1,499.3643	138.129	39.591	.25849	3.886	.767	40.075
Palmyra Island: 3								
S.....	67.7354	235.6094	72.491	22.831	.27388	2.977	.361	20.779
M.....	206.6390	838.6164	94.381	28.042	.23120	6.221	.481	29.341
Phoenix Islands:								
S.....	104.8074	386.4849	68.103	21.651	.24564	4.922	.547	20.889
M.....	507.6593	1,849.5511	98.855	29.696	.25748	4.243	.763	29.991
L.....	256.6681	846.2511	134.937	37.793	.24371	4.908	1.060	30.027
East Marshall Islands: L.....	207.6508	727.2810	136.321	37.760	.26782	1.250	.598	38.745
Bikini Island: S.....	136.5968	488.3494	59.029	18.945	.26736	3.163	.456	20.541
East Caroline Islands:								
S.....	278.3699	982.4089	65.272	20.282	.27597	2.269	.354	20.207
M.....	487.3084	2,001.3000	98.367	28.639	.23674	5.352	.510	29.026
L.....	399.8920	1,591.7800	139.727	38.840	.23308	6.272	.738	38.903

See footnotes at end of table.

TABLE A-3.—Regression statistics of yellowfin tuna samples—Continued

Character and size group ¹	Sy^2	Sxy	\bar{x}	\bar{y}	b	a	s	\hat{Y}
Central Caroline Islands:								
S.....	213.6964	681.6964	68.331	21.431	0.29080	1.560	0.674	20.462
M.....	716.5190	2,764.7333	101.034	29.502	.24001	5.253	.731	29.254
L.....	360.4895	1,028.6865	131.743	37.253	.26316	2.584	1.166	39.426
Philippines (SW. Panay):								
S.....	1,068.2601	3,489.7440	65.157	21.116	.28704	2.413	.528	21.071
M.....	526.4000	1,951.9623	90.738	27.844	.25307	4.881	.641	30.188
L.....	205.6000	614.1950	133.041	38.550	.23954	6.681	1.397	40.217
Japan; S.....	416.3374	1,434.3187	57.726	18.352	.28709	1.779	.396	20.440
Hawaii: ²								
S.....	168.6975	547.5950	52.350	16.358	.29445	1.444	.467	20.583
M.....	181.0448	647.7448	101.953	30.153	.24025	5.047	.820	29.672
L.....	2,174.4026	8,398.2667	150.041	41.741	.24758	4.594	.852	39.255
Hawaii: ³								
S.....	38.4587	110.0536	57.006	18.521	.29432	1.743	.367	20.874
M.....	96.4595	307.5490	142.960	40.045	.29229	-1.741	.605	39.180
L.....	208.4792	717.6459	79.146	25.229	.25435	5.098	.751	21.631
Northeast Africa: S.....								
Angola, Africa: ⁴								
S.....	374.2714	1,497.3414	97.643	29.643	.24704	5.521	.479	30.225
L.....	220.5800	845.3900	137.667	39.467	.24729	5.423	.679	40.044
Y ² =greatest body depth:								
Costa Rica: ² M.....	246.6014	855.8203	99.879	25.417	.26800	-1.351	.799	25.449
109°-119° W.: L.....	390.8457	1,173.1343	149.819	38.714	.32153	-9.457	.843	35.557
119°-129° W.: L.....	441.5200	1,284.4100	140.721	36.500	.25059	-8.847	1.677	35.076
129°-139° W.: L.....	1,498.6661	5,502.0583	144.948	35.383	.25467	-6.590	1.488	35.124
139°-149° W.: L.....	1,361.7169	4,091.6786	148.338	37.717	.30010	-6.799	1.118	35.215
East Line Islands:								
M.....	150.7747	621.1294	102.456	24.928	.21128	3.281	.807	24.409
L.....	1,267.7564	4,062.2382	145.061	36.236	.28108	-4.538	.910	34.813
West Line Islands:								
S.....	161.9377	599.3763	68.556	17.135	.24657	.231	.587	16.258
M.....	569.4407	2,214.7833	97.064	23.771	.22087	2.200	.985	24.287
L.....	591.7793	1,748.7343	138.179	34.204	.30106	-7.396	1.090	34.752
Phoenix Islands:								
S.....	89.1089	369.7056	67.453	16.744	.22375	1.651	.433	16.195
M.....	503.8639	1,862.3048	98.225	24.110	.24070	.467	.968	24.537
L.....	375.9088	860.0632	135.068	33.602	.24398	-6.848	1.254	34.805
East Marshall Islands: L.....	284.8236	842.8003	136.279	33.813	.30548	-7.818	.860	34.949
Bikini Island: S.....	97.7194	416.0368	59.029	14.636	.22777	1.181	.319	15.986
East Caroline Islands:								
S.....	157.5893	719.3893	65.272	16.247	.20208	3.057	.459	16.192
M.....	488.5953	1,991.5434	98.262	23.556	.23469	.495	.632	23.904
L.....	575.7756	1,882.6350	139.950	34.816	.26904	-2.920	1.123	34.830
Central Caroline Islands:								
S.....	148.8973	592.7176	67.943	16.770	.23298	.941	.556	16.085
M.....	647.5291	2,653.3177	100.875	24.103	.22524	1.332	.706	23.906
L.....	457.7347	1,252.3399	132.323	32.856	.28304	-4.597	1.223	35.020
Japan: S.....	321.5547	1,265.2073	57.607	15.013	.35191	.501	.437	16.875
Hawaii: ²								
S.....	98.9364	409.9150	52.350	13.631	.22042	2.092	.504	16.419
M.....	162.8941	602.8918	101.953	25.732	.22920	2.364	.879	25.284
L.....	3,209.8397	10,080.9737	149.943	37.965	.29905	-6.726	1.274	35.001
Northeast Africa: S.....	225.3725	774.6375	79.146	20.837	.27455	-.893	.525	16.953
Y ² =insertion ventral fin to anterior edge vent:								
109°-119° W.: L.....	288.0247	963.7465	150.212	43.518	.27889	2.376	1.267	40.721
119°-129° W.: L.....	351.6464	1,206.2371	146.721	41.583	.24097	6.228	1.164	39.964
129°-139° W.: L.....	1,719.2287	6,003.8027	144.948	41.126	.27776	.865	1.075	39.751
139°-149° W.: L.....	1,248.5543	3,883.7779	148.540	42.007	.28450	-2.253	1.143	39.577
East Line Islands:								
M.....	231.9206	799.7827	102.609	28.324	.27178	.464	.685	27.642
L.....	1,298.9754	4,141.1737	145.432	40.485	.27522	.459	1.027	38.990
West Line Islands:								
S.....	143.8737	495.3853	68.445	19.326	.27138	.751	.512	18.391
M.....	738.3841	2,687.2328	97.233	26.992	.26389	1.333	.601	27.722
L.....	459.4699	1,521.6909	138.334	38.473	.26548	1.748	1.014	38.915
Phoenix Islands:								
S.....	44.2063	145.1658	68.905	19.142	.28462	-4.470	.412	18.030
M.....	441.1425	1,627.0607	97.188	26.651	.26299	1.092	.531	27.391
L.....	211.2589	622.7878	134.289	37.594	.23995	-1.343	.960	39.250
East Marshall Islands: L.....	291.2231	838.0954	136.454	37.931	.30568	-3.780	.973	39.015
East Caroline Islands:								
S.....	278.5460	972.9090	65.272	18.670	.27330	.881	.467	18.596
M.....	608.4060	2,209.4215	98.509	27.537	.26606	1.328	.629	27.934
L.....	644.2975	2,064.3486	139.989	39.031	.29587	-2.388	.795	39.034
Central Caroline Islands:								
S.....	197.1489	680.9356	67.747	19.556	.27316	1.050	.573	18.805
M.....	817.7146	3,006.1016	100.875	28.281	.25518	2.540	.709	28.058
L.....	454.6795	1,249.9491	132.455	36.603	.29115	-1.961	1.147	38.800

¹ S, small, less than 80 cm., compared at length of 65 cm.; M, medium, 80 to 120 cm., compared at length of 100 cm.; L, large, over 120 cm., compared at length of 140 cm.

² Schaefer (1952). ³ Godsil and Greenwood (1951). ⁴ Schaefer and Walford (1950).

ORIGINS OF HIGH SEAS SOCKEYE SALMON

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ABSTRACT

To fulfill the requirements of the Protocol of the International North Pacific Fisheries Treaty, Canada, Japan, and the United States undertook a program of offshore fishery research in the North Pacific Ocean and Bering Sea. The studies have contributed much to understanding the distribution and migrations of sockeye salmon, *Oncorhynchus nerka* (Walbaum), at sea. The main objective of this report is to examine the available information concerning the origin of sockeye salmon that are found in different parts of the ocean. Several techniques have been successfully used

to identify the sources of fish at sea. These include studies of parasites, movements of tagged fish, and scale differences and other morphological characteristics. The last provides most of the basis for quantitative statements regarding origin. Nearly all of the field work was done between early May and late September; accordingly results are available for only this period. It was found that in early summer the maturing sockeye salmon north and south of the eastern and central Aleutian Islands were mainly of Bristol Bay, Alaska origin.

The Protocol to the International Convention for the High Seas Fisheries of the North Pacific Ocean states that "The Commission to be established under the Convention shall, as expeditiously as practicable, investigate the waters of the Convention area to determine if there are areas in which salmon originating in the rivers of Canada and of the United States of America intermingle with salmon originating in the rivers of Asia. If such areas are found, the Commission shall conduct suitable studies to determine a line or lines which best divide salmon of Asiatic origin and salmon of Canadian and United States of America origin . . ."

The International North Pacific Fisheries Commission (INPFC) has undertaken research for the purpose of satisfying the requirements of the protocol to the treaty. As provided by the treaty, extensive research has been conducted by Canada, Japan, and the United States in a cooperative manner. This has resulted in greatly improved understanding of the distribution of salmon at sea.

While much remains to be done in the analysis of the available data, it is worthwhile now to ex-

amine the results of the research pertinent to the protocol problem. This report deals with the sockeye salmon, *Oncorhynchus nerka* (Walbaum), one of the more important species of salmon found in the waters of the North Pacific Ocean.

The purposes here are to review the pertinent research and combine the results so that the distribution and origins of sockeye salmon in the high seas can be clarified. While this is principally concerned with the Commission's studies, reports from other sources are incorporated as well.

LIFE HISTORY

A brief review of the life history of sockeye salmon provides a background for understanding the studies to be discussed. The distribution of spawning grounds, the homing habit, the length of time spent in the sea, and other characteristics of the species control to a high degree the salmon's ocean distribution and migrations.

The sockeye salmon reproduces in streams entering the sea from the Kurile Islands (fig. 1) to the

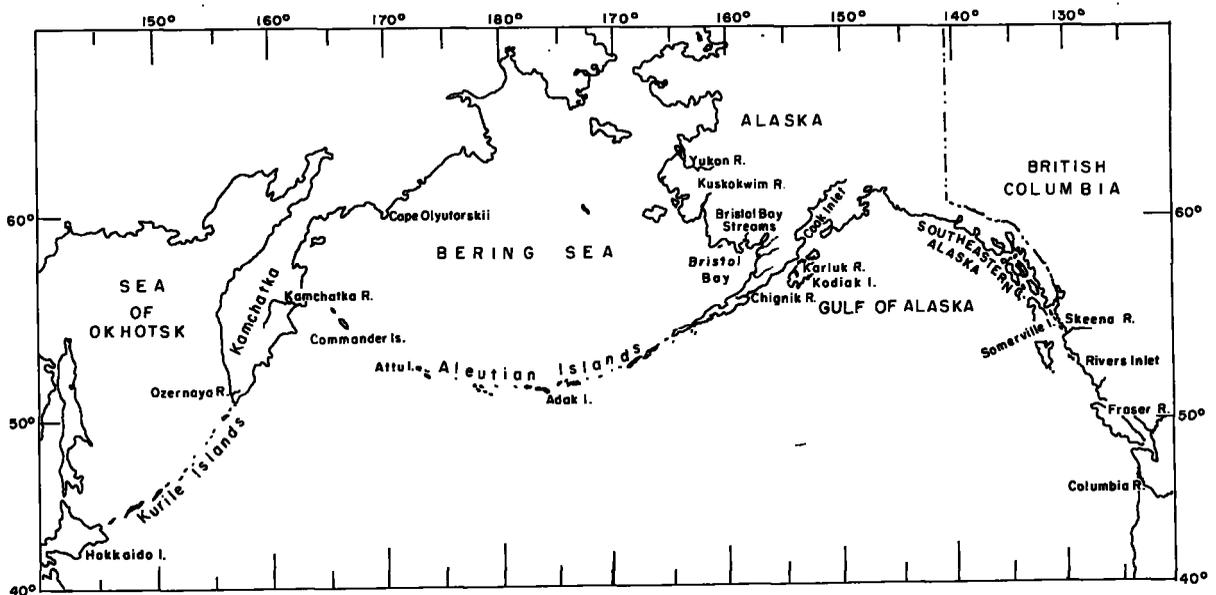


FIGURE 1.—Reference map.

northern Bering Sea¹ coast of Asia, and from the Columbia River to the northern Bering Sea coast of North America. The larger and more valuable populations tend to occur in the central portions of the species' range between lat. 49° and 60° N. According to Taguchi (1956) Asian sockeye originate preponderantly in southwest Kamchatka (mainly Ozernaya River) and in the Kamchatka River in east central Kamchatka. These two areas provided about 87 percent of the inshore Japanese catch of this species for the years 1932–41, inclusive. In North America the Bristol Bay tributaries in the north and the Fraser River in the south provide the largest stocks of sockeye. From 1955 to 1959 an average of 64 percent of the North American catch were salmon destined for these streams. The streams lying between the Fraser River and Bristol Bay produced almost all of the remaining 36 percent.

Sockeye salmon are usually found only in those river systems that have suitable lake areas for growth of the young prior to seaward migration. While this is not always the case, there appears to be no major sockeye population that does not spawn so that the young have easy access to a lake either below the spawning grounds or not far upstream.

The adult salmon spawn in the summer or autumn. The timing appears to be connected

with the temperature regimen of the spawning grounds (Royal, 1953). Because a specific range of temperatures and quantity of heat are needed to complete development within the egg at an appropriate time, spawning must occur in water that is within a favorable range of temperatures and at a suitable point in the annual temperature cycle if the young organism is to survive in its environment.

Temperature requirements are a major reason for the very strong tendency of sockeye salmon to return to the tributary, and even to that part of the tributary, in which they were hatched. There is evidence that a fish from one spawning ground generally would not reproduce as successfully in another with a different temperature regime (Royal, 1953; Andrew and Geen, 1960). Because the time of spawning is set by conditions on the ancestral spawning ground, time of migration from the sea is also influenced. The fish must arrive while river conditions are suitable for migration and must have time to complete their fresh-water migration to the spawning grounds which may be hundreds of miles from the ocean.

The precise adaptation to particular spawning grounds and the strong "homing instinct" have given rise to numerous independent or semi-independent populations of sockeye salmon. Within the Fraser River in Canada, for example, there are at least 29 unique, distinguishable populations that reproduce and flourish or fail as

¹ The Bering Sea is considered here as a separate body of water and not referred to as a part of the North Pacific Ocean.

independent units (International Pacific Salmon Fisheries Commission, 1961). The number of minor populations and subunits is certainly greater. Krogius (1958) inferred that the same situation exists in the Kamchatka River. Studies by Roos² showed that the sockeye runs of the Chignik River on the south side of the Alaska Peninsula are composed of two major stocks that enter the river at different times. The early part of the run proceeds to Black Lake tributaries and the later arriving fish spawn in the tributaries of Chignik Lake.

Stream residence is brief. The eggs are deposited in stream or lake gravels that have an adequate flow of aerated water through them. The young emerge in spring. Ordinarily, the young do not remain in the stream, but promptly migrate to the lake. Except for a small number of races in which the young migrate to the sea shortly after emerging from the gravel, lake residence is characteristic of the species.

Length of lake residence varies considerably between lakes and races. Most often, the young will spend 1 or 2 years in the lacustrine environment and migrate to sea in the first or second spring following the year of hatching. In some lakes, however, the young may remain for 3 or even 4 years. The length of fresh-water residence is a characteristic of the race and its lake. Often a lake may have seaward migrants of several different ages. Usually, the older migrants from a lake are larger than the younger migrants.

During life in the lake, young sockeye compete with other fish for food and are preyed upon by larger fish and birds. The number of seaward migrants forms a small but variable portion of the number of eggs carried into a lake system by adult females. Foerster (1955) has given an average value of 1-2 percent for British Columbia sockeye salmon.

The migration from the lake to the sea is mainly in April, May, and June. The young salmon appear to move downstream rapidly without protracted delay enroute except where a chain of lakes must be passed. In many systems migration seems to occur only during darkness, and the migrants rest in quiet areas in daylight.

From one to several years are spent growing

² Roos, John F., Red Salmon Studies—Chignik, Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, Contribution No. 77, March 1960, pp. 7-8.

and maturing in the sea. Fish which return after a single winter at sea are almost always small males, about 3 pounds in weight in the Fraser River (Killick and Clemens, 1963). Some races seem to have large numbers of these precocious individuals, while in other races they are rarely seen. Most commonly, the sockeye returns after 2 or 3 winters in the ocean and occasionally after 4 winters. The average size of the fish at the time of migration to the natal stream seems to depend to some extent upon the race, location of the spawning grounds, timing of the run, and length of sea life.

The time at which the adults re-enter their home stream is an inherited characteristic of the particular race and varies from May to September among the diverse groups. When eggs from one river have been reared in a hatchery (on some occasions far from the native stream) and released in a stream or lake other than that in which they originated, transplanted fish retain a migration timing comparable to that of their parents (Andrew and Geen, 1960). Choice of unsuitable donor stocks has been known to result in disastrously bad timing of the return.

Upon entering the stream, the adults move swiftly upstream until they reach the vicinity of the spawning grounds. Here they may spawn almost immediately or linger in the lakes or the quiet waters of the larger streams for more than a month before spawning. After spawning the salmon die.

INSHORE DISTRIBUTION

It is necessary to examine the inshore distribution, abundance, and timing because of their effect upon the distribution and abundance of sockeye salmon at sea. The area through which they are distributed must at some time include the sea approaches to their home stream. The timing of the migrations is such that the maturing fish disappear from the sea at differing times according to their race. Because the maturing fish on the high seas are the same fish that appear in the rivers a short time later, there is a strong relationship between the abundance in the rivers and the abundance at sea, although this relationship may be modified by fishing at sea.

ABUNDANCE

For the Columbia, Fraser, Skeena, Karluk, Chignik, Ozernaya, and the Bristol Bay Rivers,

the number of fish returning to the stream is known for some years, but for most other streams the number of fish in the runs is unknown or unavailable. Consequently, it is not possible to make comparisons of abundance on the basis of the total number of fish migrating to the stream. The best available common index of the abundance (catch plus escapement) of sockeye salmon in rivers of Asia and North America is the catch. For most recent years catch data have been published for the major fishing areas. In making comparisons of the runs to various areas we should keep in mind that these comparisons are based on the assumption that fishing removes the same portion of the salmon from the stock of each area. This assumption is known to be not strictly true. At various times fishery regulation has severely reduced the part of the run taken in all of the streams on the North American continent. While the extent of regulatory reduction in fishing is not as readily available for Asian streams, we can be certain that stream fishing has been curtailed there as well. According to Krogius and Krokhin (1956), the Kamchatka River fishing has been limited to a very low level since 1951. From 1940 to 1955 the catch in the Ozernaya River fishery has varied from 32 to 85 percent of the run (Semko, 1961).

Table 1 gives the sockeye salmon catch by nation for the years 1909-60. It is immediately apparent that the data do not allow close comparison before 1933 or for 1937 to 1939 because records are incomplete. Following 1952 the high seas mothership salmon fishery expanded rapidly and we are again not able to make comparisons. By 1954 the greater part of the catch by Asian nations was taken by Japan on the high seas; in 1957 the greater part of the world catch was so taken (table 2). High seas catch data have not been available in the detail necessary to accurately assign fish to the mainland areas from which they originated. In addition, the part of the catch which would not have matured in the year of capture is unknown. For these reasons, it is not possible here to credit the high seas catch to inshore areas of origin or year of spawning, and there are no means available for making comparisons of the numbers of fish produced by the various rivers even if inshore catch and escapement were known. As will be shown later, the high seas catch is taken primarily from Asian

TABLE 1.—Catch of sockeye salmon in millions of fish^{1,2}

Year	Coastal catch		Mothership fishery Japan	Total catch by Japan-U.S.S.R.	Coastal catch		Total catch by Canada-U.S.S.A.	Total catch
	U.S.S.R.	Japan ³			Canada	U.S.A.		
1909		1.3		(1.3)				
1910		1.9		(1.9)				
1911		1.8		(1.8)				
1912		1.3		(1.3)				
1913		2.5		(2.5)				
1914		0.9		(0.9)				
1915		2.0		(2.0)				
1916		2.9		(2.9)				
1917		2.4		(2.4)				
1918		4.6		(4.6)				
1919		5.7		(5.7)				
1920		4.2		(4.2)	4.3	20.2	24.5	(28.7)
1921		5.7		(5.7)	2.2	26.2	28.4	(34.1)
1922		10.6		(10.6)	4.0	85.0	39.0	(49.6)
1923		8.3		(8.3)	4.5	28.1	32.6	(40.9)
1924		8.2		(8.2)	5.0	19.9	24.9	(33.1)
1925		4.3		(4.3)	5.0	17.0	22.0	(26.3)
1926		6.6		(6.6)	4.2	31.2	35.4	(42.0)
1927		49.8		(9.8)	4.1	18.8	22.9	(32.7)
1928		+15.4		(15.4)	2.4	28.4	30.0	(46.2)
1929		+11.2		(11.2)	3.6	20.9	24.5	(35.7)
1930		+12.4	0.3	(12.7)	5.3	14.9	20.2	(32.9)
1931		+9.7	(0.6)	(10.9)	3.1	24.2	27.3	(37.8)
1932		+9.0	(1.3)	(10.3)	3.6	28.0	31.6	(41.9)
1933		+5.9	2.9	8.8	3.6	33.2	36.8	45.6
1934		+12.5	7.5	20.0	4.6	36.1	40.7	60.7
1935		+4.8	3.4	8.2	4.6	11.2	15.8	24.0
1936		+7.9	7.0	14.9	4.9	36.2	41.1	56.0
1937		5.7	10.3	(16.0)	4.6	32.1	36.7	(52.7)
1938		7.0	9.7	(16.7)	5.1	37.0	42.1	(58.8)
1939		5.0	9.2	(14.2)	4.1	25.3	29.4	(43.6)
1940	1.3	3.7	5.3	10.3	4.2	13.0	17.2	27.8
1941	1.7	3.9	5.1	10.7	5.3	17.6	22.9	33.6
1942	2.1	3.6	7.3	13.0	7.9	16.1	24.0	37.0
1943	3.0	2.4	2.9	8.3	2.1	26.7	28.8	37.1
1944	3.5	1.4	0.3	5.2	2.0	20.6	22.6	29.1
1945	4.4			4.4	3.8	15.9	19.7	24.1
1946	4.9			4.9	7.1	18.1	25.2	30.1
1947	3.8			3.8	3.9	26.3	30.2	34.0
1948	2.3			2.3	2.8	20.3	23.6	25.9
1949	3.3			3.3	3.0	13.1	16.1	19.4
1950	3.4			3.4	4.5	15.2	19.7	23.1
1951	2.9			2.9	4.4	10.8	15.2	18.1
1952	3.4		0.7	4.1	4.9	18.2	23.1	27.2
1953	1.9		1.6	3.5	5.9	14.0	19.9	23.4
1954	1.5		3.8	5.3	6.7	14.3	21.0	26.5
1955	1.1		12.5	13.6	2.8	9.6	12.4	16.0
1956	2.1		10.3	12.4	3.3	15.7	19.0	31.4
1957	1.3		20.1	21.4	3.0	11.6	14.6	36.0
1958	0.4		12.0	12.4	12.0	11.6	23.0	36.0
1959	1.5		9.1	10.6	3.3	9.9	13.2	23.8
1960	1.5		12.9	14.4	2.9	19.2	22.1	36.5

¹ From Progress Report—catch statistics for North Pacific Salmon, International North Pacific Fisheries Commission, Vancouver, B.C. (INPFC Doc. 398), October 1960, 15 pp.

² Figures in parentheses are incomplete.

³ Catch from fisheries on coast of U.S.S.R.

⁴ Combined Japan-U.S.S.R. catch.

⁵ From Pacific Salmon Catch Statistics of the Union of Soviet Socialist Republics, 1940-58, International North Pacific Fisheries Commission Secretariat, Vancouver, B.C., (INPFC Doc. 236, Revision 1), July 1961, 4 pp.

⁶ From Statistical Information on coastal catch of Far Eastern salmon by the Soviet Union for the year 1960. International North Pacific Fisheries Commission, Vancouver, B.C. (INPFC Doc. 457), July 1963, 284 pp. [Processed]; average weight of 2.6 kg. per fish used to convert weight to number of fish.

⁷ From Kasahara and Kissack (1961). See footnote 4, p. 451.

and Bristol Bay stocks of sockeye salmon. For these stocks the high seas catch exceeded the inshore catch in 1955, 1957, 1958, and 1959.

Let us examine the years for which complete catch figures are available. In table 1, the years 1933-36 and 1940-52 inclusive can perhaps best be used for this comparison. In the years 1933-52 the mothership catches were made near Kamchatka

TABLE 2.—High seas and total world catch of sockeye salmon¹

[Millions of fish]

Year	Total	High seas only	High seas catch as percent of whole
1952	27.2	0.7	2.6
1953	23.4	1.6	6.8
1954	26.3	3.8	14.4
1955	26.0	12.5	48.1
1956	31.4	10.3	32.8
1957	36.0	20.1	55.8
1958	36.0	12.0	33.3
1959	23.8	9.1	38.2
1960	36.5	12.9	35.3

¹ Derived from table 1.

TABLE 3.—Inshore catch of sockeye salmon by area of origin

[Thousands of fish]

Year	East Kamchatka ¹	West Kamchatka ²	Bristol Bay ³	Chignik River ⁴	Karluk River ⁵	Skeena River ⁶	Fraser River ⁷
1944	1,808	1,808	11,546	945	641	762	1,439
1945	3,000	1,615	7,300	553	676	1,165	1,675
1946	2,423	2,654	8,051	791	228	591	7,791
1947	2,308	1,615	18,663	1,971	110	363	4,443
1948	662	1,692	14,544	375	657	1,131	1,842
1949	192	3,192	6,449	543	450	737	2,078
1950	423	3,153	7,157	317	504	530	2,115
1951	260	2,692	4,327	257	149	689	2,425
1952	115	3,423	11,266	140	219	1,282	2,267
1953	38	1,923	6,112	301	77	246	4,024
1954	154	1,385	4,653	91	95	571	9,529
1955	269	923	4,549	350	4	157	2,115
1956	500	1,692	8,881	676	75	149	1,802
1957	231	1,115	8,276	306	91	280	3,050
1958	154	231	2,986	321	148	602	15,200
1959	577	962	4,608	428	118	196	3,393

¹ Progress Report-catch statistics for North Pacific Salmon, International North Pacific Fisheries Commission, Secretariat, Vancouver, B.C. (INPFC Doc. 389), October 11, 1960, 15 pp.; mainly Kamchatka River.

² From INPFC Doc. 389; mainly Ozernaya River.

³ From Bristol Bay Sockeye Salmon catch in numbers of fish by river system—1893-1960, International North Pacific Fisheries Commission, Secretariat (INPFC Doc. 444), Dec. 7, 1960, 2 pp.; includes Ugashik, Egegik, Naknek, Kvichak, Nuslagak, and Togiak Rivers.

⁴ From U.S. Fish and Wildlife Service (1940-53); Simpson (1960).

⁵ 1944-53 from Rounsefell (1958); 1954-59 from Simpson (1960).

⁶ 1944-52 from Foskett (1953) converted at 47 pounds of raw fish per case; 1953-59 from Department of Fisheries, Canada.

⁷ From INPFC Doc. 389; INPFC Annual Report, 1959.

and probably were almost all, if not entirely, Asian sockeye salmon. During these years the total catch varied from 18 to 61 million sockeye salmon. The percentage of Asian fish in the total catch varied from 9 to 37 percent with a 17-year mean of 23 percent. The Asian portion of the total recorded catch for the other years from 1920 to 1945 in each instance falls within the limits given above. In other words, for the years for which the continent of origin appears certain, the catch of Asian sockeye salmon was generally less than one-third of the total and averaged about one-fourth.

The inshore catch of salmon has generally declined in the years between 1920 and 1960. In the 20 years 1920-39 the total catch averaged

41 million fish (table 1); from 1940 to 1959 it averaged 28 million fish. This decline has not been uniform. Some streams on the American continent have had runs of more or less the same size throughout the period. In Asia, the sockeye catches have dropped to low levels in recent years (table 3). Information available for the Kamchatka River shows that in 1948 the catch suddenly declined to a fraction of its former size. In North America, the trend of catch in Bristol Bay and in the Chignik and Karluk Rivers has been generally downward. The runs to the Skeena River in Canada were relatively stable until a landslide in the Babine River in 1951 (removed in 1952-53) interfered with the passage of adult fish. A similar fate befell the Fraser River in 1913. The runs of Fraser River sockeye dwindled thereafter until means of upstream passage were provided in 1946. Since then, the numbers of fish have been restored to a large degree.

Although the inshore catch records are not complete, and the fishing intensities on the stocks of the various rivers may not be equal, the catch records are the best available data for comparing the relative abundance of the fish between North American and Asian streams. In the years for which comparable records are shown, the average portion of the world catch originating in Asian streams was 23 percent; and in North American streams, 77 percent. In the past several decades the stocks of most major streams have tended to decline. In the 6 years beginning with 1955, from 33 to 56 percent of the world catch was made on the high seas and cannot now be assigned to stream or spawning year.

TIMING

The time of arrival of sockeye salmon at their natal streams is quite consistent for each stream, but varies between streams. Asian streams are typical in this respect. Taguchi (1956) showed that the greater part of the Asian sockeye population is produced by the Ozernaya and Kamchatka Rivers. Let us then consider the arrival of adults making up these runs. The Ozernaya River sockeye arrival may be determined by the periods given for the Yavina fishery (Taguchi, 1956). The run lasts from June 30 to August 30 of each year, and the peak of the run occurs between July 25 and August 5. The percent of the run represented in the period containing the peak is

not clear, but about 70 percent of the catch was made during the last 10 days of July and the first 10 days of August. The run to the other major sockeye producing area of Asia, the Kamchatka River, arrives at that stream somewhat earlier. Taguchi stated that the Kamchatka River run lasts from June 9 to September 5, and peaks between June 13 and July 5. The peak interval appears to account for about 75 percent of the fish, with only 22 percent of the catch shown as taken before June 1 or after July 1. Birman (1958) stated that the Kamchatka River run finishes mainly on July 25 and the principal migration in the Ozernaya begins in the first days of August. In fact, the run is nearly over in the Kamchatka River when the bulk of the run appears in the Ozernaya River.

The peaks of the runs in the minor fisheries of northwestern Kamchatka and the Okhotsk Sea coast generally occur between mid-July and mid-August according to Taguchi. In this respect they resemble the Ozernaya more than the Kamchatka River. The peak period for the minor fisheries for sockeye salmon in northeastern Kamchatka is between June 28 and July 12, and appears to resemble the Kamchatka River fisheries in timing. The Asian sockeye salmon may, therefore, be placed into two broad groups: the earlier runs of eastern Kamchatka which reach their streams in June or early July and the later runs of western Kamchatka which reach their streams in the latter half of July and in August.

Timing of the runs to North American streams seems more complex.³ The peak of the migrations of sockeye salmon to Bristol Bay streams generally occurs in the first 2 weeks of July, although some numbers enter as early as June 15 or as late as August 15. The Chignik River fish first appear in late May, reach a maximum between June 10 and July 15, and continue to enter until late September. The run to the Karluk River begins in mid-May, lasts until mid-October, and has two peak periods. The first lasts from early June to July 1, and the second from late July to mid-September (Rounsefell, 1958). The catch in Cook Inlet is supported by several streams. The fish appear from late May until late August but are most abundant from

mid-July to early August. The catch in South-eastern Alaska is supported by fish from many streams, most of which have small runs. Fish appear in early June, reach maximum numbers in late July and early August, and are scarce after early September. The Skeena River sockeye arrive from late June until mid-August, and the run peaks between July 15 and August 1. The peaks of the Fraser River runs are most variable. Because the tributary systems have their own unique races, the characteristics of the peaks in a particular year depend upon which races are dominant in that year. Several peaks occur within a year as each major race approaches the river. Sockeye enter the Fraser River from early July until late September, and the dominant peak usually occurs between the latter part of July and early September.

The variation in the times when sockeye salmon reach their spawning streams is evident (fig. 2). Fish begin to arrive in large numbers in the Karluk River as early as June 1, and may continue to arrive in large numbers in the Fraser and Karluk Rivers until mid-September. With the exception of these rivers, the duration of heavy migration tends to be shorter, occurring within 6 weeks, and generally lasting less than a month for the major runs. These differences in timing must have a pronounced effect upon the distribution of maturing sockeye salmon in the sea. After the middle of July, for example, one would not expect to find in the sea any large part of the mature fish destined for the Kamchatka River or Bristol Bay rivers. If the speed of fish migration is considered with the time of their arrival at a particular stream, it should be possible to define areas of the sea which,

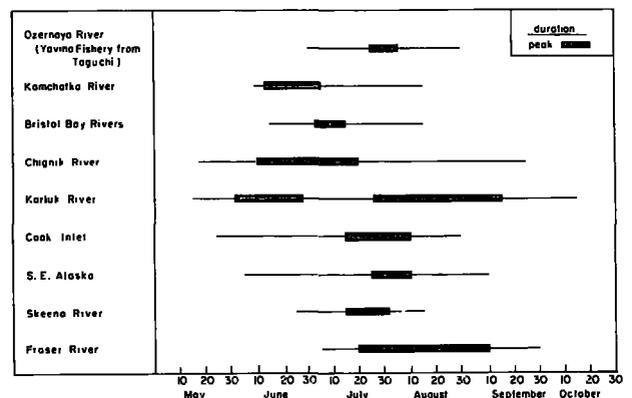


FIGURE 2.—Timing and duration of sockeye salmon migrations.

³ International North Pacific Fisheries Commission, Proceedings of the Seventh Annual Meeting, 1960, Vancouver, B.C. (INPFC Doc. 432) March 1961, 284 pp. [Processed.]

after a given date, would not contain maturing sockeye salmon from that stream. This feature may determine the origin of some groups of fish found on the high seas.

HIGH SEAS DISTRIBUTION

While the data related to the high seas distribution of salmon have not yet been analyzed thoroughly, there is information available from partial analyses and from the catch records of research vessels of Canada, Japan, and the United States, as well as from the Japanese high seas mothership fisheries. The data are deficient in two respects: First, almost all of the fishing has been done between May 1 and September 30, and second, comparable areas have not been fished each year.

SURFACE

Fishing with surface gill nets has shown that sockeye salmon are widely distributed in the North Pacific Ocean and Bering Sea from North America to Asia. Sockeye salmon have been caught in May as far south as lat. 45° N. in the western Pacific Ocean, and as far south as lat. 47° N. in the eastern Pacific Ocean (Bureau of Commercial Fisheries chartered research vessel *Bertha Ann*, March 1962). In June they have been caught at lat. 62° N. in the Bering Sea.⁴ It is likely that the ocean range of the species exceeds these boundaries; indeed they are regularly found, at least in restricted localities, outside of these latitudes. Every year they enter the Columbia River (lat. 46° N.) and the Noatak River⁵ (lat. 62° N.).

Little is known of the oceanic distribution of sockeye salmon from October through April. If, as has been commonly assumed, the fish at sea move southward in the winter, the area in which they are found in May might be taken to approximate that occupied during the preceding winter. During May, 1956, three Japanese vessels, *Eiko Maru*, *Takuyo Maru*, and *Etsuzan Maru*, explored an area bounded roughly by long. 160° E. to 175° W. and from lat. 40° N. to 50° N.⁶ The southern limit to which sockeye (maturity not stated) were found is shown in figure 3. The

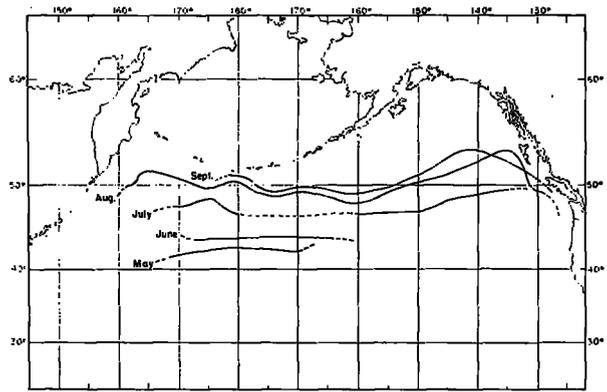


FIGURE 3.—Southern limits of sockeye salmon see footnote 7.

northern boundary of sockeye salmon between long. 175° E. and 180° appeared to be near lat. 50° N. The evidence indicates that by late May 1956, sockeye salmon had not moved as far north as the Aleutian Chain. This supposition is supported by the distribution of the Japanese high seas fishery which takes place well south of the Aleutian Islands in May. However, the supposition that the salmon all move south in winter, is contradicted by the catches of the Bureau's research vessel *Bertha Ann*. She caught considerable numbers of sockeye salmon as far north as lat. 51° N. at long. 175° W. in February 1962, and lat. 57°28' N. at long. 175° E. in February 1963. Fishing was not done further north.

The seasonal changes in the north to south distribution are poorly understood; however, figure 3 clearly shows a northerly displacement of oceanic sockeye salmon in successive months from May to September 1956.⁷

The distribution of the maturing salmon and the immature fish must be somewhat different because of their different requirements. As the spawning time approaches, the maturing fish must migrate to their streams to reproduce. To flourish, immatures must be distributed in whatever manner best suits survival and growth. The distribution of maturing and immature salmon should be considered separately for these reasons. Favorite⁸ in figures 23 and 24 (also INPFC, 1960, p. 91) shows a persistent decline in the size

⁴ Kasahara, H., and L. M. Kissack, Statistical Yearbook 1960, International North Pacific Fisheries Commission, Vancouver, B.C., 1961, pp. 1-67.

⁵ Reported by Clifford H. Fiscus, U.S. Fish and Wildlife Service, Seattle, report of 1955 field activities.

⁶ Konda, Mitsuo, Distribution area of salmon in the High Seas, *Suisan chō* (Fisheries Agency of Japan). In two parts—(INPFC Doc. 309 (1) and 309(2)). [Part I—English summary, 10 pp.; part II—Japanese text 8 pp. and 22 pp. in English.]

⁷ Manzer, J. I., Salmon Distribution and Abundance in the northeast Pacific, 1956-57. Fisheries Research Board of Canada, Nanaimo, B.C. (INPFC Doc. 195), 1958, 8 p. [Processed].

⁸ Favorite, Felix, Progress Report of Oceanography, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 319), 1950, 8 pp. [Processed.]

of sockeye salmon as fishing proceeded in a southerly direction. This is indicative of increasing percentages of immature salmon to the south. We have reason to believe from the results of high seas fishing that sometime during the winter the immature sockeye retreat to the south in the middle and western parts of the northern Pacific Ocean. Although information for the Gulf of Alaska is meager, Manzer's data for that area also suggest a southward retreat in winter. Data on the winter distribution of sockeye salmon are almost totally lacking. With the onset of maturation the maturing individuals separate from (if they were mixed) the immature elements of the stocks.

The research vessels in the Aleutian Region in June catch principally maturing fish (Hartt, 1962; and Margolis, 1963.) The maturing fish continue to be relatively abundant in the central and eastern Bering Sea, and along the Aleutian Islands until late June. Off southeast Kamchatka their abundance decreases in July and they become comparatively rare by August.

The distribution of maturing sockeye salmon in the Gulf of Alaska is less well known. Experimental catches have not been as large as in the Aleutian area. Maturing fish have been taken throughout the region north of lat. 50° N. and east of long. 150° W. (INPFC, 1957), between May and July. Intermittent fishing has shown them to be present at sea south of the Alaska Peninsula.

The maturing sockeye precede the immature fish in the more northern waters. In late May or early June the immature sockeye salmon appear to be situated south of the maturing individuals in the Aleutian Islands area (Hanavan, 1961). In the western Gulf of Alaska (south of Kodiak Island and the Alaskan Peninsula), immature salmon are found in fair abundance. In late June immature sockeye begin to replace the maturing fish in the catches off east Kamchatka and near the Aleutian Islands. By July immature fish are generally dominant from southeast Kamchatka along the Aleutians and well into the Gulf of Alaska. In August the fish are chiefly immature in the catches along the east coast of Kamchatka (Ishida and Miyaguchi, 1958). This is also true in the Aleutian Islands area, in the Bering Sea, and in the western Gulf of Alaska.

SUBSURFACE

The ocean distribution described above has been determined by surface fishing, however, the subsurface distribution may be different. Relatively little is known of the sockeye salmon in the deeper layers of the sea. Fishing in the Gulf of Alaska⁹ demonstrated that in the absence of a thermocline, this species is found to depths of at least 200 feet. A seasonal change in depth distribution in the Gulf of Alaska may be associated with the development of the thermocline. During summer when a marked thermocline existed, the fish were caught only in the layer above the thermocline. The depth distribution of maturing and immature sockeye salmon appeared to be about the same.¹⁰ It is not known whether the same vertical distribution pattern occurs elsewhere. The experiments indicated that salmon made diurnal migrations and were most abundant near the surface at night. This may explain the pattern of the Japanese mothership fishery in which the catch is taken at night with surface nets.

MIGRATION

Sockeye salmon are caught across the North Pacific Ocean and Bering Sea; consequently, some of them must migrate at least to midocean at the latitudes in which they are found. Because immature fish are believed to be scarce or absent in the Bering Sea in the colder months and from the southern part of their ocean range in the warmer months, they probably undertake considerable migrations in a north-south direction.

There are several possible methods of studying the migrations of sockeye salmon in offshore waters. First we will consider what can be discovered of the migrations from fishing indices.

Analysis of high seas catches of sockeye salmon could probably identify migration of major groups of salmon. Differences in numbers of fish, their size, sexual development, age, and timing of migration might be used to trace movement. Analysis of research vessel data, however, has not been completed, and detailed data needed from the mothership fisheries are not generally available.

⁹ Manzer, J. I., and R. J. LeBrasseur. Further Observations on Vertical Distribution of Salmon in the Northeast Pacific, Fisheries Research Board of Canada, Nanaimo, B.C. (INPFC Doc. 311), 1959, 9 p. [Processed.]

¹⁰ Neave, Ferris, Observations of the Vertical Distribution of Salmon in Northeast Pacific, 1960, Fisheries Research Board, Canada (INPFC Doc. 408), October 1960, 5 p. [Processed.]

Two interesting papers on migration are those by Johnsen ¹¹ (1962) and Hartt (1962). Johnsen examined data on the direction from which salmon entered the gill nets fished by U.S. research vessels

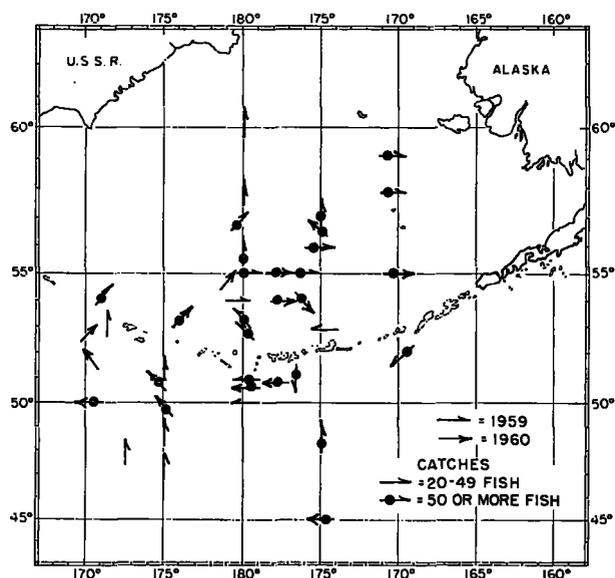


FIGURE 4.—Dominant direction of movement of red salmon indicated from gill net catches during May and June 1959 and 1960.

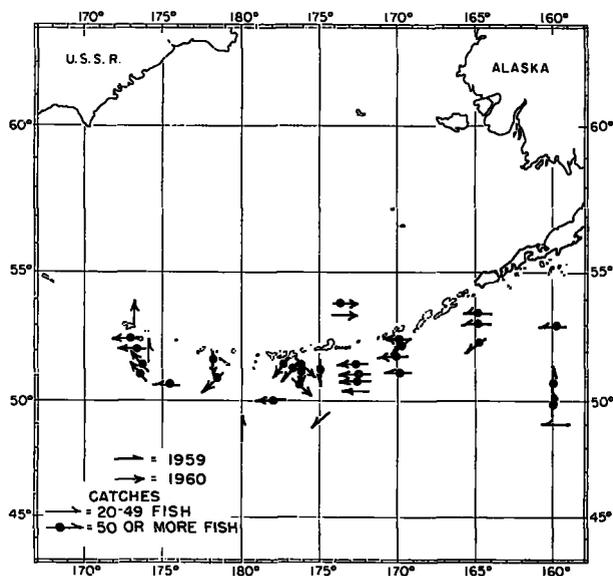


FIGURE 5.—Dominant direction of movement of red salmon indicated from gill net catches during July and August 1959 and 1960.

¹¹ Johnsen, Richard C., Directional Movement of Salmon in North Pacific Ocean and Bering Sea as indicated by Surface Gill Net Catches, 1959-60, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 569), 1962, 63 pp.

in 1959 and 1960. These data are grouped by May-June and by July-August catches (figs. 4 and 5). The May-June catches are predominantly maturing fish, and the July-August catches predominantly immature sockeye salmon. (The movement of fish is shown as being perpendicular to the axis of the gill net on each set.) Caution must be used in interpreting these figures. Where direction of migration is shown by an arrow, fish could have approached the net from somewhat different directions, but if they entered the net from the same side, the differences would not be detected. The situation where fish are shown to be moving about equally in opposite directions could also arise if the fish were caught while moving in a general direction more or less parallel to the net. Therefore, we must question the instances in which fish are shown to be moving equally in opposite directions, and consider that where movement is shown to be predominantly in one direction, the direction shown is not precise.

For maturing fish (fig. 4) the direction of movement in the North Pacific Ocean was westward as far west as long. 180°. At long. 175° E. the migration was north or west. Near long. 170° E. it was west, northwest, north, and northeast. In the Bering Sea, movement was generally in a northerly or easterly direction, although there are some marked exceptions at long. 180° and 175° W.

Immature fish in July and August (fig. 5) showed northerly or westerly movement in the western Gulf of Alaska and westerly movement in the North Pacific Ocean to long. 173° W. Between long. 175° W. and 175° E. the direction of movement was confused. Between long. 175° and 170° E. the direction again became strongly north and west. Too few catches of immature sockeye salmon are shown in the Bering Sea to provide an indication of the pattern of movement.

Hartt (1962) used the direction in which purse seine nets were set to study the direction in which sockeye salmon were migrating in the ocean. He pointed out that for the seine to catch fish in the manner it did, the fish must have been actively moving through the water. The purse seine is set to catch fish approaching from only one side of the net. By comparing the numbers caught when the net was set in opposite directions, the relative directional movement was revealed.

In the North Pacific Ocean he found that the catches "clearly illustrate the pronounced west-

ward movement along the south side of the Aleutians for both mature and immature reds (sockeye) as far as 175° East longitude . . . opposed movement to be only slight or lacking. West of 175° East longitude, movement becomes more mixed, but westward movement is still pronounced. Northward movement through Amchitka and Buldir Passes is indicated positively only later in the season when immatures were present. In the Bering Sea, the eastward route near the Pribilofs is shown between June 16 and 30."

These two sources indicate that from May through August, both the mature and immature sockeye salmon found in the North Pacific Ocean show a strong westward (and presumably northward) migration from long. 165° W. to 170° E. Although Hartt's observations were for the years 1956, 1957, and 1958 and Johnsen's were for 1959 and 1960, the results are quite similar. From the Bering Sea observations, the movement of maturing sockeye seemed to be mainly to the north and east. No observations were available with reference to movement in the Gulf of Alaska or in waters west of long. 170° E.

ENVIRONMENT

The migrations of sockeye in the sea, particularly during the homeward migration, seem to be related to the hydrography of the North Pacific Ocean and the Bering Sea. Taguchi (1957b) showed that the distribution of salmon in the Pacific Ocean west of long. 180° coincides with that of the dichothermal water which shows Oyashio (cold) water, and that the southern boundary of the distribution lies along the belt where the Kuroshio encounters Oyashio water. Taguchi (1957a) further stated that the oceanic migration of salmon coincides with the movement of water and that the best catches (presumably reflecting greatest abundance) will be made where a tongue of cold water intrudes into a branch of the Kuroshio.

Work by Favorite (INPFC, 1958) clearly shows that adult sockeye salmon which were going to Bristol Bay, Alaska, were moving along and quite close to the body of cold water (less than 3° C. from surface to bottom) near lat. 57° N. and long. 170° W.

In the central North Pacific Ocean, in the region where salmon are found, the movement of water

is easterly, except for the narrow return flow south of the Aleutian Islands. If the ocean migration of maturing fish were always with the prevailing current, the sockeye salmon should be moving easterly in the central regions when beyond the influence of the west current immediately south of the Aleutian Islands. Available evidence (figs. 4 and 5) indicates that this is not true; therefore, factors other than current direction may influence the direction of migration.

It is certain that the ocean environment strongly affects the distribution of salmon on the high seas. Favorite and Hanavan¹² showed that the southern limit of salmon as determined by surface gill net catches may be more directly related to subsurface than to surface conditions. Favorite¹³ and INPFC (1958) showed good correlation between the surface distribution of salmon and temperature at depth. During fishing operations along long. 155° W., surface temperature varied little. When the subsurface temperature minimum was no longer present, however, no salmon were caught at the surface. Although the temperature at the surface was about the same, sockeye salmon did not occur over the area which had warmer subsurface temperatures. For these reasons we might conclude that temperature may be only an indicator of the water inhabited by sockeye salmon, and not a precise limiting factor.

Konda¹⁴ stated that sockeye salmon were caught in surface nets when water temperatures ranged from 4.3° to 6.9° C. and that they were most abundant between 5° and 6.9° C. Manzer,¹⁵ however, reported that they were caught in the Gulf of Alaska at temperatures from 7° to 15.9° C. Fish seemed most abundant between 7° and 11.9° C. in 1956 and between 9° and 13.9° C. in 1957. These variations suggest that at surface water temperatures between 4° and 16° C., factors other than temperature may control the distribution of sockeye salmon.

¹² Favorite, Felix, and Mitchell G. Hanavan, Oceanographic condition and salmon distribution south of Alaskan Peninsula and Aleutian Islands 1956, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 415), 1960, 34 p.

¹³ Favorite, Felix, Progress report on oceanography, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 152), September 1957, 8 p. [Processed].

¹⁴ Kondo, Heihachi, Progress report on tagging experiments conducted in 1961 and additional recovery information for 1960 tagging, in Japanese (English translation by INPFC Secretariat, INPFC Doc. 485), October 1961, 3 p.

¹⁵ Cited by Manzer in footnote 7, p. 451.

It is possible that the oceanic environment in which maturing sockeye salmon are found might not be particularly favorable. The migration to their natal stream might take them into environments that are unfavorable, but which are tolerated in order to reach the spawning grounds. Thus, the circumstances in which the maturing fish are found may not represent optimal conditions, but merely an area through which they must pass.

In summary, the sockeye salmon inhabit a band of ocean reaching from Asia to North America. The position and perhaps the width and density of this band shifts with seasonal changes in the environment. In fall the fish seem to retreat from the Bering Sea and Aleutian Islands area. In late spring and summer, they reappear. It is most likely that features of the environment, such as food supplies and temperature strongly influence this distribution. Because the characteristics of the Gulf of Alaska are less affected by seasonal changes than the sea near Kamchatka, it seems likely that the displacement of sockeye salmon would be less marked. The shift is nevertheless apparent, but the fish apparently do not move as far southward. The distribution of these fish in the high seas is continually changing. Maturing fish are found over wide areas of the sea in early summer and disappear when they migrate to their streams. Immature fish (fish which are not going to mature within the calendar year of capture) are usually scarce at sea near the Aleutian Islands while maturing sockeye salmon are present; by July immature fish are abundant in this area.

Seasonal distribution combined with spawning time and location of spawning ground determines to some extent the direction of homeward migration. If the fish are south of lat. 50° in May in the central Pacific Ocean their spawning migration would probably have a northerly directional component because most of the major spawning streams lie north of this latitude. This would also be the case for Bristol Bay fish in the Gulf of Alaska, but not for Fraser River fish. Fish which begin a spawning migration in June would probably tend to go more directly east or west.

We can now reconstruct partially the oceanic migrations of sockeye salmon. Their movements are obscure after they leave the river mouth until they begin their second summer in the sea. In

June of their second summer at sea, sockeye salmon are found to be moving northward. This situation persists through the summer. From both fishing observations and tagging results, there appears to be a strong movement of immature fish to the westward along the south side of the Aleutian Islands. In the region of the Commander Islands movement seems to be predominantly to the north. This movement should shift the abundance of fish to the west and north. It is not clear if an individual fish will travel, for example, from the eastern end of the Aleutian Islands to the Commander Islands and northern Kamchatka. More extensive study of the migrations of immature salmon is needed.

After the end of summer the young salmon evidently migrate south to spend their second winter in the sea. The following spring we again find them distributed across the ocean and engaged in a general northward movement. This might not be so marked in the Gulf of Alaska as it is farther west. Migration south of the Aleutian Islands (and to some extent further east) is predominantly westward. Maturing fish which have spent two summers and winters at sea precede those which have been at sea equally long but which are not maturing.

From the tagging results which are discussed later it seems that maturing sockeye salmon destined for Kamchatkan streams continue to move west, but that the Bristol Bay fish go west for a distance, turn north through one of the passes into the Bering Sea, and proceed north and east to Bristol Bay. Evidently, most of the maturing fish south of the Aleutian Islands migrate westward regardless of whether their final destination lies to the east or west. Fishing provides no evidence that any substantial eastward movement by maturing fish exists south of the Aleutian Islands. Some exceptions to this must be in fish that are traveling to the Chignik River, Kodiak Island, or the British Columbia coast. Presumably, sockeye salmon that were going to Kamchatka from the Aleutians area would migrate west and then either north or south to reach the east or west coast of Kamchatka.

All sockeye salmon do not mature after their second winter in the ocean. These immature "two winter" fish, which are nearly as large as those which matured, apparently behave in the manner described for them as immatures a year earlier.

ORIGIN OF SOCKEYE SALMON IN OFFSHORE WATERS

From the preceding discussion it is evident that sockeye salmon travel far during their ocean existence. They are widely distributed on the high seas, and fish from rivers of both Asia and North America may be found in approximately the same part of the sea simultaneously. We then may consider origins of stocks caught on the high seas, and also, where they are of more than one origin, the relative proportion of each. This problem is complicated by the constantly changing distribution. Evidence now available indicates that before June there may be relatively few maturing salmon in the Pacific Ocean near the Aleutian Islands or in the southern Bering Sea. By the end of June large numbers of fish have entered these waters, traveled through them to various destinations, and have disappeared. Thus it is plain that to speak precisely of quantities of fish from each of several different streams is difficult. The numbers and destinations of fish in any area are apt to be changing. Further, as shown earlier, by far the greater numbers of salmon originate in a relatively few streams. It is almost impossible to discover and trace the very small groups that inhabit some of the streams along the Pacific Ocean rim. There are many streams each of which has a total run of only about one thousand salmon.

Although some information is available from other sources, knowledge of the origin of sockeye salmon on the high seas is principally from earlier work by Japanese scientists or from studies made by Canada, Japan, and the United States for the International North Pacific Fisheries Commission. This origin problem has been studied using tagging, scales, distinctive parasites, serology, and morphology. These studies have dealt separately with maturing and immature sockeye because of the marked difference in their distribution and movements. The work with maturing fish has progressed more rapidly than that with immature fish.

TAGGING STUDIES

The results of tagging experiments add enormously to our knowledge of the origins of sockeye salmon in the high seas.

Japanese scientists have studied oceanic migrations of sockeye salmon over a period of years.

From the results of tagging, Sato (1938, 1939) determined that the sockeye salmon offshore of southeast Kamchatka went north to the Kamchatka Gulf in May and south to the west coast of Kamchatka later in the year. He presents a schematic chart which shows sockeye salmon proceeding westward from the area south of Attu Island (ca. long. 173° E.) to the coast of Kamchatka and then proceeding north and south. He estimated that the average speed of travel of sockeye salmon at sea was 12.5 miles per day for mature fish traveling from Cape Kronotski (southeast Kamchatka) to the Ozernaya River in west Kamchatka.

Taguchi and Nishikawa (1954) gave a more detailed review of the movements of sockeye salmon in the western Pacific Ocean. The description they gave corroborates and extends the earlier work. They found fish traveling from the oceanic area southeast of the Kamchatka Peninsula north to the Kamchatka River and minor streams beyond, or south and west to the streams on the west coast of the Kamchatka Peninsula. They gave 3.3 to 9.3 miles per day as the average speed for directional movements along the west coast of Kamchatka.

In 1958, 1959, 1960, and 1961 (Japan Fishery Agency, 1959, 1960, 1961, and 1963) Japanese scientists conducted extensive high seas tagging experiments (fig. 6). The discussion here is limited to returns within the year of tagging in an effort to eliminate immature fish from consideration, but some of those taken by the high seas fishery might have been immature. The reports are not clear on this point. Most fish were released in June; some were tagged in July near Kamchatka in 1958. Some of the sockeye salmon tagged north of lat. 50° N. and west of about long. 165° E. were recovered in Asia. No American recoveries were made of fish tagged in this area. According to Sato (1939), the maturing fish from this area went to both east and west Kamchatka.

Recoveries in North America are shown for the sockeye salmon tagged north of about lat. 50° N. and east of about long. 170° E. in the North Pacific Ocean and Bering Sea. The one inshore recovery from tagging in the Bering Sea west of long. 180° was from Bristol Bay. No Asian recoveries resulted from tagging in these areas. The inshore recoveries were made mostly in Bristol Bay, Alaska, from tagging in both the

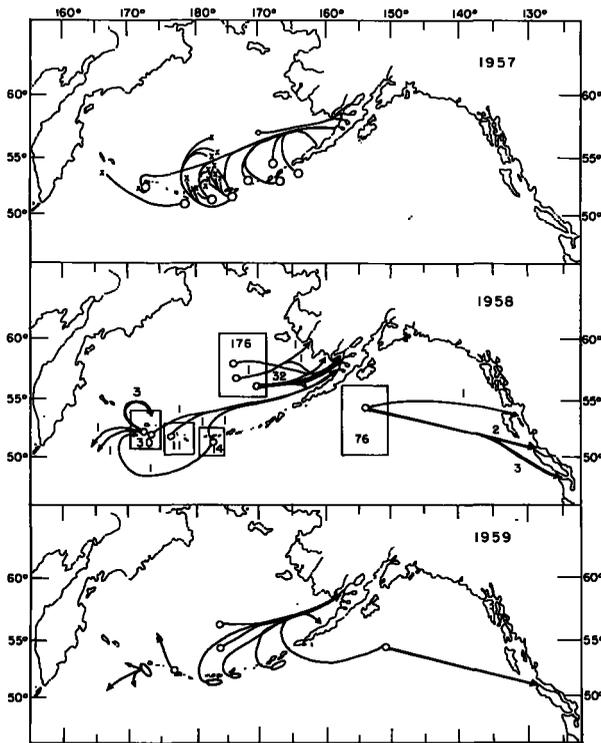


FIGURE 8.—Ocean migrations of sockeye salmon tagged by United States (INPFC, 1958, 1959, 1960c).

and in the Bering Sea nearly as far west as long. 180°. Again, nearly all of the inshore returns were from Bristol Bay, Alaska. There were also recoveries from other areas: one in Chignik River (1956) and one in Cook Inlet (1961) from fish tagged in the North Pacific Ocean near long. 165° W. (not shown), a recovery in the Kuskokwim River of a fish tagged in the Bering Sea near long. 175° W. and seven recoveries on the British Columbia coast of fish tagged between long. 150° W. and 155° W. south of Kodiak Island. Most of the seven were probably destined from the Fraser River. Fish that were released closer to Kodiak Island in 1961 had a different migration pattern (Hartt, 1963) and were recaptured from only Western and Central Alaska. Fish tagged near lat. 56° N. and long. 140° W. were recovered from Southeastern Alaska and northern British Columbia.

Hirano and Kondo¹⁷ reviewed the results of high seas tagging by Japan and the United States. They examined the recoveries of mature sockeye

¹⁷ Hirano, Yoshimi, and Heihachi Kondo, Salmon Tagging experiments in high seas of North Pacific, Fisheries Agency, Japan (INPFC Doc. 324), September 1959, 10 pp.

salmon according to the month of tagging. Most of the fish, however, were tagged in June. The May experiments were small, and in July the mature fish were no longer caught in the high seas areas. Their discussion of maturing sockeye salmon is primarily concerned with the distribution of the Bristol Bay fish. They express the opinion that from late May to June red salmon of Bristol Bay origin are distributed in the Bering Sea east of the line drawn between Attu Island and the Yukon River as well as along the Aleutian Islands, and that the Bristol Bay fish mix with red salmon originating from the Asian continent in the waters around Attu to Adak Island in May and June. Hirano and Kondo suggest that the direction of migration shown by tagged fish retaken on the high seas indicates that some sockeye of Asian origin also occurred south of the Aleutian Islands west of Adak Island.

Tagging recoveries show the eastward extent of migration for maturing Asian salmon and the westward extent for maturing North American salmon (figs. 9 and 10). The results of all of the sockeye salmon tagging experiments discussed earlier were employed in constructing these figures. In figure 9 the seaward limits of Asian and North American sockeye salmon are shown to the extent that they have been proved by recoveries in the home streams. Recoveries of tagged maturing sockeye salmon have been made in Asian streams from tagging in the North Pacific Ocean as far east as about long. 175° E. (Hirano, 1953). Although tagged fish have been released in the Bering Sea, none have been recovered in Asia. Tagged fish

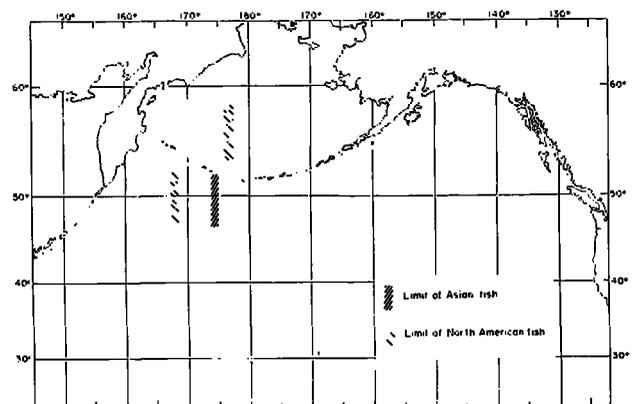


FIGURE 9.—Seaward limits of maturing sockeye salmon migration as shown by tag recoveries in or near spawning streams.

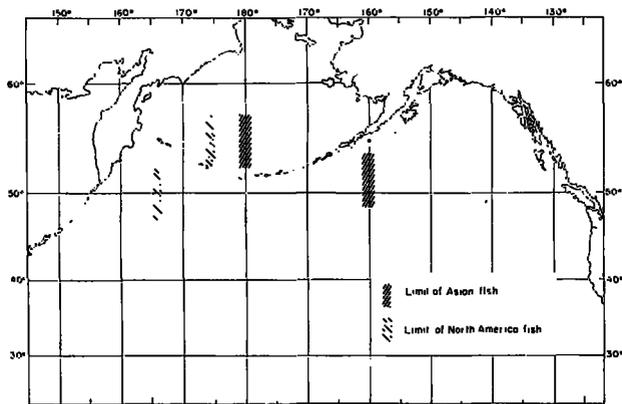


FIGURE 10.—Seaward limits of maturing sockeye salmon as inferred from direction of movement by salmon recovered on high seas.

have returned to North American streams from tagging operations near long. 167° E. in the North Pacific Ocean and from operations near long. 175° E. in the Bering Sea.

The recoveries shown in the figures are maturing salmon except where noted. If we assume that the ultimate destination can be inferred from the direction in which the fish traveled prior to capture, it is possible to speculate on the migrations which some of the fish captured on the high seas were undertaking (fig. 10). On this basis, maturing Asian fish appear to be migrating homeward from as far east as long. 159° W. in the North Pacific Ocean and from long. 179° W. in the Bering Sea. American fish appear to be migrating homeward from as far west as about long. 165° E. in the North Pacific Ocean and from about long. 175° E. in the Bering Sea. These limits can perhaps be useful in examining the extreme distances at which maturing Asian and North American fish might be found.

The procedure used in figure 10 is of doubtful validity. It is not known for certain that all of the high seas recoveries were maturing fish enroute to their spawning stream. In some instances they probably were immature fish of unknown origin engaged in a feeding migration. Further, the maturing fish enroute to the rivers generally move westward along the south side of the Aleutian Islands even when their ultimate destination is in Bristol Bay, which lies to the eastward. For these reasons we must conclude that we are unable to identify with any certainty the ultimate destination of a tagged fish recovered on the high seas.

The movements of immature sockeye salmon in the ocean are less clear than those of maturing sockeye. High seas recoveries of salmon tagged as immatures usually cannot be assigned to any final destination. Most were tagged during one summer season and recovered a year later. Because the intervening movements could have been and probably were extensive, it is difficult to place significance on distance between release and recovery points. With the exception of one that was released near lat. 52° N. and long. 172° E. and recovered in Kamchatka Bay, stream recoveries of salmon tagged as immatures were obtained only from North America. These again are chiefly from Bristol Bay, Alaska, and from fish tagged in the preceding summer at sea in the waters immediately south of the Aleutian Islands between long. 167° W. and 173° E. In addition, one fish tagged when immature at long. 177° E. was recovered at Rivers Inlet, British Columbia; another that was tagged south of Kodiak Island at long. 156° W. was caught at the mouth of the Fraser River, British Columbia.

From the discussion of high seas migrations it is clear that in the North Pacific Ocean maturing Kamchatkan sockeye salmon have been found in June as far east as long. 175° E. Maturing sockeye salmon tagged as far west as long. 167° E. and as far east as long. 150° W. have been recovered in Bristol Bay. Sockeye salmon tagged as far west as long. 177° E. in the Bering Sea in June were recovered in Bristol Bay.

Most of the maturing sockeye salmon tagged south (fig. 8) of the Aleutian Islands as far west as long. 175° E. appear to have been migrating westward when caught and tagged. Recoveries were mainly from Bristol Bay or the Bering Sea east of long. 180°. Although there are certain exceptions, tagged fish released near the south side of the Aleutian Islands usually did not proceed as much as 10 degrees of longitude further westward. However, those shown in figure 6 migrated from near long. 160° W. to almost 180°, and showed a distinct northward movement as well.¹⁸ With one exception, they did not appear west of long. 180°. From the recoveries from these tagging experiments we infer that the maturing sockeye salmon found south of the Aleutian Islands are mainly of Bristol Bay origin.

¹⁸ See footnote 14, p. 454.

The fact that maturing Bristol Bay sockeye are intercepted by tagging vessels in a westward movement south of the Aleutian Islands when they are on a spawning migration to Bristol Bay, which lies to the east, makes it evident that these fish do not travel home by the shortest and most direct route. The work by Sato (1939) and Taguchi (1956) which was discussed shows that Asian sockeye salmon tend to travel first west, and then north or south when on their spawning migration to Kamchatka streams.

Early summer tagging has yielded some information concerning the origins of maturing sockeye salmon in the eastern Aleutian Islands area and in the Gulf of Alaska. Fish from Chignik, Kodiak Island, Cook Inlet, and northern British Columbia have been tagged in the North Pacific Ocean in the vicinity of long. 170° W. to 175° W. Sockeye returning to Kodiak Island, Cook Inlet, Copper River, Southeastern Alaska, northern British Columbia, and the important Fraser River have been tagged in the central Gulf of Alaska as shown by the preceding figures. While it is evident that the data are too few to describe the areas occupied by the runs to the streams of North America south of Bristol Bay, all of the runs seem to be represented in the region south of Kodiak Island.

The origin of immature salmon is poorly defined by tagging results. Examination of the tagging references considered earlier shows that immature fish which were probably Asian were tagged as far east as about long. 175° E. in the North Pacific Ocean. Immature North American (Bristol Bay) fish were tagged in the North Pacific Ocean as far west as long. 173° E. and in the Bering Sea as far west as long. 171° E.

From the tagging studies it is possible to reach certain conclusions concerning the origin of maturing sockeye salmon found in various areas of the North Pacific Ocean and Bering Sea.¹⁹ Tag returns cannot be used to calculate precisely the percentages of fish of various origins in areas of the high seas unless it is known that inshore recovery rates are equal or can be adjusted. Little information is available on this point. However, Hartt (1962) pointed out that the complete lack of Asian returns is incompatible with the assumption that large numbers of maturing Asian sockeye salmon were present among his tagged fish. Con-

sidering these points with the tagging returns, it appears that most of the maturing sockeye found in June and July off the southeast coast of Kamchatka at least as far east as long. 170° E. were of Asian origin. Maturing sockeye salmon are found here in May, June, and the first half of July. In the tagging areas south of the Aleutian Islands where maturing fish are caught in late May and in June, the tagged fish were of Bristol Bay origin at least as far west as long. 175° W. in 1956, 1957, and 1958, long. 178° W. in 1959 and 1961, and long. 177° E. in 1960.

In the Bering Sea east of long. 177° W., virtually all of the sockeye salmon present along the north side of the Aleutians and in the Pribilof Islands area were of Bristol Bay origin. Although relatively fewer tags were released in the Bering Sea between long. 177° W. and long. 177° E., the only inshore recoveries were made in Bristol Bay, suggesting that Bristol Bay fish formed a majority of the maturing sockeye in this area. Maturing sockeye are found in the Bering Sea principally in June. From the Aleutian Islands eastward, less is known about the relative numbers of fish of various origins. Additional tagging is required.

MORPHOLOGICAL STUDIES

Differences in the morphological characteristics of North American and Asian sockeye salmon were used by Fukuhara, Murai, LaLanne, and Sribhibhadh (1962), Fukuhara (1961), and Landrum and Dark (1963) to determine the origin of sockeye salmon occurring in the Aleutian Islands area of the North Pacific Ocean and Bering Sea. In these studies, reference morphotypes or classificatory categories were chosen, certain morphological characters were selected to measure the racial differences between reference morphotypes, and a discriminant function analysis was employed to classify sockeye caught in the Aleutian Islands area.

Samples taken from the sockeye runs returning to Southwest Kamchatka and Bristol Bay-Chignik-Karluk River systems were chosen as reference morphotypes. These selections were based on evidence from tagging studies, parasite studies (which will be discussed later), and generalized distance function analyses (INPFC, 1958, 1959), all of which indicated that most of the maturing sockeye salmon in the Aleutian Islands area originated in Kamchatka or Western Alaska, and from

¹⁹ See footnote 14, p. 454, and INPFC 1963.

information on the sizes of sockeye runs to various inshore areas, which showed that the Ozernaya River produced over three-fourths of the total Kamchatka catch while almost all Western Alaska sockeye originated in the rivers of Bristol Bay or Chignik and Karluk Rivers.

Seven morphological characters were used to measure the racial differences between the two reference morphotypes (scales in lateral line, vertebrae, caudal vertebrae, gill rakers, ventral gill rakers, pectoral fin rays and fin elements, and position of haemal arch). Each of these characters was carefully examined to make certain that no appreciable intra-morphotype variation was introduced by counting methods or differences in sex, age, life history, and time of sampling. The correlation between each character and fish length was determined to be negligible.

From samples obtained at sea off southwest Kamchatka and from streams in Western Alaska in 1956, the seven morphological characters were combined in a discriminant function. The amount of overlap between the two reference morphotypes was determined, rules of classification were established, and errors of misclassification were estimated. Since the Western Alaska reference morphotype was composed of several runs with differing errors of misclassification, it was necessary to obtain a weighted average error of misclassification for this morphotype. This was accomplished by weighting the error of misclassification for each run by its relative abundance as estimated from escapement counts.

Fukuhara et al. (1962) reported the classificatory results obtained by applying the discriminant function derived from the 1956 reference samples to high seas samples collected in 1956 and 1957. The authors also reported the details of the statistical analyses, tests of underlying assumptions, and empirical verification of the efficacy of the discriminant function. Classifications of the high seas samples taken in 1958 and 1959 and the development of confidence intervals for the classificatory results were discussed by Fukuhara (1961).

In each of the 4 years 1956-59 the samples taken in the Aleutian Islands area were divided into three groups: those taken in May and June; those taken in July; and those taken in August. The samples taken in May and June were composed mainly of maturing fish; the samples taken in July and August were mainly immature fish. Because the

distributions of mature and immature sockeye were not the same, and underlying assumptions have not been satisfied for immature fish, the classification results were discussed separately.

Landrum and Dark (1963) used the discriminant functions derived from the 1956 reference samples to classify the 1960 collections. The average error of misclassification for Bristol Bay salmon was weighted by the relative abundance of the component stocks in the 1960 escapement.

The run to Bristol Bay in 1960 was very large (about 37 million according to Royce, 1961). We expected that the maturing sockeye salmon in large areas of the ocean, particularly in the Bering Sea east of long. 180° would be predominantly of Bristol Bay origin. As anticipated, all samples taken east of long. 175° E. in the Bering Sea were found to be chiefly of the Western Alaska morphotype. East of long. 180° the samples contained an estimated average of over 90 percent sockeye of Western Alaska morphotype. The upper 90 percent confidence limit averaged about 104 percent, and the lower limit averaged about 79 percent.

In the North Pacific Ocean in May and June 1960, maturing Bristol Bay sockeye salmon predominated in samples taken east of long. 180° with percentages ranging from 59 to 100 percent. West of long. 172° E. Kamchatkan sockeye salmon predominated by percentages ranging from 60 to 100 percent in samples that were mainly of maturing salmon.

Landrum and Dark further concluded that "the general trends in the east-west distribution of Kamchatkan and Bristol Bay stocks in both the Bering Sea and North Pacific Ocean are similar for the years 1956 through 1960."

A further matter of interest is the development of confidence limits for the point estimates of western Alaska type sockeye salmon (Fukuhara, 1961). The error caused by misclassification of fish was found to be a limiting factor in developing precise point estimates. For 1956 and 1957 (with errors of classification about 21 percent) samples of 150 to 200 fish had 90 percent confidence limits of about ± 8 percent. For 1959 (with an error of classification of about 30 percent) the 90 percent confidence limits were about ± 15 percent.

The origin of the maturing fish that were taken on the high seas seems best described by the summary given in Proceedings of the Seventh

Annual Meeting, International North Pacific Fisheries Commission.²⁰ In table 4 (taken from page 101 of that document) the percentages of Western Alaska morphotype in late May and June were averaged by 5-degree intervals of longitude for the North Pacific Ocean and for the Bering Sea according to year of sampling. These averages are shown in figure 11 and are referred to in 5-degree bands centered on the longitude indicated.

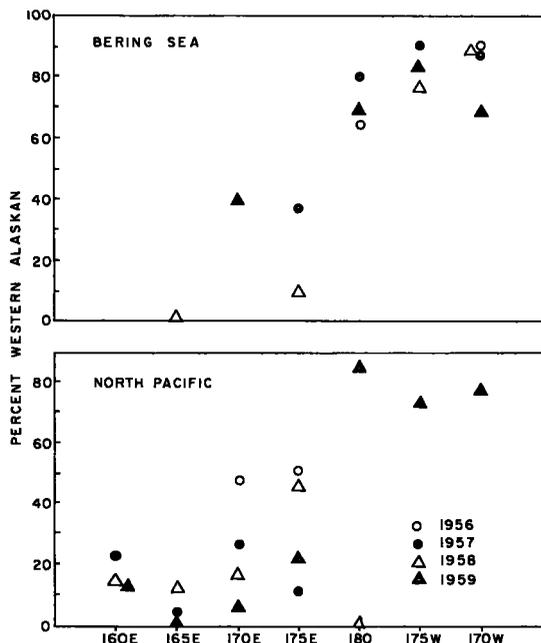


FIGURE 11.—Average percentages of Western Alaska morphotype in samples taken in the Bering Sea and North Pacific Ocean in late May and June 1956–59. (The 1958 sample at long. 180° was entirely of immature fish.)

These percentages show the following:

(1) In the Bering Sea, in the 180° band and eastward, the average percentage of Western Alaska morphotype in the samples ranged from 65 to 90 percent. Westward from this bank, the average percentages of Western Alaska morphotype in the samples decreased. In the 175° E. band and westward, the average percentage of southwest Kamchatka morphotype ranged from 61 to 100 percent. (2) In the North Pacific Ocean, from the Asian coast out to the 170° E. band, the average percentages of Western Alaska morphotype in the samples ranged from 0 to 40 percent. In the 175° E. band, the average percentages of Western Alaska morphotype ranged

²⁰ See footnote 3, p 450.

from 11 to 45 percent, except for 67 percent in 1956. In the 180° band and eastward, the average percentage of Western Alaska morphotype ranged from 72 to 85 percent in 1959, but in 1958 the single sample (taken in the 180° band) contained none of this type. (3) In the Bering Sea eastward from the 180° band and in the North Pacific westward from the 175° E. band, sampling from 1956 to 1959 was sufficiently intensive to suggest that the approximate ranges of percentages cited above reflect the relative proportions of the southwest Kamchatka and Western Alaska morphotypes present in these areas.

The morphological research cited above shows some interesting features of the high seas distribution of immature sockeye salmon in August. Because maturing sockeye are still present in the waters near Kamchatka and near spawning streams of North America in July, the samples in these areas may be either mature or immature. By August, maturing sockeye become relatively rare in the open ocean. As shown in the INPFC annual reports for the years 1959 and 1960 (INPFC, 1960, 1961) immature sockeye of the southwest Kamchatkan type appear to be distributed through the western Bering Sea as far east as long. 180°. They appear to be distributed as far east as long. 175° W. in the North Pacific Ocean and possibly as far east as long. 165° W. Because sockeye from British Columbia rivers inhabit this area, and the discriminant function incorrectly classifies most of such fish as south-

TABLE 4.—Average percentages of Western Alaska morphotype in samples taken in the Bering Sea and North Pacific Ocean, late May and June, 1956–59.^{1 2 3}

Location and year	Mid-points of 5° intervals						
	160° E	165° E	170° E	175° E	180°	175° W	170° W
Bering Sea:							
1956					65 (1)		90 (1)
1957				36 (1)	80 (2)	90 (6)	87 (4)
1958		0 (2)		9 (1)		78 (1)	89 (3)
1959			39 (3)		70 (10)	84 (6)	70 (3)
North Pacific Ocean:							
1956			48 (2)	51 (5)			
1957	23 (1)	5 (3)	28 (4)	11 (3)			
1958	15 (1)	12 (1)	18 (5)	45 (2)	0 (1)		
1959	14 (3)	0 (2)	8 (10)	23 (5)	85 (2)	72 (4)	78 (2)

¹ The numbers of samples used for computing the averages are shown in parentheses.

² Taken from table 8, page 101 of (Proceedings of the seventh annual Meeting, 1960, International North Pacific Fisheries Commission, Vancouver B.C. INPFC Doc. 432, March 1961, 284 pp. (Processed).

³ Deletion of samples containing more than 25 percent immature fish would eliminate the entries for the Bering Sea in 1957 at 175° E., and for the Pacific Ocean in 1957 at 175° E., and in 1958 at 180°. Deletion would also increase the average percentage in the Bering Sea 180° interval to 74 in 1956 and 78 in 1959. In the Pacific Ocean the average for 170° E. would change to 17 in 1958; in 1959, the averages become 10 for 170° E., 26 for 175° E. and 73 for 175° W.

west Kamchatkan morphotype, there is no way of determining whether the immature sockeye salmon of the western part of the Gulf of Alaska which are classified as Kamchatkan fish come from Kamchatka or from streams east of Kodiak Island.

Immature sockeye salmon of the Western Alaskan morphotype were found in August 1959 as far west as long. 170° E. in the Bering Sea. Indeed, a sample taken about 80 miles south of Cape Olyutorskii in 1959 showed strong evidence of immature Western Alaska type fish. In the North Pacific Ocean, Western Alaska type immature salmon were found from long. 160° W. to long. 175° E. Samples are lacking for the waters farther west. Landrum and Dark (1963) found that the Bristol Bay morphotype dominated all samples of immature sockeye salmon to long. 172° E. in July and August 1960. As in earlier years, the degree to which Bristol Bay fish dominated was not as pronounced in immature samples as in samples of maturing fish.

This may be the result of segregation of maturing fish into groups of common origin, or it could be caused by the presence of immature fish from areas other than Asia or Western Alaska. The analysis assumes that all fish are from these two sources. This assumption has been tenably justified for maturing salmon only. Although there is little evidence to negate the hypothesis for immature fish, there is a distinct possibility that sockeye salmon from North American streams other than those of Western Alaska may occur in the area. Analysis shows that the discriminant function used would misclassify these Kamchatkan salmon. A further but less serious error lies in the fact that the errors of misclassification for samples of immature salmon were not weighted in accordance to their abundance at maturity.

Analyses of the morphological characteristics of salmon east and south of Kodiak Island have not yet been reported. Preliminary studies have been made using the generalized distance function analysis with sockeye salmon data. This work is discussed briefly in the Annual Report for the year 1957 (also for 1958) of the International North Pacific Fisheries Commission (INPFC, 1958, 1959). This preliminary work using the distance function showed approximately the same distribution for Asian and North American sockeye salmon as was found by using the discriminant function.

Gilbert (1914-20) noted and described differences in scale patterns between races of Fraser River salmon on their spawning grounds. Various scientists since that time have used sockeye salmon scales in assigning fish of unknown origin to a particular spawning group. Scales of fish from different streams often have unique patterns. The use of scales for identification of the origin of sockeye salmon in the high seas is particularly attractive. When compared to alternate means of identifying high seas fish, scales are found to be relatively inexpensive to collect, store, and examine. Consequently, there has been a considerable amount of study designed to develop means of using scales to determine the origin of high seas sockeye salmon.

Although offering marked advantages over other means of identification, scale studies have difficulties that are not found in other methods. The usefulness of the scale method generally depends upon precisely counting or measuring various groups of circuli or areas of the scale. That scale reading has not yet developed into an exact science on a worldwide basis is evident. During the 1956 meeting of International North Pacific Fisheries Commission scale scientists, comparisons of age determinations were made on 436 sockeye salmon scales. Among a test panel of six scientists from Canada, Japan, and the United States, there was a disagreement of some sort concerning the total age of 55 percent of the test scales. This does not imply disagreement by all six on this percentage. Two scientists who had previously worked together disagreed on 11 percent between themselves, and their final conclusions disagreed by 4 percent from the ages considered to be correct. Relatively little difficulty was experienced with scales from Canadian fish; the disagreement was much greater for fish originating farther north. The range of disagreement for the six scientists was from 11 to 26 percent when compared with the age judged to be correct. There is no way at present of being certain that the ages judged to be correct really were. From subsequent tests it appeared that the difficulty lay chiefly in determining the number of annular marks in the fresh-water zone of the scale. This is of particular importance because most methods for identifying the origin of high seas sockeye salmon depend upon separat-

ing them into groups according to fresh-water life and total age.

The methods further require consistent measurement of the features employed to identify origin of the fish. Because scales are often very irregular in structure, exact criteria describing annuli are difficult to establish. Studies of the variation in number and spacing of circuli at various angles of the anterior field of the scales have not been formally reported, although experts commonly refer to this variation. There seems to be no published definition of the point at which measurements and counts start or stop for any particular study. Because of the lack of definitive descriptions of techniques and the lack of analyses of their reliability in general, it is nearly impossible to gauge the accuracy of the results unless some other means of measuring reliability is provided. Keeping the possible errors in mind, we can proceed to discuss the classification of high seas salmon to their origins. There is need to make the use of scales more precise.

Krogius (1958) discussed the variation in Kamchatkan sockeye salmon scales in considerable detail. She described the patterns found in the Kamchatka, Bolshaya, Ozernaya, Kukhtua, Pylga, and Paratunka Rivers, which include the major sources of sockeye salmon in Asia. Distinctive differences were found in the number of circuli formed in each year of fresh-water life, the size of the scale at the end of each year, and the relative numbers of crooked or broken circuli. Using these features, she identified Kamchatka, Ozernaya and Bolshaya River sockeye salmon taken in the North Pacific Ocean from Kamchatka to about long. 175° E. She stated that the origins of fish taken in the ocean could be determined from scales characteristics but that the method is in need of further development.

Kubo²¹ reported the results of an extensive study of sockeye salmon scales and developed a method which he employed to identify the origin of maturing 5₂ and 6₃ salmon caught on the high seas. The first number in this terminology refers to the year of life when the fish was caught, and the subscript number to the year of life in which it migrated from fresh water. His scale comparisons included: (1) total radius (anterior), (2)

length of anterior field for ocean growth only, the ratio of (2)/(1), the ratio of the spacing of ocean circuli 21 to 30 to ocean circuli 11 to 20 and the anterior radius of the fresh-water zone excluding the so-called "plus growth." Plus growth is indicated by the widely spaced circuli which in some fish follow the last fresh-water annulus and are believed to occur in fresh water just prior to the salmon's migration to the sea. He determined that the radius of the fresh-water growth zone was most efficient in identifying the origin of sockeye salmon in the high seas. Like Fukuhara et al. (1962), he concluded that the maturing sockeye salmon in the North Pacific Ocean and Bering Sea between Asia and long. 165° W. were principally of Kamchatkan or Bristol Bay origin in late May and June. He constructed and used frequency curves of fresh-water radii to correct for overlap in this character between Kamchatka and Western Alaska sockeye salmon. Figure 12 shows the adjusted result of identifying samples of salmon taken on the high seas.

The method employed by Kubo promises to be useful in determining the origin of salmon. His test for scale differences between sexes and the effect of fish length on scale characters might be improved by utilizing fish of a single, known origin instead of a high seas sample of unknown, and perhaps mixed, origin. A mixture of fish with varying scale characters might obscure the relationships he is examining. It is doubtful that any large error has been introduced, however.

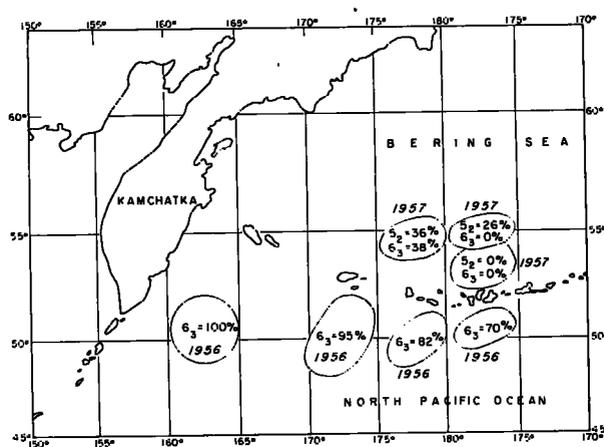


FIGURE 12.—Distribution of Asiatic sockeye salmon estimated by RF (fresh-water radius) composition in samples from various areas of the high seas.

²¹ Kubo, Tatsuro, Study of Sockeye Salmon Stocks by means of the Growth Pattern of Scales (Preliminary Report). Faculty of Fisheries, Hokkaido University, Japan (INPFC Doc. 206). August 1958, Part 1, 15 pp. (Text.) Part II-2, 16 pp.

The most serious difficulty with Kubo's results arises from the use of only the 5₂ and 6₃ fish. The failure to include the 4₂ and 5₃ groups prevents interpreting the results in terms of the relative numbers of Kamchatkan and Bristol Bay sockeye that may be present in the area. The proportion of the runs that return as 4₂, 5₃, 5₂, or 6₃ to Kamchatka or Bristol Bay varies widely from year to year. If only part of the fish are considered for any one year it is easily possible to overlook the major part of the maturing fish present. To illustrate this, table 5 shows the estimated numbers of fish of 4₂, 5₃, 5₂, and 6₃ categories that returned to Bristol Bay streams from 1956 to 1959. These figures are based on combined catch and escape-ment statistics. In 1956, 20.5 million of the 24.5 million fish returning to Bristol Bay were 4₂ and

TABLE 5.—Age composition of Bristol Bay sockeye salmon runs
[Figures in millions of fish]*

Year and District	4 ₂	5 ₃	Sub-total 2-ocean	5 ₂	6 ₃	Sub-total 3-ocean	Totals
1956							
Nushagak	0.914	0.316	1.230	1.090	0.126	1.216	2.446
Naknek							
Kvichak	10.371	6.701	17.072	1.045	1.003	2.048	19.120
Ugashik	.528	.129	.657	.049	.057	.106	.763
Egegik	.292	1.326	1.618	.201	.418	.619	2.237
Totals	12.105	8.472	20.577	2.385	1.604	3.989	24.566
Percent.	49.3	34.5	83.8	9.7	6.5	16.2	-----
1957							
Nushagak	.267	.033	.300	.659	.069	.728	1.028
Naknek							
Kvichak	.018	1.953	1.971	5.187	1.217	6.404	8.375
Ugashik	.130	.117	.247	.261	.062	.323	.570
Egegik	.015	1.158	1.173	.260	.735	.998	1.171
Totals	.430	2.261	2.691	6.367	2.086	8.453	11.144
Percent.	3.9	20.3	24.2	57.1	18.7	75.8	-----
1958							
Nushagak	1.139	.137	1.276	.946	.084	1.030	2.306
Naknek							
Kvichak	.181	.561	.742	.080	.908	.988	1.730
Ugashik	.024	.381	.405	.234	.085	.319	.724
Egegik	.002	.406	.408	.050	.257	.307	.715
Totals	1.346	1.485	2.831	1.310	1.334	2.644	5.475
Percent.	24.6	27.1	51.7	23.9	24.4	48.3	-----
1959							
Nushagak	2.888	1.320	4.208	.436	.097	.533	4.741
Naknek							
Kvichak	1.307	2.684	3.991	1.030	.342	1.372	5.363
Ugashik							
Egegik							
Totals	4.195	4.004	8.199	1.466	.439	1.905	10.104
Percent.	41.5	39.6	81.1	14.5	4.3	18.9	-----

* Age composition estimated from catch samples only.

¹ Not available.

² Total run to the four districts was 12,622 million fish in 1959. Thus, the percentages given fairly accurately depict age composition of total Bristol Bay run in 1959.

³ From research files of the University of Washington Fisheries Research Institute and the Bureau of Commercial Fisheries.

5₃. Only 16 percent of the run was composed of 5₂ and 6₃ fish. In 1957 the situation was reversed. About 8.5 million returned as 5₂ and 6₃ fish, and they formed about 76 percent of the run of 11.1 million sockeye salmon. Therefore in a study in which only 5₂ and 6₃ fish were used, if the ocean distribution were the same for all age categories, estimates of the percent of the fish present of Bristol Bay origin would be expected to be very low in 1956 and high in 1957. Comparable figures are unfortunately not available for all major Kamchatkan streams.

When figure 12 is considered with the data of table 5, it appears that the estimates of the numbers of Asian fish given for the North Pacific Ocean are probably high, because only 1956 samples are considered. Bristol Bay fish would be under-represented. The run to Bristol Bay was relatively large in 1956, but the dominant age categories involved did not enter the calculations. Kamchatkan runs appear to have high percentages of 5₂ and 6₃ fish every year. The degree to which bias occurs is determined by the relative proportions of fish of the same age categories in the runs to Kamchatka and Bristol Bay, and by whether fish from both origins are present at the time and place of sampling.

Kubo and Kosaka²² reported a similar study which was concerned only with the origin of 5₃ sockeye salmon caught on the high seas. Because the anterior radii of the fresh-water zones (from the focus to the last fresh-water annulus) was distinctly larger in fish which matured as 5₃ than those which remained in the ocean and matured as 6₃, they concluded that the radius of the fresh-water zone was not suitable to separate Kamchatkan and Bristol Bay sockeye salmon. The maturity of the samples was not considered to be known with sufficient certainty. Therefore a 5₃ taken at sea might actually have remained to migrate as a 6₃ a year later.

They further concluded that the anterior radius of the fresh-water zone divided by the combined width of the first two ocean zones provided the best means of identifying the origin of maturing 5₃ sockeye salmon in the Aleutian Islands area. Although it is not explicitly stated, the 1956 samples from the Kamchatka region and from

²² Kubo, Tatsuro, and Jun Kosaka, Study of Sockeye Salmon Stocks by means of the Growth Pattern of Scales, Fisheries Agency, Japan (ENPFC Doc. 326), August 1959, 8 p.

Bristol Bay were evidently employed to define the population parameters that were used to calculate the percentage of high seas fish of Kamchatkan and Bristol Bay origins. The results of these calculations are shown in figure 13.

These results are difficult to interpret for the reasons discussed in connection with Kubo's 1958 report.

Neither of the above papers provides a method of judging the accuracy with which high seas samples are assigned to the correct origin. An empirical test in which independent samples of known origin are identified would be useful. It would still be necessary, however, either to find some means of weighting the samples or to develop a method by which all of the age categories caught could be suitably treated. Without this, there is no way of knowing what portion of the fish in any particular sample originated in Kamchatka or Bristol Bay.

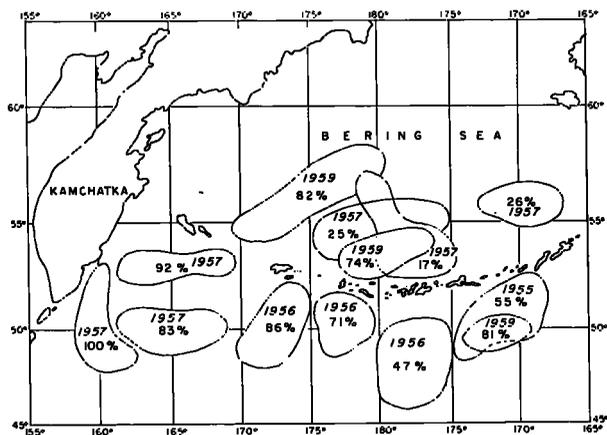


FIGURE 13.—Distribution of Asiatic salmon estimated by RF/RS₂ ratio (fresh-water radius/radius to fourth annulus) composition in samples from various areas of the high seas (from Kubo and Kosaka, 1959).

Mosher²³ in a similar study examined the number of circuli in the fresh-water zone and first ocean zone of sockeye scales. Scale samples taken in or near Kamchatka and in Bristol Bay streams provided the population parameters and a test of the accuracy of his identifications.

²³ Mosher, Kenneth H., Racial analysis of the offshore samples of red salmon (*Onchorhynchus nerka*, Walbaum) from central north Pacific and Bering Sea from May 1 to July 15, 1956-57 by means of scales. Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 312), October 1959, 29 p. [Processed.]

The fish were divided according to whether they had migrated to sea in their second, third, or fourth years and whether the sample came from Kamchatka or Bristol Bay streams. For each of the six categories a bivariate tabulation was made of the number of circuli in the fresh-water and first ocean year zones, except for the fourth year fish for which length of these zones was used. The bivariate frequencies were then weighted to 100 to adjust for unequal sample size. Next, the frequencies were superimposed, the Kamchatkan frequencies being placed on those for Bristol Bay of the same fresh-water age. The numbers in each cell were compared, and each cell was judged to be Kamchatkan or Bristol Bay according to which had the larger frequency.

When the 1957 samples of maturing fish of known origin which were used to construct the tables were identified by using the bivariate charts, 85.4 percent of the fish from near Kamchatka and 86.5 percent of the fish from Bristol Bay were correctly identified. Of an additional 261 scale samples from near or in Kamchatka in 1957, which were not used in deriving the continental standards (for lack of data on the area of the fish from which scales were taken), 237 or 91 percent were correctly assigned to Kamchatka.

Samples of fish taken in other years were also used to examine the accuracy of the classificatory procedure. Of 648 sockeye salmon taken in or near Kamchatka and 786 sockeye taken from Bristol Bay in 1956, 77.2 percent and 82.3 percent respectively were correctly identified.

For 1955 samples (again using the 1957 reference data) 77 percent of 168 Asian fish and 72 percent of 303 Bristol Bay fish were correctly identified. The average misclassification was roughly 14 percent for the 1957 samples, 21 percent for the 1956 samples, and 25 percent for the 1955 samples. This seems to indicate a moderately increasing error in classification as the year in which the standards were taken becomes more remote. No difference was found between sexes in the scale characters.

Using the charts developed with 1957 inshore samples, Mosher classified the sockeye salmon in high seas samples for 1956 and 1957. The initial classifications of the fish into area of origin were adjusted for the average error of misclassification for that year (fig. 14). The average

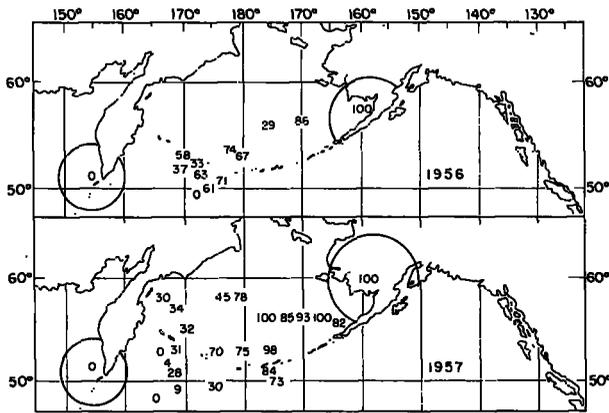


FIGURE 14.—Percentage of Bristol Bay type sockeye salmon in scale samples taken from mid-May to mid-July.

adjustment of 21 percent produces a bias favoring Bristol Bay fish in 1956.

There are other possible sources of bias. The high seas samples used were mostly maturing fish, but contained some immature fish, especially in July. The samples contained a mixture of fish of various year classes and age categories. No definitive mention is made of the variation that might occur in the scale characters of the high seas samples due to differing year classes, ages of maturity, length selectivity, or similar factors. Kubo and Kosaka²⁴ presented data which indicated that the anterior radius of the fresh-water zone was larger among those fish which matured in 1956 as 5₃, than in fish of the same brood year which returned in 1957 as 6₃. The effect of this on Mosher's results is obscure. Further, the error of misclassification is given for the combined samples; it is not clear whether or not this error was the same for all three fresh-water ages. If it were markedly different, the adjustments could be inaccurate.

With only moderate increases in error, Mosher, however, was able to identify the continental origin of sockeye in samples from years (1955 and 1956) other than that used in constructing the tables. This would indicate that differences between adjacent year classes or variations in life history do not upset the method. Consequently, the inclusion of immature fish on the high seas should not introduce serious error.

Mosher, Anas, and Liscom (1961) applied the

same method to the 1958 high seas samples. Using 1958 samples taken near Kamchatka, they determined an average error of misclassification of 28.8 percent for 584 Asian fish; using Bristol Bay samples yielded a 15.6 percent error for Bristol Bay fish. These errors were applied as adjustment factors to estimate the numbers of Kamchatkan and Bristol Bay sockeye in the high seas samples (fig. 15).

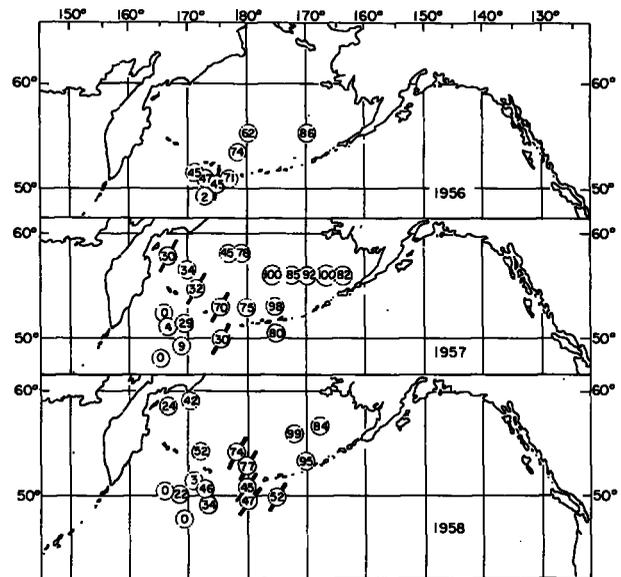


FIGURE 15.—Percentage of Western Alaska type sockeye salmon in scale samples taken from mid-May to mid-July (from Mosher et al., 1961). Samples containing more than 25 percent immature fish have been marked with a diagonal line.

Excepting the bias factor, this paper shares the difficulties discussed for Mosher,²⁵ as well as the benefit of general verification by empirical means. A further problem appears when the results of classification of the 1956 samples are compared (figs. 14 and 15). In figure 15 the 29 percent sample at about long. 175° W. in figure 14 is no longer present, and the seven samples shown for the western North Pacific Ocean in 1956 in figure 14 became five samples in figure 15. Mosher has stated (personal communication) that these changes have been brought about by correction of errors, revision of the manner in which the samples were grouped, elimination of very small samples, and elimination of immature fish. In some instances

²⁴ See footnote 22, p. 465.

²⁵ See footnote 23, p. 466.

the original groups contained samples from quite different times and places.

Because the distributions of maturing and immature sockeye salmon are different, further separation in the samples used by Mosher, Anas, and Liscom is desirable. The original data have been examined, and those samples shown in figure 15 that contained more than 25 percent immature fish are marked by a diagonal line. If these samples are omitted when considering the origins of the salmon, the major change is an absence of midocean samples. Those which remain are similar to the adjacent ones deleted.

As stated in the proceedings of the Seventh Annual Meeting of the International North Pacific Fisheries Commission,²⁶ the Asian standards are not necessarily adequate for estimating the proportion of Asian stocks in samples from near northeast Kamchatka. Nevertheless, the studies indicate for 1956, 1957, and 1958 that in the period from mid-May until mid-July in the Bering Sea, maturing sockeye salmon of Kamchatkan origin predominated from Kamchatka to long. 170° E. and occurred at least to long. 180°. In the North Pacific Ocean they were generally predominant to about long. 175° E. Bristol Bay fish were predominant from Bristol Bay to west of long. 180° in the Bering Sea.

Using scales,²⁷ Mosher, Anas, and Liscom (1961) tentatively identified high seas caught sockeye salmon to be from the British Columbia coast. These studies suggested that maturing fish of the River's Inlet and Smith Inlet types were found in the Gulf of Alaska as far west as long. 155° W. and that immature fish from these areas were found as far west as long. 170° W.

PARASITE STUDIES

Margolis (1963) reported the use of parasites to detect the continent of origin of sockeye salmon taken on the high seas. He found that a larval tapeworm, *Triaenophorus crassus*, was acquired by sockeye salmon in their early life in fresh water. It was found in smolts and returning spawners only in certain areas of western Alaska, chiefly in Bristol Bay, but

not in Asian sockeye salmon. A nematode, *Dacnitis truttae*, was found in samples of sockeye salmon taken near Kamchatka and in the Okhotsk Sea, but was not found in any samples of smolts or adults from North American rivers. This parasite also infects the young fish while in fresh water. Thus, he identified two "tags," one limited to western Alaskan and the other to Kamchatkan sockeye salmon. While the incidence of the parasites varies between years and streams, *Triaenophorus* seems to be more prevalent in Bristol Bay sockeye than is *Dacnitis* in Kamchatkan fish. His report shows levels of 4 to 12 percent of Kamchatkan samples infected with *Dacnitis* and 3.5 to 21.7 percent of the Bristol Bay samples infected with *Triaenophorus*.

Margolis' work reports are valuable in determining the origin of salmon stocks found on the high seas. The presence of *Dacnitis* or *Triaenophorus* in a sample is positive evidence of the origin of the fish bearing the parasites. The origin of the uninfected fish in samples is harder to interpret. Because of the variable and often low level of infection, some samples of Kamchatkan or Bristol Bay sockeye probably would not contain any infected fish. It is also possible that some samples containing no infected fish were sockeye which originated in neither Kamchatka nor Bristol Bay. Therefore it is difficult to place any quantitative interpretation on the fact that *Dacnitis* has never been found in maturing sockeye salmon east of long. 175° E. in the North Pacific Ocean or that *Triaenophorus* has never been found in maturing sockeye salmon west of long. 168° E. It would seem, however, that they do not ordinarily exceed these limits in large numbers during the May-June sampling period.

More samples were taken for parasite studies in 1959 than in any other year. Data from these samples indicated that between 10 and 13 percent of the sockeye salmon returning to Bristol Bay were infected by *Triaenophorus*. When this range of infection is compared with the rates of infection in the high seas samples (fig. 16, from Margolis, 1963) it is possible to reach some conclusions concerning the origin of maturing sockeye salmon occurring in oceanic areas in May and June of 1959. It is evident that, in many of the high seas samples, the incidence of *Triaenophorus* closely resembled the rate of infestation found in Bristol Bay sockeye

²⁶ See footnote 3.

²⁷ Manzer, J. I., T. H. Bilton, and K. H. Mosher. The ocean distribution of sockeye salmon originating in rivers and Smith Inlet. Fisheries Research Board of Canada and Bureau of Commercial Fisheries (INPFC Doc. 407), October 1959, 5 pp. [Processed.]

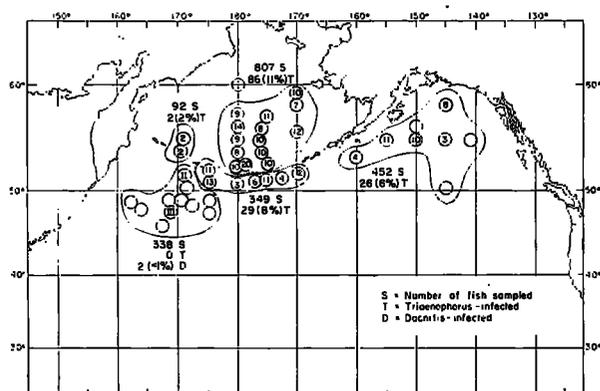


FIGURE 16.—Percentage of infected sockeye salmon in samples of maturing fish in 1959 (Margolis, 1963).

salmon. On this basis it is probable that these samples are comprised mainly of Bristol Bay sockeye salmon. This probability requires that Bristol Bay salmon of each river and each age group have the same relative distribution at sea. July and August are not shown, because as stated earlier, maturing fish become relatively scarce then.

The following summary²⁸ succinctly outlines the conclusions which may be drawn from this study:

(1) In the Bering Sea from 170° W. to 180° samples taken in the latter half of June consisted largely of fish of Bristol Bay origin. Between 180° and 171° E. samples were lacking. At 171° E. in early June the proportion of Bristol Bay sockeye in the two samples examined was greatly reduced. Presumably the majority of sockeye in these samples were of Asian origin. Samples of maturing fish from west of 171° E. in the Bering Sea were not obtained.

(2) Immediately south of the Aleutians, from about 169° W. to 175° E. in late May and early June, there was greater variation in the incidence of *Triclaenophorus* between samples than in the eastern half of the Bering Sea and no trend was evident. The combined samples in this area consisted predominantly of fish of Bristol Bay origin, but to a lesser extent than in the eastern half of the Bering Sea. The area of origin of the maturing sockeye other than those from Bristol Bay could not be determined. Samples from close to the south side of the Aleutians west of 175° E. were not examined.

(3) To the south and west of the waters bordering the extreme western Aleutians, from 175° E. and westward, no Bristol Bay sockeye, but two Asian sockeye, were identified in the samples collected from late May to late June. It seems most likely that the maturing sockeye in these samples were mainly of Asian origin.

In the Gulf of Alaska in a sample of maturing sockeye taken towards the middle of June at 55° N., 155° W., and in samples taken in late May at 55° N., 150° W., and 58° N., 145° W., a large proportion were of Bristol Bay origin.

²⁸ See footnote 3, p. 450.

Toward mid-June Bristol Bay sockeye appeared to be absent from a sample taken at about 55° N., 155° W., suggesting that maturing Bristol Bay sockeye move out of the Gulf of Alaska quite rapidly. Eastward from 150° W., along 55° N., in the latter half of May the proportion of Bristol Bay sockeye diminished and none were identified at 141° W. It seems most probable that the predominant stocks of sockeye in these samples from the eastern Gulf of Alaska were from North American areas to the south and east of the Alaska Peninsula.

Although most Bristol Bay maturing sockeye were found in samples taken in late May or June, two were also identified in Bering Sea samples (at 170° W. and 173° E.) taken in early July and one in the mid-Aleutian area in early August.

The results obtained from the 1959 samples of maturing sockeye confirm and considerably extend the results obtained from examination of less adequate samples of the years prior to 1959, as presented in Document 303.

The parasite studies also add much to our knowledge of the origin of the immature fish caught at sea. Immature sockeye salmon from Kamchatka were found from Kamchatka to as far east as long. 170° W. in the North Pacific Ocean and as far east as long. 175° W. in the Bering Sea. Immature salmon from Bristol Bay were found as far east as long. 145° W. and as far west as long. 175° E. in the North Pacific Ocean. In the Bering Sea, immature Bristol Bay sockeye salmon were found as far west as long. 170° E. One was taken in 1958 about 30 miles southeast of Cape Olyutorski in Asia.

SEROLOGICAL STUDIES

Investigations have been undertaken to discover blood differences that could be used to identify the streams of origin of sockeye salmon caught on the high seas. Ridgway and Klontz (1960) demonstrated the existence of blood groups in salmon and through isoimmunization showed that considerable antigenic diversity exists in sockeye salmon. Ridgway, Cushing, and Durall (1958) found differences in the reactions of sockeye salmon erythrocytes with pig sera. The degree of reaction was found to differ between sockeye salmon from different streams. There was considerable evidence that the differences in reactions were genetically controlled.

Ridgway, Klontz, and Matsumoto (1962) reported the development of a modification of Ouchterlony's method of double diffusion precipitin analysis in agar and its application to the problem of identifying the origin of sockeye salmon taken on the high seas. They found that antiserum produced by injecting rabbits with sockeye

salmon serum reacted with the serum of 96.8 percent of the sockeye salmon taken from American streams, and only 7.9 percent of the samples taken near Kamchatka. By testing sera from hatchery-reared fish, they were able to show that the antigens responsible for the reaction were present for at least a year prior to maturation, and that the antigens are a sufficiently permanent feature of the salmon's sera for use in identifying the origin of fish taken at sea.

The serological method was difficult to apply to high seas samples. It became apparent that the method of handling and storing the samples from the high seas was either partially destroying the antigens in the blood of American fish or inhibiting the reaction. The portions of the samples taken in the eastern Bering Sea in June identified as North American by Ridgway, Klontz, and Matsu-moto seem to be lower than might be reasonably expected. This is not clearly evident in their tables, because the samples are small and no distinction is made between mature and immature salmon. Because the distribution of immature sockeye salmon is not the same as that for maturing individuals, it is not possible to make direct quantitative comparisons between this work and the studies using tagging, morphology, scales, and parasites.

The Japan Fishery Agency ²⁹ reported the results of experiments with the haemoglobin fraction of the blood of sockeye salmon. It was possible to identify three separate groups of samples from the Pacific Ocean and Bering Sea. The samples taken south of the central Aleutian Islands were more similar to those taken near Kamchatka than were the samples taken north of the Aleutian Islands.

DISCUSSION

We have considered briefly the several techniques employed to determine the origin of the maturing sockeye salmon found in the high seas. Our information is more complete for the fish in the sea between long. 165° W. and Kamchatka than for fish in waters to the east. In the Pacific Ocean west of long. 165° W., it appears that the salmon mainly move north and west in the spring; those going to Kamchatka continue west, and

those going to Bristol Bay pass into the Bering Sea and turn east. There is an area between long. 180° and 170° E. (and possibly wider) that for a time may contain large numbers of fish from both of these sources. As these fish continue their homeward migration, segregation into stream groups becomes increasingly complete. The relative numbers of maturing fish from Kamchatka and Bristol Bay that may be found in the area of mixing in May and June probably varies with the year and date of sampling.

The runs of fish to the rivers vary widely in size from year to year (table 3). If, for example, the spatial distribution at sea of Kamchatka River fish were identical from year to year, they would certainly be scarcer at sea at a particular place and time in years when the stock for that river was low. We would then expect the percentage of fish from a particular area to fluctuate in accord with their abundance, unless all of the stocks found in that part of the sea were undergoing similar fluctuations. Because there seems to be no close year-to-year relationship in these fluctuations between Kamchatka and Bristol Bay, we may expect that the percentage of the fish from both of these will fluctuate in the high seas samples taken in the area of mixing.

In the period 1956-59, both Kamchatka and Bristol Bay appear to have had salmon runs of widely varying numbers. The 1956 Bristol Bay run of 24.6 million fish was fairly large, and the 1958 run of 5.5 million fish was fairly small. The sizes of the Kamchatka runs are not as well known, but the 1957 run might have been quite large. Unless the bulk of the Japanese high seas catch of 20.1 million fish were of Bristol Bay origin, the potential run to Kamchatka in 1957 must have been numerous, at least at sea. The high seas catch might not have been preponderantly from Kamchatkan sockeye salmon, however. It is not clear whether maturing sockeye salmon from a particular stream are distributed in the same relative manner from year to year. The available data do not seem to allow more than speculation on this point. From table 5, however, it is evident that the age composition of the stocks returning to an area may vary between years. In 1956 the Bristol Bay runs were mainly fish which had spent 2 years at sea; in 1957 the runs had predominantly spent 3 years at sea. Unless the immature fish return to the same part of the

²⁹ Japan Fisheries Agency, Studies to determine the origin of northern sea salmon by serological methods. Fisheries Agency, Japan (INPFC Doc. 222), October 1958, 21 p. [Processed].

ocean to spend each succeeding winter, it is conceivable that those fish which remain at sea an additional year might become more dispersed.

EFFECT OF TIME OF SAMPLING

In addition to the sources of variation mentioned above, it is pertinent to examine the distribution of the samples in time. Because the maturing fish are moving rapidly to their home streams, samples, unless taken sufficiently early in certain areas, could not be expected to contain fish from the more distant streams. Jones (1961) provided data on the rate of travel of sockeye salmon from various points on the high seas to Bristol Bay, Alaska. Some variation was evident in the mean rate of travel for fish tagged at different locations, and he stated that the salmon tagged later traveled more rapidly. Assuming that the tagged fish traveled in a straight line from Adak Island to their final destination, he found that the average rate of travel per day varied from about 22 to 34 nautical miles. A mean rate of 30 nautical miles per day for Bristol Bay sockeye salmon seems reasonable. This rate, which would place the peak of the Bristol Bay runs between long. 180° and long. 175° W. in mid-June and near the Pribilof Islands in late June, which is in agreement with fishing information. It is not clear whether the rates presented by Taguchi and Nishikawa or Sato are suitable for this use because they deal with inshore movements.

Jones's study provides a basis for examining the effect of date of sampling upon the number of Bristol Bay salmon found in a sample. A mean migration rate of 30 miles per day was used to construct figure 17. The time of migration was calculated from lat. 50° at various meridians along straight lines to Bristol Bay streams. The end of the period of peak run in Bristol Bay was considered to be July 15. The dates at which most of these fish would have passed these meridians were estimated, and the diagonal line for Bristol Bay located on the figure. We would then expect that samples occurring above this diagonal would have been taken too late to contain Bristol Bay fish at that particular longitude. Because variation in latitude of sampling introduces distance discrepancies, only samples taken in the Pacific Ocean were used. This does not eliminate all of the variation, and the position of the diagonal line is not precise with respect to the samples shown. The

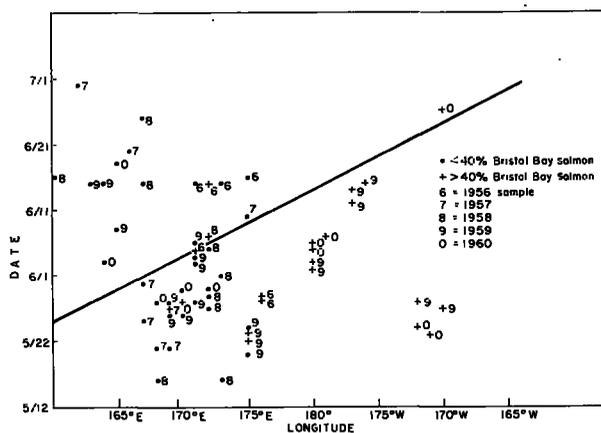


FIGURE 17.—Effect of time of sampling on origin of samples from Pacific Ocean. Samples below line could contain fish from Bristol Bay if we accept a 30-mile per day homeward migration. Lines are based on distances from stream to lat. 50° N. for various longitudes. Samples from Fukuhara et al., 1962; Fukuhara, 1961; and Landrum and Dark, 1963.

samples listed in Fukuhara et al. (1962), Fukuhara (1961), and Landrum and Dark (1963), were used to examine the effect of sampling time upon the classification of the fish in the samples.

The 1956 samples were all taken in the vicinity of long. 170° E. to 175° E., and one sample estimated to contain more than 40 percent Bristol Bay fish was taken 9 days later than might have been expected. The runs in Bristol Bay, however, were still quite heavy after July 20, 1956, which might account for apparent discrepancy.

When the data for the 5 years together are examined the migration rate of 30 miles per day is reasonably consistent with the results of morphological classification. Excepting the sample in 1956, all of the samples taken in the North Pacific Ocean that were found to contain more than 40 percent Bristol Bay sockeye salmon fall either very near to the Bristol Bay "disappearance line" or below it, as predicted. The line seems reliable in 21 of 22 instances. If we accept this, we must then suspect that over one-third of the sampling was too late to detect the distribution of maturing Bristol Bay salmon west of long. 180° in the North Pacific Ocean. This would tend to depress the average percentages of maturing Bristol Bay fish found in the western samples for the May-June period.

Because of the uncertainty of the migration rates for Kamchatkan sockeye salmon, figures for these

runs are not presented. However, if July 5 and August 5 are used as the end of the period of peak runs for the Kamchatka River and the Ozernaya River, respectively, and a 30-mile per day migration rate is assumed, it is found that sampling in the North Pacific Ocean west of long. 180° and lat. 50° N. has been done early enough to intercept these runs. There seems, however, to be very little information available to establish the rate of travel for these fish, although it should be possible to make estimates from the detailed records of the Japanese high seas fisheries.

ORIGIN OF SOCKEYE SALMON

It is worthwhile to consider together the results of morphology, scale, and tagging studies to see what quantitative conclusions may be drawn concerning the origin of maturing red salmon on the high seas. Although the distribution of sampling is neither regular nor complete for any technique during 1956-60, some estimates can be obtained because one study sometimes provides information where another does not.

The combined results of the studies during 1956-60 for maturing fish in late May and June are shown in figure 18. The results of the morphology and scale studies are taken directly from the sources cited earlier. Tagging results were employed only where the migration from the point of tagging appeared to be wholly to Asia or North America. Where more than one method gave the same result for a locality, only one was plotted. In the instance where two methods gave divergent results, both were entered. For this figure, samples which yielded estimates of more than 60 percent Kamchatkan salmon were considered dominantly Kamchatkan (K); those with estimates of 40 to 60 percent were considered indeterminate (O), and those with estimates of over 60 percent Western Alaska type were considered to be Western Alaska sockeye salmon (A).

These figures show: (1) No examples of dominance of maturing Kamchatkan salmon east of long. 175° E. in May and June 1956, 1957, 1958, 1959, and 1960 with the exception of one sample in the eastern Bering Sea in 1959 which is considered to have been too far from Kamchatka on June 27 to be reasonably considered as Kamchatkan. (2) Data for the Western Bering Sea are scanty. The few observations available suggest that the dividing line between areas

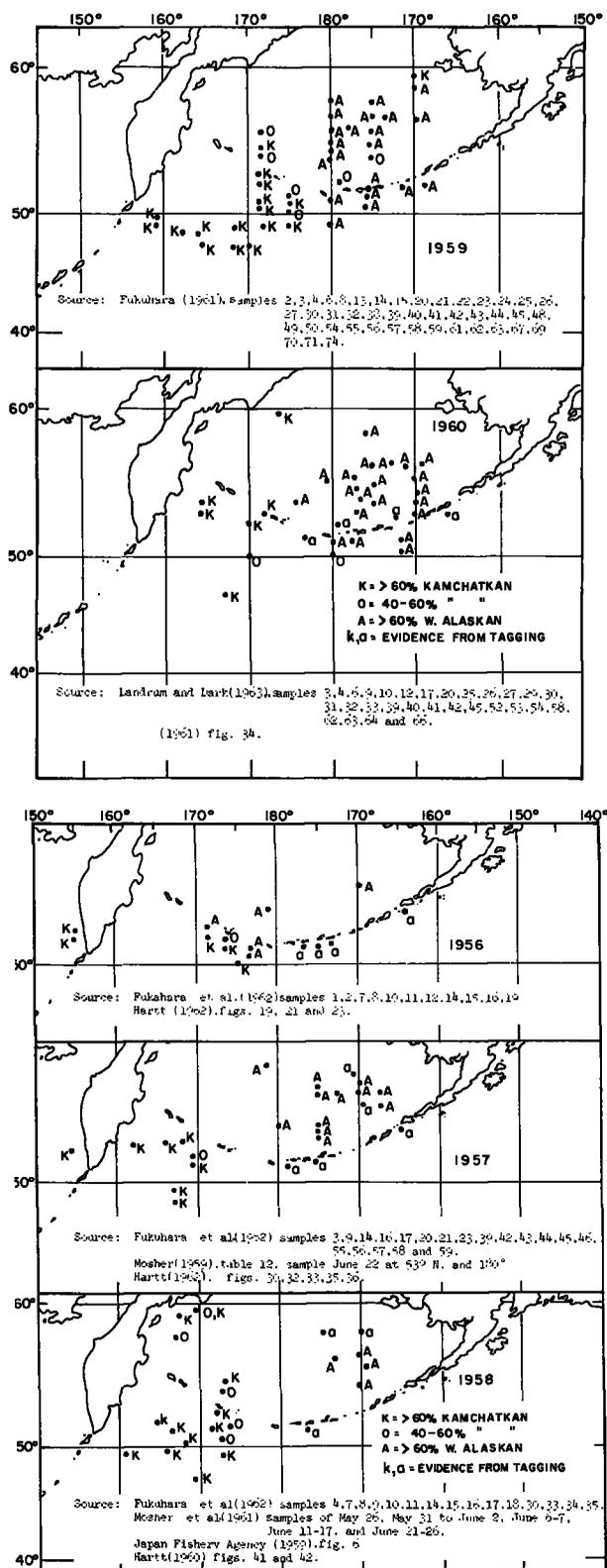


FIGURE 18.—Origin of maturing sockeye salmon in May and June.

dominated by Kamchatkan and Western Alaska sockeye salmon was about long. 175° E. (3) Maturing Western Alaska salmon were dominant in the Bering Sea to or west of long. 180° in the 4 years (1956, 1957, 1959, and 1960) for which samples were available. There was only one sample near long. 180° in 1956 and none in 1958. (4) Dominance of Bristol Bay fish in the North Pacific Ocean west to long. 175° E. in 1956, to long. 177° W. in 1957 (with no data between long. 177° W. and 170° E.) to long. 180° in 1959, and west of long. 180° in 1960.

According to the studies that have been discussed in the previous paragraphs, and the results of parasitological studies (fig. 16), there appears to be a zone of about 10 degrees of longitude (from long. 170° E. to long. 180°) between the areas consistently dominated by maturing Kamchatkan or Bristol Bay sockeye salmon in May and June.

With the data in figure 18, it is possible to summarize the results of the studies of the origin of maturing sockeye salmon as follows: For the 5 years 1956, 1957, 1958, 1959, and 1960, the samples in the Bering Sea near and east of long. 180° are generally heavily dominated by Bristol Bay salmon. Bristol Bay salmon dominated one sample near long. 180° in 1956, two in 1957, seven in 1959, including one at long. 175° E., and three in 1960. Near long. 175° W., however, there are six samples in 1957, two in 1958, five in 1959, and eight in 1960 that show an eastward continuation of Bristol Bay dominance observed at long. 180° in the Bering Sea. Because these years include both very large and very small runs in Bristol Bay and considerable variation in the hydrography of the area, it appears that maturing Bristol Bay sockeye consistently dominate the sockeye salmon catches in the Bering Sea near and east of long. 180°.

The situation in the North Pacific Ocean appears to be somewhat different (fig. 18). The data for 1956, 1958, and 1959 indicate a dominance of Kamchatkan sockeye salmon as far east as long. 175° E., with little information on the eastward extent of Kamchatkan dominance in 1957 and 1960. Dominance of Bristol Bay salmon is indicated as far west as long. 175° E. in 1956 and 1960, and as far west as long. 180° in 1957 and 1959. Data for the central Aleutian Islands area are almost lacking in 1957 and 1958. Figure 17 shows that west of long. 180° four of the 1956 samples,

three of the 1957 samples, three of the 1958 samples, three of the 1959 samples, and two of the 1960 samples were taken too late to have intercepted the Bristol Bay runs. In those samples taken sufficiently early, we find strong representation of Bristol Bay fish to long. 175° E., with lesser numbers appearing to the westward. The samples taken west of long. 175° E. prior to the time that Bristol Bay fish might have left mainly show dominance of Kamchatkan salmon in each year. It can be tentatively concluded, therefore, that dominance shown for Kamchatkan fish west of long. 175° E. is not primarily caused by time of sampling, and that the data support the view that the maturing sockeye salmon were predominantly of Kamchatkan origin.

The samples of maturing sockeye salmon taken in May and June in the North Pacific Ocean east of long. 180° (fig. 18) were preponderantly of Bristol Bay origin from 1956 to 1960. No indication of dominance by Kamchatkan salmon is found in the results of either the morphological or tagging studies.

It appears from these data that maturing Bristol Bay sockeye dominate the North Central Pacific Ocean as far west as long. 180° in late May and in June. The change in sockeye samples from predominantly fish of Alaska origin to predominantly fish of Kamchatka origin appears to occur near long. 175° E. In the Bering Sea in late May and in June maturing Bristol Bay fish are consistently dominant westward to at least long. 180°. We may conclude that the dominance of Kamchatkan and Bristol Bay sockeye salmon in these areas are consistent features of the system of distribution under the conditions prevailing during the 5 years of observation.

CONCLUSIONS

1. On the basis of catch statistics, Asian stocks of sockeye salmon provide about 23 percent of the total catch and North American stocks about 77 percent.
2. Sockeye salmon enter their home streams from May until October, but for any stream the duration of heavy migration is usually less than 1 month.
3. Sockeye salmon are found from North America to Asia in the North Pacific Ocean during spring and summer. Information is lacking for fall and winter.

4. The oceanic distribution appears to shift southward in winter and northward in summer.

5. Immature Asian sockeye salmon have been shown to migrate as far east as long. 170° W. in the North Pacific Ocean and long. 175° W. in the Bering Sea. Immature Bristol Bay sockeye have been shown to migrate as far east as long. 145° W. and as far west as long. 173° E. in the North Pacific Ocean, and as far west as long. 170° E. in the Bering Sea.

6. In May and June maturing Kamchatkan sockeye salmon predominate in the North Pacific Ocean from Kamchatka to about long. 175° E. and Bristol Bay sockeye salmon predominate westward to at least long. 180°. Maturing Kamchatkan sockeye salmon have been tagged as far east as long. 165° E. and Bristol Bay fish have been tagged as far west as long. 167° E. In the Bering Sea, maturing sockeye salmon are almost entirely of Bristol Bay origin from Bristol Bay to west of long. 180°.

7. The major areas dominated by Kamchatkan or Bristol Bay sockeye salmon appear to have been consistent in 1956, 1957, 1958, 1959, and 1960.

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LITERATURE CITED

- ANDREW, F. J., AND G. H. GEEN.
1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. International Pacific Salmon Fisheries Commission, Bulletin XI, 259 pp.
- BIRMAN, I. B.
1958. [On the occurrence and migration of Kamchatka salmon in the northwestern part of the Pacific Ocean.] O rasprostraneni i migratsiakh kamchatskikh lososēi v severo-zapadnoi chaste Tikhogo okeana. In Materialy po biologii morskogo perioda zhizni dal'nevostochnykh lososēi, pp. 31-51. Vsesūznyi Nauchno-issledovatel'skii Institut Morskogo Rybnogo Khozāistva i Okeanografi (VNIRO). [Translation by R. E. Forester, 24 pp., Fisheries Research Board of Canada, Translation Series No. 180.]
- FOERSTER, R. E.
1955. The Pacific salmon (genus *Oncorhynchus*) of the Canadian Pacific Coast, with particular reference to their occurrence in or near fresh water. International North Pacific Fisheries Commission, Bulletin No. 1, pp. 1-56.
- FOSKETT, D. R.
1953. Contributions to the life history of the sockeye salmon (No. 38). Province of British Columbia, Provincial Department of Fisheries Report for year ended December 31, 1952, pp. L33-L56.
- FUKUHARA, F. M.
1961. Analysis of red salmon morphological data—1958 and 1959. International North Pacific Fisheries Commission, Annual Report, 1960, pp. 99-107.
- FUKUHARA, F. M., S. MURAI, J. J. LALANNE, AND A. SRIBHIBHADH.
1962. Continental origin of red salmon as determined from morphological characters. International North Pacific Fisheries Commission, Bulletin No. 8, pp. 15-109.
- GILBERT, CHARLES H.
1914-1920. Contributions to the life history of the sockeye salmon. (Nos. 1-6). Province of British Columbia, (Annual) Report of the Commission of Fisheries for the years 1913-19. Various pagination.
- HANAVAN, M. G.
1961. Distribution and racial sampling of salmon on the high seas. International North Pacific Fisheries Commission, Annual Report for the year 1960, pp. 76-81.
- HARTT, ALLAN C.
1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956-1958. International North Pacific Fisheries Commission, Bulletin No. 6, 157 pp.
1963. Tagging studies [in 1961]. International North Pacific Fisheries Commission, Annual Report, 1961, pp. 83-91.
- HIRANO, YOSHIMI.
1953. The outline of results of tagging experiments on the Pacific salmon. Hokkaido-ritsu Suisan Shikenjo, goju Shunen Shuppan (Hokkaido Government Fisheries Research Station, 50th Anniversary Publication), 134 pp. [In Japanese, with English abstract pp. 44-46.]
- INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION (INPFC).
1957. Annual report for the year 1956. International North Pacific Fisheries Commission. 88 pp.
1958. Annual report for the year 1957. International North Pacific Fisheries Commission, 86 pp.
1959. Annual report for the year 1958. International North Pacific Fisheries Commission. 119 pp.

1960. Annual report for the year 1959. International North Pacific Fisheries Commission, 116 pp.
1961. Annual report, 1960. International North Pacific Fisheries Commission, 116 pp.
1963. Annual report, 1961. International North Pacific Fisheries Commission, 127 pp.
- INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION.
1959. Annual report, 1958. International Pacific Salmon Fisheries Commission, 33 pp.
1961. Annual report, 1960. International Pacific Salmon Fisheries Commission, 36 pp.
- ISHIDA, TERUO, AND KIICHI MIYAGUCHI.
1958. On the maturity of Pacific salmon (*Oncorhynchus nerka*, *O. keta*, and *O. gorbuscha*) in offshore waters, with reference to the seasonal variation in gonad weight. Bulletin of the Hokkaido Regional Fisheries Research Laboratory (Yoichi, Japan) No. 18, pp. 11-22. [In Japanese, with English summary. Translation by Kunio Yonezawa, 7 pp., Fisheries Research Board of Canada, Translation Series No. 190.]
- JAPAN FISHERIES AGENCY.
1959. Report of research on salmon conducted by Japan in 1958 for the International North Pacific Fisheries Commission. International North Pacific Fisheries Commission, annual report for the year 1958, pp. 50-73.
1960. Report on the investigations by Japan for the International North Pacific Fisheries Commission—1959. International North Pacific Fisheries Commission, Annual report for the year 1959, pp. 54-78.
1961. Report on the research by Japan for the International North Pacific Fisheries Commission during the year 1960. International North Pacific Fisheries Commission, Annual report for the year 1960, pp. 57-75.
1963. Report on research by Japan for the International North Pacific Fisheries Commission during the year 1961. International North Pacific Fisheries Commission, Annual report for the year 1961, pp. 48-82.
- JONES, B. F.
1961. Ocean migration of Pacific salmon revealed by tagging and recovery. International North Pacific Fisheries Commission, Annual Report, 1960, pp. 108-115.
- KILLICK, S. R., AND W. A. CLEMENS.
1963. The age, sex ratio and size of Fraser River sockeye salmon 1915 to 1960. International Pacific Salmon Fisheries Commission, Bulletin XIV, 140 pp.
- KROGIUS, F. V.
1953. [On the scale pattern of Kamchatka sockeye of different local populations.] O stroenii cheshui Kamchatskoĭ krasnoĭ raznykh lokal'nykh stad. In Materialy po biologii morskogo perioda zhizni dal'nevostochnykh lososeĭ, pp. 52-63. Moscow, Vsesŭznyi Nauchno-issledovatel'skii Institut Morskogo Rybnogo Khozĭalstva i Okeanografi (VNIRO). [Translation by R. E. Foerster, 10 pp. Fisheries Research Board of Canada, Translation Series No. 181.]
- KROGIUS, F. V., AND E. M. KROKHIN.
1956. [Results of a study of the biology of sockeye salmon, the conditions of the stocks and the fluctuations in numbers in Kamchatka waters.] Rezulytaty issledovaniĭ biologii nerki-krasnoĭ, sostofaniĭ ee zapasov i kolebaniĭ chislennosti v Vodakh Kamchitki. Voprosy Ikhtiologii, No. 7, pp. 3-20. [Translation by R. E. Foerster, 21 pp., 1956, Fisheries Research Board of Canada, Translation Series No. 176.]
- LANDRUM, B. J., AND T. DARK.
1963. Morphological classification of 1960 red salmon. International North Pacific Fisheries Commission, Annual Report, 1961, pp. 108-114.
- MARGOLIS, LEO.
1963. Parasites as indicators of the geographical origin of sockeye salmon, *Oncorhynchus nerka* (Walbaum), occurring in the North Pacific Ocean and adjacent seas. International North Pacific Fisheries Commission, Bulletin No. 11, pp. 101-156.
- MOSHER, KENNETH H., RAYMOND E. ANAS, AND KENNETH L. LISCOM.
1961. Study on scales. International North Pacific Fisheries Commission, Annual Report, 1960, pp. 88-95.
- RIDGWAY, G. J., J. E. CUSHING, AND G. L. DURALL.
1958. Seriological differentiation of populations of sockeye salmon, *Oncorhynchus nerka*. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 257, 9 pp.
- RIDGWAY, GEORGE J., AND GEORGE W. KLONTZ.
1960. Blood types in Pacific salmon. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 324, 9 pp.
- RIDGWAY, G. J., G. W. KLONTZ, AND C. MATSUMOTO.
1962. Intraspecific differences in the serum antigens of red salmon demonstrated by immunochemical methods. International North Pacific Fisheries Commission, Bulletin No. 8, pp. 1-13.
- ROUNSEFELL, GEORGE A.
1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 130, vol. 58, iv+ pp. 83-169.
- ROYAL, LOYD A.
1953. The effects of regulatory selectivity on the productivity of Fraser River Sockeye. The Canadian Fish Culturist, No. 14 (October), pp. 1-12.
- SATO, ROKUJI.
1938. On the migratory speed of salmon and the stock of red salmon estimated from the tagging experiments in the northern North Pacific. Bulletin of the Japanese Society of Scientific Fisheries, vol. 7, No. 1, pp. 21-23. [In Japanese, with English summary. May 1938. Translation by Lorry Nakatsu, U.S. Fish and Wildlife Service, Pacific Salmon Investigations, Seattle, Wash., Translation Series No. 5.]

SATO, ROKUJI.

1939. On salmon tagging experiments in the northern North Pacific in 1937 and 1938. Bulletin of the Japanese Society of Scientific Fisheries, vol. 8, No. 4, pp. 178-184. [In Japanese, with English summary. Translation by Robert Ting, U.S. Fish and Wildlife Service, Pacific Salmon Investigations, Seattle, Wash., Translation Series No. 3.]

SEMKO, R. S.

1953. [The stocks of west Kamchatka salmon and their commercial utilization.] Zapasy zapadno kamchatskikh lososei i ikh promyslovoe ipolzovanie. Izvestiia Tikhookeanskovo Nauchno-is-seledovatel'skovo Instituta Rybnovo Khoziaistva; Okeanografi (Vladivostok) (TINRO) 41, pp. 3-109. (Translation by R. E. Foerster and L. V. Sagen, 1960, Fisheries Research Board of Canada, Translation Series No. 30.)

1961. Contemporary changes in the abundance of Pacific salmon and their fundamental causes. Sovrenennye izmeneniia chislennosti Tikhookeanskikh lososei i ikh osnovnye priohiny. In Trudy Soveshchaniia po dinamiko chislennosti tyb, edited by E. N. Pavlovskii, pp. 117-129. Moskva, Akademiia Nauk SSSR. Ikhtiologicheskaiia Komissia, Trudy Soveshchaniia, vyp. 13.

SIMPSON, ROBERT R.

1960. Alaska Commercial Salmon Catch Statistics 1951-1959. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Statistical Digest No. 50, 115 pp.

TAGUCHI, KISABURO.

1956. The salmon fisheries and salmon resources of the northern waters. Northern Waters Fisheries Resources Investigation Conference (Hokuyo Shi-

gen Kenkyu KyōgiKai), 1956. 290 pp. [In Japanese, with English summary]. (Revised edition published by Nichiro Gyogyo Kabushiki Kaisha [Nichiro Fishing Co., Ltd. 1, 1957. 166 pp. In Japanese].)

1957a. The seasonal variation of the good fishing area of salmon and the movements of the water masses in the waters of Western North Pacific. II. The distribution and migration of salmon populations in offshore waters. Bulletin of the Japanese Society of Scientific Fisheries, vol. 22, No. 9, pp. 515-521. The Japanese with English summary.

1957b. The seasonal variation of the good fishing area of salmon and the movement of water masses in the waters of the Western North Pacific. III. Relation between the distribution of salmon population and oceanographical condition mainly in the southern waters of 48° N. lat. Bulletin of the Japanese Society of Scientific Fisheries, vol. 22, No. 10, pp. 609-617. The Japanese with English summary.

TAGUCHI, KISABURO, and KIYOSHI KISHIKAWA.

1954. Some knowledge on the migration of salmon in Asiatic region inferred from the data of the past. I. Red salmon (*Onchorhynchus nerka*). Bulletin of the Japanese Society of Scientific Fisheries, vol. 20, No. 7, pp. 581-585. The Japanese with English summary.

U.S. FISH AND WILDLIFE SERVICE.

1946-1953. Alaska fishery and fur seal industries—1944 to 1950. U.S. Department of the Interior, Fish and Wildlife Service, Statistical Digests, Nos. 13, 15, 17, 20, 23, 26 and 29. Various pagination.

RELATION BETWEEN SPAWNING-STOCK SIZE AND YEAR-CLASS SIZE FOR THE PACIFIC SARDINE *SARDINOPS CAERULEA* (GIRARD)

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ABSTRACT

A high degree of inverse correlation between spawning-stock size and year-class size (based on indices of total fish caught) was found for the Pacific sardine (*Sardinops caerulea*). Over the 26-year period for which data are available it appears that catch, on which the indices are based, was determined primarily by popula-

tion size and secondarily by availability and effort. The data indicate that spawning-stock size influences year-class size and that this is not merely a secondary result of year classes occurring in cycles which generate similar cycles of spawning populations several years later.

The object of this paper is to explore the relationships between spawning-stock size and year-class size for the Pacific sardine, *Sardinops caerulea* (Girard). It also treats to a lesser extent some of the other related factors involved in the population dynamics of the sardine.

The introductory paragraphs of Clark and Marr (1955) sum up the considerations of the problems as follows:

At the present stage of our knowledge, there is rather universal agreement that the only way Man can affect a population of marine fishes is by fishing (and, perhaps, by pollution in special situations). That is, we cannot economically fertilize large areas of the sea, nor can we treat epidemics in fish populations, nor hope to stock the ocean by means of hatchery-reared fish. There is further agreement that Man can affect fish populations by varying the amount of fishing and by varying the method of fishing. There is, however, disagreement about the nature and magnitude of such effects.

According to one theory, big spawning populations produce bigger year-classes than do small spawning populations. Therefore, one might suppose that reducing the total catch would make the spawning population bigger and therefore result in the production of bigger year-classes. Although this assumption has been made many times, it has not been demonstrated for any marine fish. The possibility that this theory does not conform to the fact will be discussed below. Unfortunately, this assumption is perhaps more often made tacitly than explicitly.

There must, of course, be a critical population size below which the population will not be able to perpetuate itself.

And further:

The death rates from fishing and from natural causes can clearly be variable and will be influenced by many factors, so that it is difficult to generalize about them. Two features are of interest, however. One of these concerns the fact that when fishing mortality is imposed on a population, natural mortality is to some extent replaced by fishing mortality. That is, some of the fish which would have died naturally during a given time interval are caught instead. The other feature, and by far the most important one, is that as far as we can judge from all the observations that have been made, fishing and natural mortality exert their greatest influence on the size of the population existing at the time they occur. Opinions differ about their effect on the size of future additions to the population, i.e., year-class which will be produced subsequent to the time the mortalities occur.

There must, of course, be some "critical," minimum spawning stock size below which year-class size is a function of stock size, as we have already stated. This critical stock size has not yet been measured for any marine fishes. Above this minimum stock size all present evidence indicates that the magnitude of additions to the population (the size of individual year-classes) is not determined by the number of eggs spawned, but rather by variations in survival rate between the time the eggs are spawned and the time the resulting fish have grown large enough to enter the population. This means that the size of any particular year-class is determined, not by the number of adult fish

(above minimum) which produce it, but rather by variations in the environment which affect survival rate after the eggs are spawned.

Clark and Marr were unable to agree on whether the size of the spawning stock determined the size of the year class. Their disagreement centered on whether or not large spawning stocks produced large year classes and small spawning stocks produced small year classes. The present paper extends their data from 19 to 26 years and re-examines the problem from a different point of view.

SOURCES OF DATA

The index of spawning population size and the index of year-class size used in this paper are essentially those used by Clark and Marr (1955), which they call "accumulated age estimates." The spawning-stock size in any given season is considered to consist of all fish having scales with three or more annuli taken in the following fall-winter fishery and all fish of these year classes taken in subsequent years plus one-half of the fish having two annuli taken in the following fall-winter fishery and one-half of the fish of this year class taken in subsequent years.

The northern fishery of the earlier years was actually a summer-fall fishery, and the expanded Mexican fishery of more recent years is pursued throughout the year although the heaviest landings generally coincide with the southern California fall fishery.

Estimates of a year class are derived by summing all fish of that year class caught during its life span with the following exceptions: only one-half of the fish with one annulus and one-fourth of the fish with no annuli are included. Fish in their first year were seldom taken by the commercial fishery, and fish with only one annulus were taken in appreciable quantities in only a few years. Most of the commercial sardine catch is made up of 2- and 3-annulus fish.

The above measure of spawning-stock size is used because it is the same as that used by Clark and Marr (1955). Actually age at first spawning varies over the geographic range of the sardine, apparently occurring earlier in the south and later in the north; it also varies from year to year. Also if the spawning-stock size is considered to be either all fish 2 years old or older or all fish 3 years old or older, and if the year class either includes or excludes fish taken at less than 2 years of age,

the correlations obtained between year-class size and spawning-stock size are as good as those obtained from the measurements used in this paper.

The age composition of the commercial sardine catch was obtained from the following sources:

Year:	Author
1932 through 1937-38.....	Eckles (1954).
1938-39 through 1940-41....	Wolf (1961).
1941-42 through 1946-47....	Felin and Phillips (1948).
1947-48.....	Mosher et al. (1949).
1948-49 through 1955-56....	Felin et al. (1949, 1950, 1951, 1952, 1953, 1954, 1955, 1958).
1956-57.....	Wolf et al. (1958).
1957-58.....	Daugherty and Wolf (1960).
1958-59.....	Wolf and Daugherty (1961).

Data for the 1959-60 and 1960-61 seasons were made available by Robert Wolf of the Bureau of Commercial Fisheries, and data for the Mexican fishery not already in the above reports by Makoto Kimura also of the Bureau of Commercial Fisheries. The only data available for some ports in a few of the earlier years are tons landed. These have been converted to age and numbers of fish on the basis of known age compositions of landings at the nearest ports having similar age composition landings in other years.

ANALYSIS OF DATA

The magnitude of the commercial catch depends upon 1) sardine population size, 2) fishing effort, and 3) availability of sardines to the fishing fleet. Over the 26-year period covered by this paper, the population size is the primary factor determining catch. Effort and availability may be considered as sampling errors whose effect is not great enough to negate the use of an index of population size based on catch. During the early years covered by the data, effort was increasing. This would cause earlier estimates of population size and year-class size to be lower with the latter less underestimated because of the 2-year lag. During the late 1940's to the present there have been first considerable fluctuation in fishing effort and finally a decrease in effort, both of which appear to be primarily responses to population size (as measured by catch) in the immediately preceding fishing seasons.

Although the range of the sardine has contracted considerably, and these fish are no longer available

in commercial quantities in the northern portions of their former range, the sardine population still shifts northward in the summer and southward in the winter.

The population as a whole has shown fluctuations in availability as evidenced by changes in total mortality rates from year to year. In some years all year classes in the catch show a negative total mortality which cannot be accounted for by increased effort. This must result from increased availability. The seasonal shifts in sardine population do not seem to be constant from year to year, and consequently availability has its greatest effect in the most northern portion of the range.

The method of accumulating ages tends to offset the errors of changing effort and availability but not as much as it would in a longer lived species of fish. Changes in both availability and effort undoubtedly account for some of the variation in the correlations between spawning-stock size and year-class size.

Direct correlation methods are usually applied to frequency series rather than time series unless, in the latter case, neither of the time series is marked by a definite secular trend. The direct correlation of time series data can easily give a fortuitously high correlation. One method of circumventing this difficulty is to determine trends for the data and correlate the deviations from the trends. This method applies only when the parameters involved react to one another relative to their trends, rather than absolutely without regard to trends.

A third degree parabolic trend line, $Y_c = 5.079 + 0.5475X - 0.06670X^2 + 0.001497X^3$, in which Y_c = calculated spawning-stock size index in billions of fish and X = trend year, was fitted to the spawning-stock size indices (fig. 1). Similarly a third degree parabolic trend line, $Y_c = 2.463 + 0.6050X - 0.06754X^2 + 0.001614X^3$, in which Y_c = calculated year class size index in billions of fish and X = trend year was fitted to the year-class size indices (fig. 2).

The deviations of the observed values from calculated values were obtained. These data are presented in table 1. In figure 3 the two sets of deviations are plotted as anomalies from their trends. Year-class size deviations are plotted against spawning-stock size deviations in figure 4. The least squares regression line $Y_c = 0.000136 - 0.6774X$ is also plotted. The correlation co-

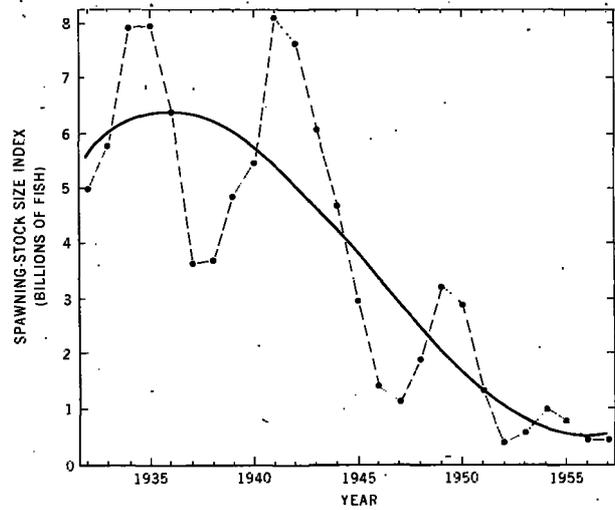


FIGURE 1.—Apparent trend of sardine spawning-stock size index, 1932-57.

efficient, r , equals -0.699 , with a probability that such a correlation could be obtained by chance alone of less than one in a thousand.

As stated above the method of correlating deviations from trend guards against spuriously high correlations that may be obtained if trend data are directly correlated. In the present case the fact that two sets of parameters having such closely coincident trends do not have a high direct positive correlation is in itself significant. As we have seen this is caused by the fact that the parameters are inversely related with respect to trend.

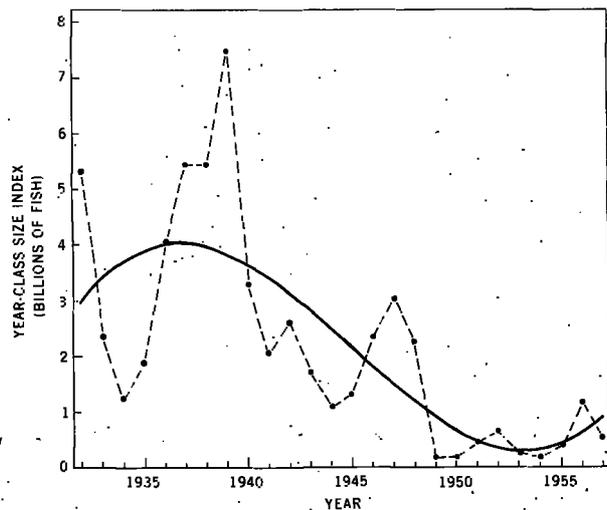


FIGURE 2.—Apparent trend of sardine year-class size index, 1932-57.

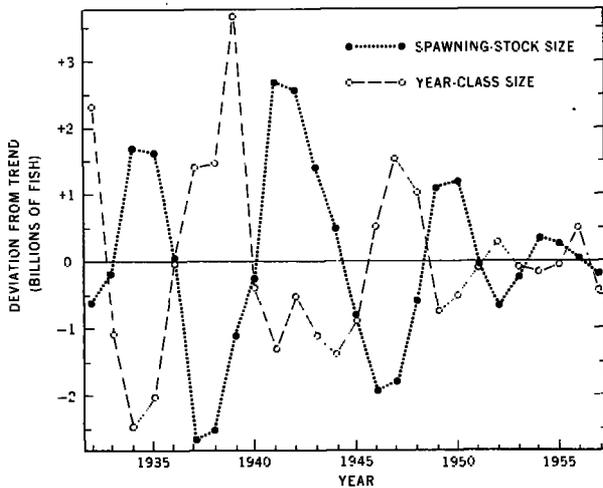


FIGURE 3.—Deviations from trends of sardine spawning-stock size index and year-class size index, 1932-57.

TABLE 1.—Indices of spawning-stock size and year-class size of the Pacific sardine. Observed and computed values and deviations

[Billions of fish]

Year	Trend year	Spawning-stock size			Year-class size		
		Observed	Calculated	Deviation	Observed	Calculated	Deviation
1932	1	4.96	5.56	-0.60	5.83	3.00	2.83
1933	2	5.76	5.92	-.16	2.37	3.42	-1.05
1934	3	7.87	6.16	1.71	1.26	3.71	-2.45
1935	4	7.94	6.31	1.63	1.89	3.91	-2.02
1936	5	6.34	6.34	.00	4.08	4.00	1.08
1937	6	3.64	6.29	-2.65	5.44	4.01	1.43
1938	7	3.07	6.16	-2.49	5.42	3.81	1.61
1939	8	4.33	5.96	-1.63	7.47	3.81	3.66
1940	9	5.44	5.70	-.26	3.27	3.61	-.34
1941	10	8.09	5.38	2.71	2.07	3.37	-1.30
1942	11	7.61	5.02	2.59	3.59	3.10	-.51
1943	12	6.04	4.63	1.41	1.69	2.79	-1.10
1944	13	4.69	4.22	.47	1.07	2.46	-1.39
1945	14	2.95	3.78	-.83	1.27	2.13	-.86
1946	15	1.39	3.34	-1.95	2.32	1.79	-.53
1947	16	1.11	2.90	-1.79	3.08	1.47	1.61
1948	17	1.88	2.47	-.59	2.22	1.16	1.06
1949	18	3.18	2.06	1.12	.14	.89	-.75
1950	19	2.89	1.68	1.21	.15	.65	-.50
1951	20	1.31	1.33	-.02	.41	.46	-.05
1952	21	.39	1.08	-.64	.68	.33	.30
1953	22	.58	.79	-.21	.22	.27	-.05
1954	23	.97	.61	.36	.16	.29	-.13
1955	24	.78	.50	.28	.36	.40	-.04
1956	25	.43	.48	-.05	1.16	.60	.56
1957	26	.41	.55	-.14	.52	.91	-.39

As also stated above, the trend method cannot be applied to parameters that react to one another absolutely, which is generally the case when biological parameters are involved. In fact, one would expect this to be the case in the present instance. As will be shown later, the period of years involved may be divided into three more or less distinct phases of population contraction. The same phenomena of population dynamics seem to be functioning within successively smaller population ranges. This permits the population

data to be treated as a trend that allows the data for all years to be included in a single correlation.

By using the trend method, the total fish caught spawning-stock size index may be compared to a second, more frequently used population size index, catch per unit of effort. Such data are available for 23 seasons for the California fishery from 1932-33 through 1954-55 (Marr, 1960).

Catch per unit of effort data (tons of sardines landed per boat-month) are presented in table 2. A third degree parabolic trend line ($Y_c = 693.76 - 28.854X - 0.034874X^2 - 0.0047127X^3$ in which $Y_c =$ computed catch per unit of effort and $X =$ trend year) was fitted to these data (fig. 5). When the deviations from trend of spawning-stock size index are correlated with the deviations from trend of catch per unit of effort for the 23 seasons, a positive correlation coefficient of 0.822 is obtained. The data were fitted to the least squares regression line, $Y_c = -0.0057656 + 0.011304X$, in which $Y_c =$ computed spawning stock size deviation and $X =$ catch per unit of effort deviation (fig. 6).

There is no reason to believe that catch per unit of effort is necessarily a better measure of

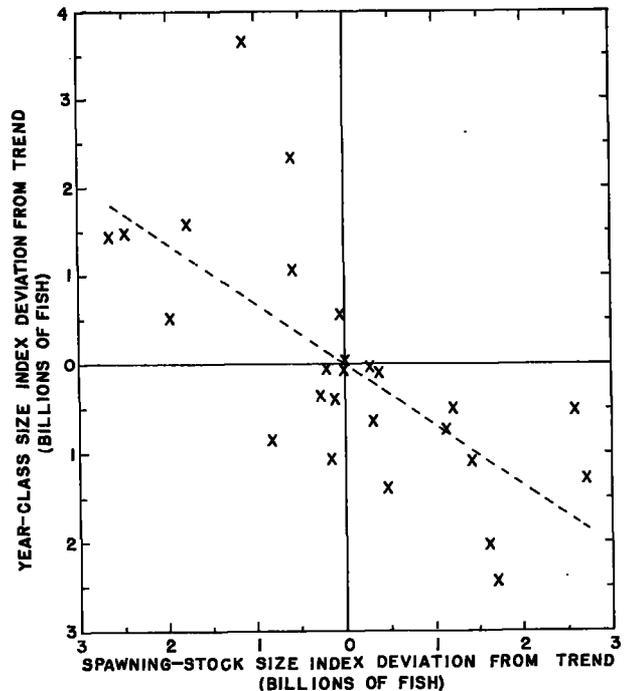


FIGURE 4.—Deviation from trend of year-class size plotted against deviation from trend of spawning-stock size for 26 years (1932-57).

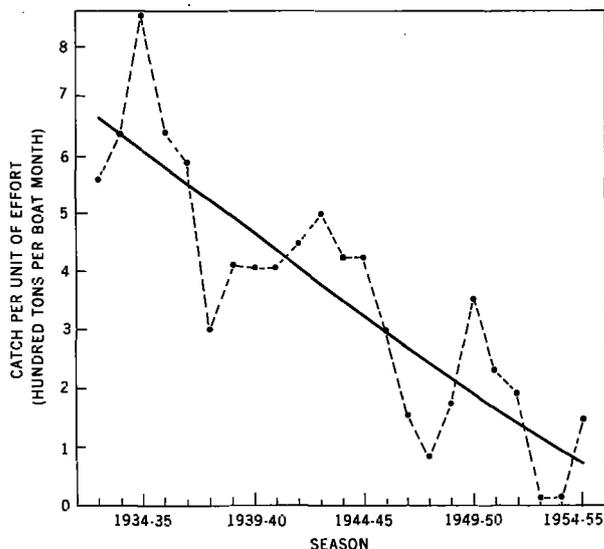


FIGURE 5.—Apparent trend of sardine catch per unit of effort, 1932-33 through 1954-55 seasons.

population size than the total fish caught index. The former accounts for changing effort but measures only the population available to the fishery in that year. The latter tends to average the effects of both effort and availability over several years. At relatively low levels of fishing effort directed against a stable fish population one might reasonably expect that changes in effort would result in directly proportional changes in catch. However, at relatively high levels of fishing effort a "saturation point" is reached above

TABLE 2.—Observed and calculated California catch per unit of effort data (tons per boat-month) and deviations compared with spawning-stock size index deviations

Year	Trend year	Observed catch per unit of effort	Computed catch per unit of effort	Deviation	Spawning-stock size index deviation
1932-33	1	557	665	-108	-0.60
1933-34	2	636	636	0	-.16
1934-35	3	835	607	228	1.71
1935-36	4	638	578	60	1.63
1936-37	5	586	549	37	.00
1937-38	6	302	520	-218	-2.65
1938-39	7	409	492	-83	-2.49
1939-40	8	405	463	-58	-1.13
1940-41	9	404	435	-31	-.26
1941-42	10	447	406	41	2.71
1942-43	11	497	378	119	2.59
1943-44	12	422	351	71	1.41
1944-45	13	420	323	97	.47
1945-46	14	302	296	6	.83
1946-47	15	153	269	-116	-1.95
1947-48	16	81	242	-161	-1.79
1948-49	17	173	216	-43	-.59
1949-50	18	352	191	161	1.12
1950-51	19	229	165	64	1.21
1951-52	20	187	140	47	-.02
1952-53	21	10	116	-106	-.64
1953-54	22	11	92	-81	-.21
1954-55	23	145	69	76	.36

which relatively large changes in effort result in relatively small changes in catch. This effort saturation point seems to have been exceeded throughout most of the period covered in this paper as later data will indicate. The above conditions will tend to impair the accuracy of the catch per unit of effort index to a greater extent than the total fish caught index. The excellent correlation between the two indices, however, is evidence of their validity as measures of population size.

Another method of demonstrating the relation between year-class size and spawning-stock size (fig. 7) involves fitting a parabola directly to the data. Ricker (1954) gives a number of examples of reproduction curves of somewhat similar nature. The curve I have fitted in figure 7 is a transformation of the straight line fitted to recruits per spawner plotted against spawning-stock size. That is, if Y equals year-class size and X equals spawning-stock size, a straight line may be fitted to $\frac{Y}{X} = 1.28867 - 0.1265SX$. Multiplying through

by X gives a second degree parabola: $Y = 1.28867X$

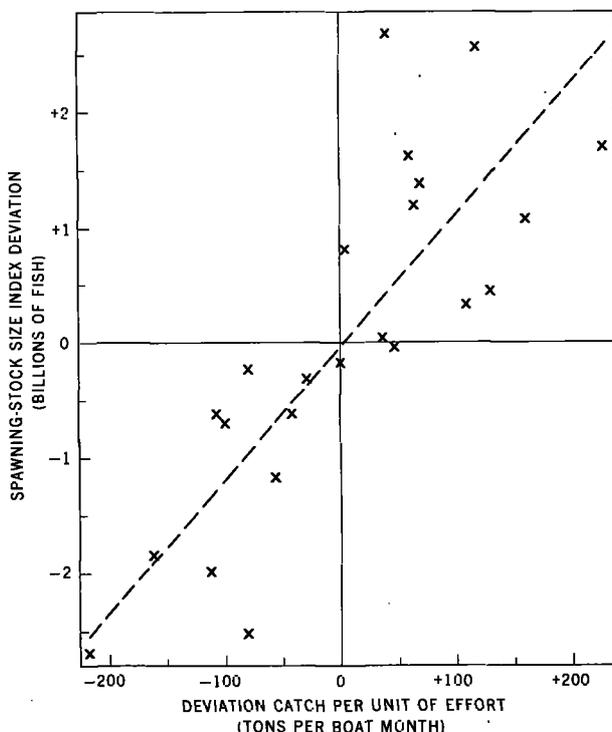


FIGURE 6.—Deviation from trend of spawning-stock size plotted against deviation from trend of catch per unit of effort for 23 seasons (1932-33 through 1954-55).

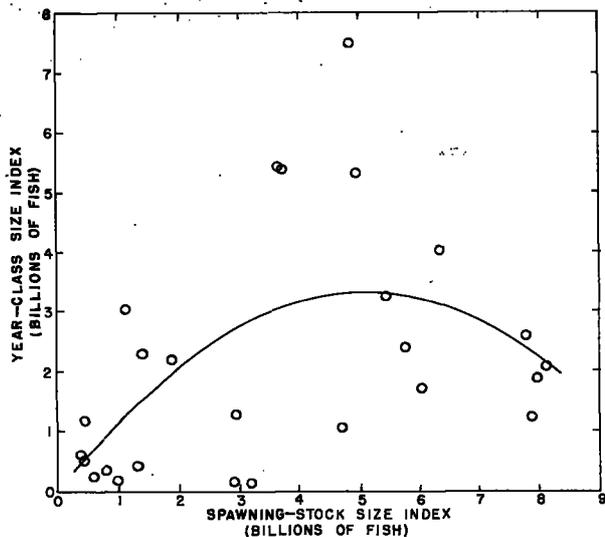


FIGURE 7.—Sardine year-class size plotted against spawning-stock size with fitted second degree parabola, $Y=1.23867X-0.12658X^2$, $r=0.539$, $p<.01$.

— $0.12658X^2$. A straight line may be fitted to random numbers as above and will yield a significant correlation if enough pairs of random numbers are used, but the transformation of such a line will, of course, no longer show a significant correlation.

In figure 8 spawning-stock size and year-class size indices are plotted against time for the sardine data. In figure 9 the observed spawning-stock size index and the computed values for year-class

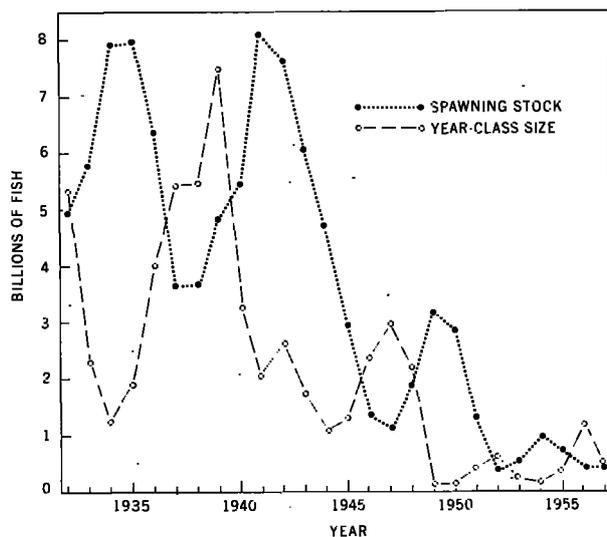


FIGURE 8.—Sardine year-class size and spawning-stock size plotted against time, 1932-57.

size obtained from the curve in figure 7 are plotted against time. A comparison of these two figures indicates that the curve is not an adequate description of the data. It is difficult to see how this curve would describe such a relationship when the fish species is fairly short-lived, year-class size is measured after the fish enters the fishery, and the data follow a somewhat cyclical pattern. In order for the population to pass over from the right limb of the curve to the left limb, it would have to move through a period of large year-class production which would throw it back to the right limb again.

Although the method of analyzing the data by trend deviation is satisfactory for the entire period covered, a more illuminating analysis may be obtained by breaking the data down into three periods of no trend which may be treated separately. The data are presented in this manner in figure 10. The straight line on the right is fitted

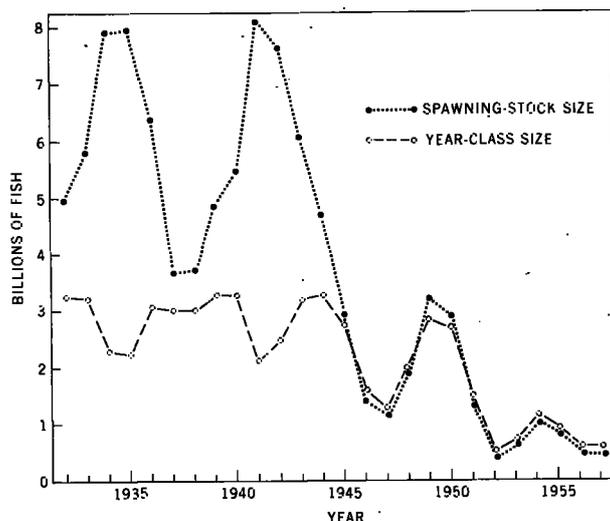


FIGURE 9.—Sardine year-class size index computed from curve (fig. 7) and observed spawning-stock size index plotted against time (1932-57).

to the data for the 11 years 1932-42; the line in the middle is fitted to the 6 years 1945-50; and the line on the left is fitted to the 6 years 1952-57. The years 1943 and 1944 marked the beginning of the first collapse of the fishery. Both of these collapses were associated with reductions in the range of the sardine. In the mid-1940's the sardine disappeared in commercial quantities from British Columbia to Central California and the Central California fishery became sporadic. The

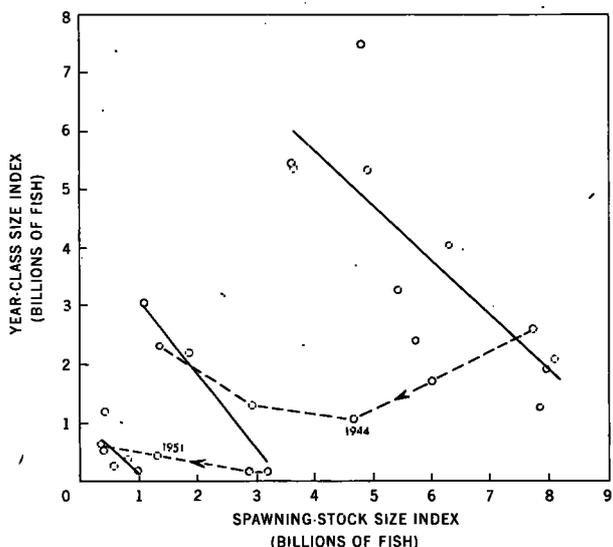


FIGURE 10.—Sardine year-class size index plotted against spawning-stock size index and lines fitted to each of the three periods 1932-43, 1945-50 and 1952-57.

San Pedro fishery remained relatively unaffected. In the early 1950's the Central California landings became negligible or absent and the San Pedro fishery became sporadic. It appears, however, that the same inverse relationship between spawning-stock size and year-class size persisted but within reduced ranges.

In figure 11 spawning-stock size and year-class size indices based on San Pedro landings only are plotted against time. Two fishery periods and one collapse are evident here. In figure 12 a

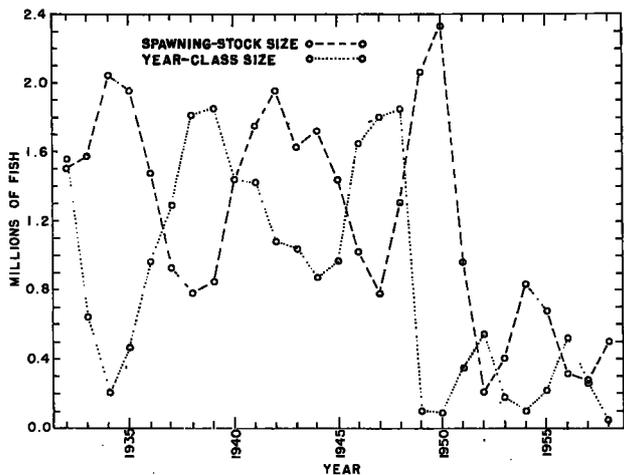


FIGURE 11.—Sardine year-class size index and spawning-stock size index plotted against time (1932-57) San Pedro, California, only.

straight line has been fitted to the 19-year period 1932-50 on the right, and a second straight line to the 7-year period 1952-58 on the left.

The three fitted lines ($Y=a+bX$) for all ports and the two for San Pedro are presented in figure 13. Correlation data for these lines are presented in table 3. It is noteworthy that the regression lines all have about the same slope and that the periods of fishery collapse originate and cross over from the lower right-hand area of the regression lines rather than going "over a curve."

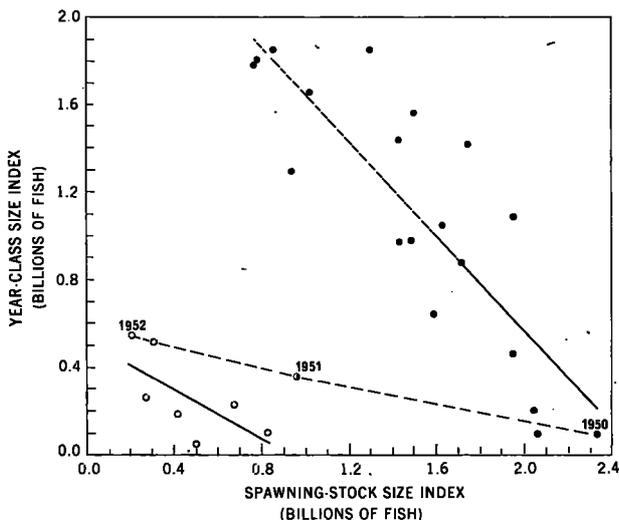


FIGURE 12.—Sardine year-class size index plotted against spawning-stock size index and lines fitted to each of two periods, 1932-50 and 1952-58, San Pedro only.

TABLE 3.—Correlation between spawning-stock size and year-class size

	N	r	P
Index based on—			
All ports:			
1932-43	11	-0.820	0.001
1945-50	6	-.936	.01
1952-57	6	-.669	.1
San Pedro:			
1932-50	19	-.845	.001
1952-58	7	-.691	.1

The existence of good correlations between spawning-stock size and year-class size does not in itself mean that spawning-stock size necessarily affects year-class size. On the other hand it is axiomatic that year-class size (as measured after the fish have entered the fishery or spawning stock) affects spawning-stock size a few years later. By using the method of correlating deviations from trend, an excellent negative correlation

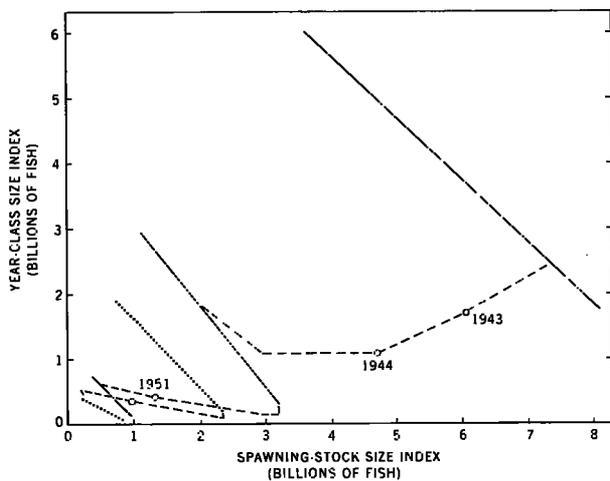


FIGURE 13.—Comparison of computed lines for three periods shown in figure 10 (all ports) and two periods shown in figure 12 (San Pedro) with transitional years plotted.

was found between spawning-stock size and year-class size. A slightly better positive correlation, however, may be found between year-class size and spawning-stock size 3 years later. Correlation coefficients of year-class size on spawning-stock size for a series of lagged and advanced years are presented in figure 14.

From the above we may hypothesize either 1) that the apparent cause and effect relationship between spawning-stock size and year-class size is merely a byproduct of the known effect of year-class size on subsequent spawning-stock or 2) that spawning-stock size actually determines year-class size. If the former is true, year-class size could either fluctuate or follow cycles. If the latter is true, year-class size would follow a cycle. Examination of the data reveals that they do appear to follow a cyclical pattern, and, in fact, if they did not, the excellent negative correlation between spawning-stock size and year-class size could not be found. Also this correlation would not result unless the length of the cycle was approximately twice the mean age of the spawning stock.

Therefore, although the effect of year-class size on subsequent spawning-stock size could cause the apparent relationship between spawning-stock size and year-class size, the circumstances under which this could occur are limited. If this hypothesis were true the factors determining year-class size would have to occur in cycles approxi-

mately equal to twice the mean age of the spawning stock. At present, the only known factor that follows this pattern is spawning-stock size.

Figure 15 presents eight population models based on the sardine data. These models illustrate what correlations would exist between spawning-stock size and year-class size if there were no cause and effect relationship between these two parameters and if the correlation resulted from the cause and effect relationship between year-class size and subsequent spawning-stock size alone. Figure 15 shows that the length of cycle determines whether or not the cycles are in or out of phase and consequently the degree and direction of the correlation. These data are presented in somewhat different form in figure 16 to which the plot of the observed correlation coefficient has been added. The factors controlling the cyclical pattern of year-class size would have to vary in approximately an 8- to 10-year cycle in order for the high observed correlation coefficient to obtain. No environmental factor varying in such a manner has yet been found.

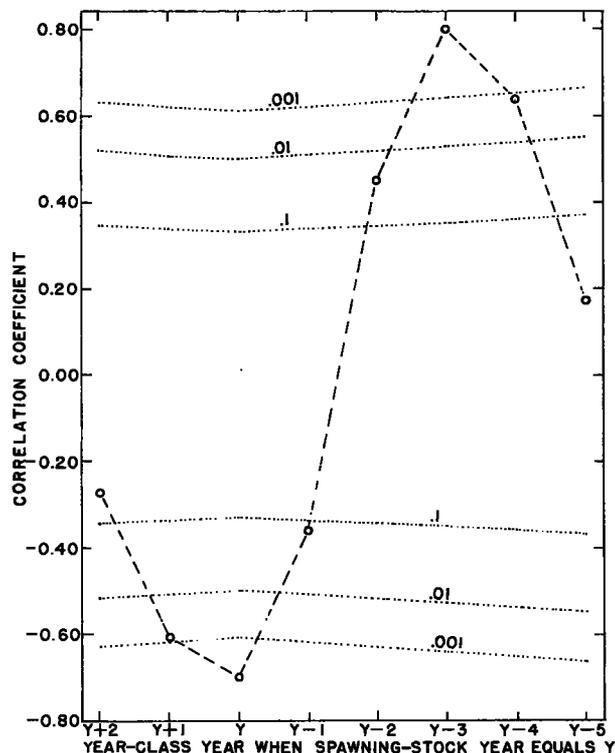


FIGURE 14.—Correlations between year-class size index deviations from trend in year, y , each of the 2 succeeding years and each of the 5 preceding years and spawning-stock size index deviations from trend in year, y .

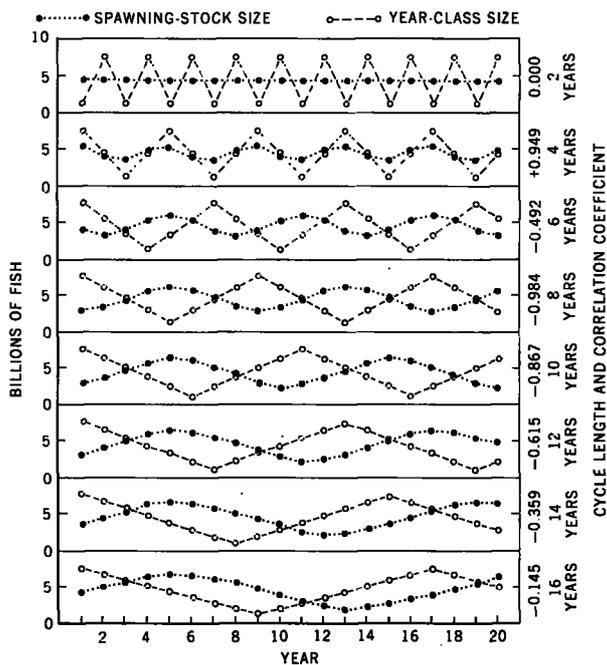


FIGURE 15.—Population models (based on sardine data) illustrating the effect (for eight cycles of different lengths) of year class strength on subsequent spawning stock size when spawning stock size exercises no influence on year-class size.

On the other hand, if spawning-stock size causes year-class size, Ricker (1954) has pointed out that the length of the cycle should be twice the mean length of a generation (interval from egg to egg). This appears to be applicable to the present data. In fact there is a shortening of the cycle length over the period covered coincident with a decrease in the mean age of spawning stocks resulting from the disappearance of the longer lived later maturing northern fish.

If it is assumed that spawning-stock size alone causes year-class size the population model, based on the sardine data, shown in figure 17 would prevail. Starting with the largest observed spawning-stock size index spawning-stock size and year-class size would fluctuate inversely in cycles of constant length but decreasing amplitude until, after many years, an equilibrium population was attained. Any environmental factors that affected the spawning-stock composition would, of course, once again initiate the fluctuating cycles.

Data comparable to those presented for the sardine may be found for the haddock (Herrington, 1948). Catch per unit of effort indices for haddock

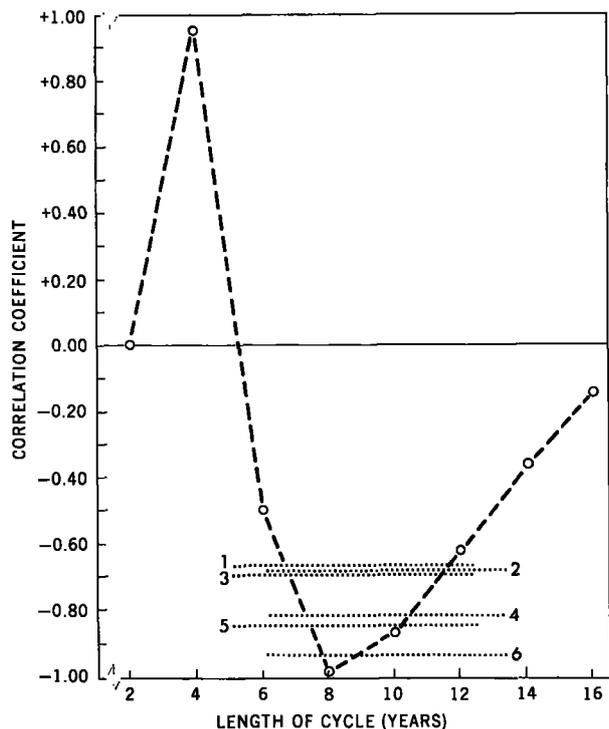


FIGURE 16.—Correlation coefficients plotted against length of cycle for data in figure 15. Observed correlation coefficients for spawning stock size index and year class size index indicated by dotted lines: No. 1 all ports 1952-57, No. 2 San Pedro 1952-58, No. 3 all ports 1932-57 (deviations from trend), No. 4 all ports 1933-42, No. 5 San Pedro 1932-50, No. 6 all ports 1945-50.

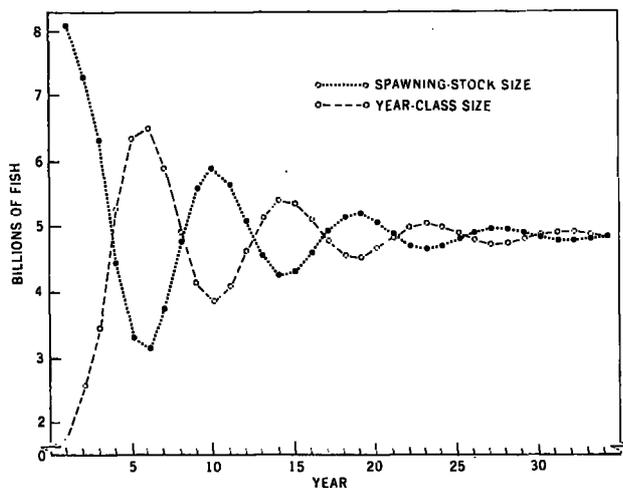


FIGURE 17.—Population models (based on sardine data) illustrating the effect of spawning-stock size on year-class size when spawning stock size determines year class size according to the straight line formula determined for sardines for all ports, 1932-43.

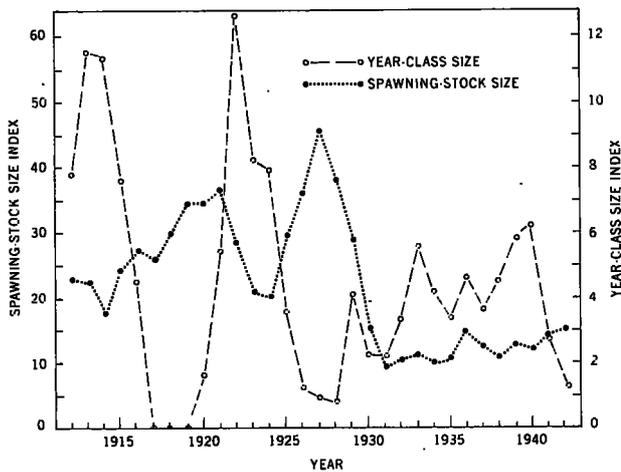


FIGURE 18.—Haddock spawning stock size index and year class size index plotted against time.

spawning-stock size and year-class size plotted against time are shown in figure 18. According to Ricker (1954) there was a radical change in fishing methods about 1930. The good inverse correlation between spawning-stock size and year-class size that prevailed until 1929 is no longer apparent after that date (figs. 18 and 19). The haddock has not undergone any great reduction of range comparable to that exhibited by the sardine.

The use of spawning-stock size and year-class size indices assumes that total sardines caught

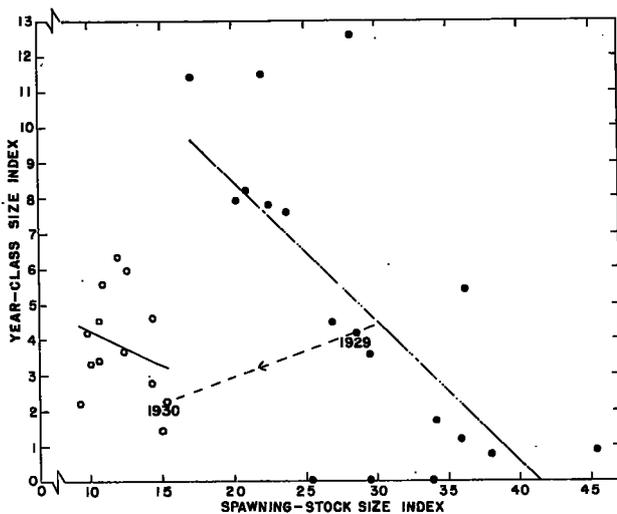


FIGURE 19.—Haddock year-class size index plotted against spawning-stock size index and computed regression lines for two periods (1912-29 and 1930-42).

adequately reflects the actual population size and year-class size present in the ocean. Although this certainly appears to be true in the case of the sardine, there are several other factors that may cause some error in the estimates. One of these is effort.

California catch (thousands of tons) and effort (boat months) (Marr, 1960) are plotted in figure 20 and also presented in table 4.

When these values are directly correlated a correlation coefficient of 0.533 ($P=0.01$) is obtained. However, if catch is correlated with effort 1, 2, or 3 years later, even higher correlations are obtained as follows:

Catch year	Effort year	Years	r
y -----	$y-1$	22	0.172
y -----	y	23	.533
y -----	$y+1$	22	.631
y -----	$y+2$	21	.636
y -----	$y+3$	20	.538
y -----	$y+4$	19	.419

These data are plotted with levels of probability in figure 21.

The above correlations appear to be caused at least in part by trend. Third degree parabolas were fitted to catch and effort data, and deviations obtained. These deviations are plotted for the 23 years in figure 22. The coefficient of correlation and the rank coefficient of correlation for various lagged and advanced series of years are as follows:

Catch year	Effort year	Years	r	Pr
y -----	$y-2$	21	-----	-0.472
y -----	$y-1$	22	-0.366	-.570
y -----	y	23	.208	.081
y -----	$y+1$	22	.197	.206
y -----	$y+2$	21	.106	.221
y -----	$y+3$	20	-----	.178

These data are plotted with levels of probability in figure 23. The great deviation in effort in the 1950-51 season tends to depress the correlation coefficients especially those of effort years $y+1$ and $y+2$ of trend deviations. The effort peaks also seem to follow the catch peaks in the earlier years and more nearly coincide with them in latter years. If the deviations from trend are correlated directly for the 1932-33 through 1948-

TABLE 4.—California sardine catch and effort 1932-33 through 1954-55

Season	Catch	Effort
	Thousands of tons	Boat months
1932-33	248	447
1933-34	382	600
1934-35	597	715
1935-36	557	874
1936-37	724	1,236
1937-38	413	1,368
1938-39	572	1,401
1939-40	531	1,312
1940-41	455	1,125
1941-42	584	1,306
1942-43	505	1,008
1943-44	479	1,123
1944-45	555	1,304
1945-46	404	1,313
1946-47	234	1,487
1947-48	121	1,356
1948-49	184	918
1949-50	334	943
1950-51	351	1,531
1951-52	127	594
1952-53	4	466
1953-54	3	298
1954-55	66	458

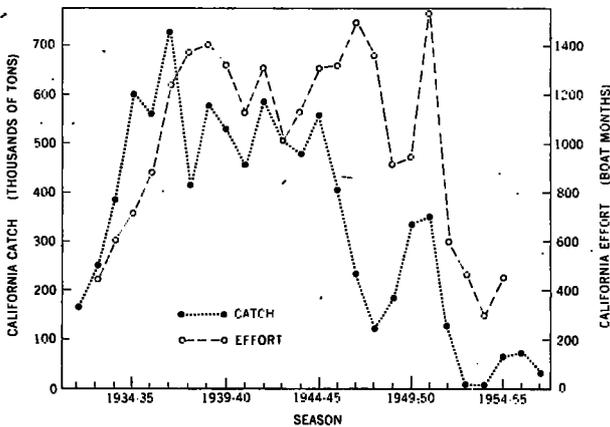


FIGURE 20.—California catch and effort plotted against time for 23 seasons.

49 period only, the following correlation coefficients are obtained:

Catch year	Effort year	Years	<i>r</i>
<i>y</i> -----	<i>y</i> -3	14	-0.062
<i>y</i> -----	<i>y</i> -2	15	-.434
<i>y</i> -----	<i>y</i> -1	16	-.618
<i>y</i> -----	<i>y</i>	17	-.171
<i>y</i> -----	<i>y</i> +1	16	.117
<i>y</i> -----	<i>y</i> +2	15	.618
<i>y</i> -----	<i>y</i> +3	14	.569

These data are plotted with levels of probability in figure 24.

The above analysis of catch and effort data indicates that catch causes effort rather than vice versa. The lag in effort appears to be more nearly 3 years at the beginning of the period and closer to 1 year at the end of the period. It is especially

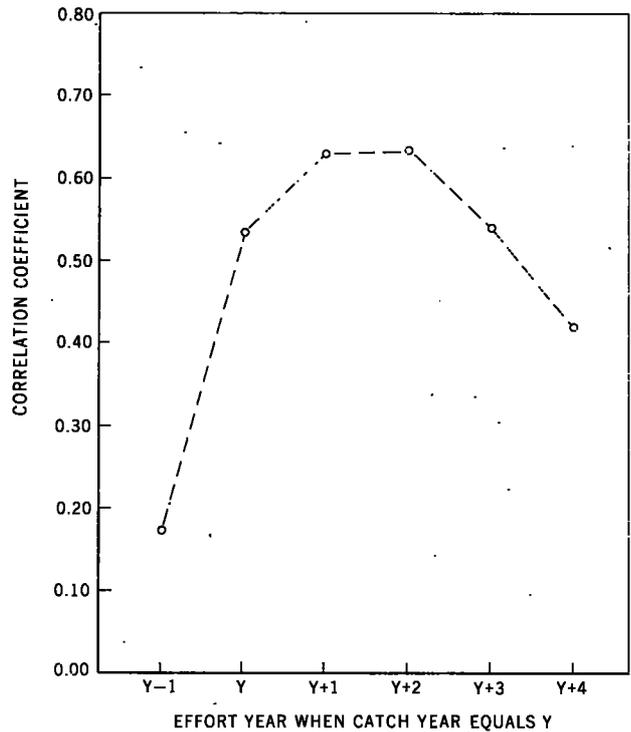


FIGURE 21.—Correlations between California catch in year, *y*, and effort in year, *y*, the preceding year, and the 4 subsequent years.

noticeable also that toward the end of the period effort is low in some years because of the scarcity of fish in those same years. When pre-season evidence indicates a scarcity of fish, many boats will not begin to fish and others will stop fishing within the first month or two of the season; and conversely, when fish are abundant, effort will remain high throughout the season.

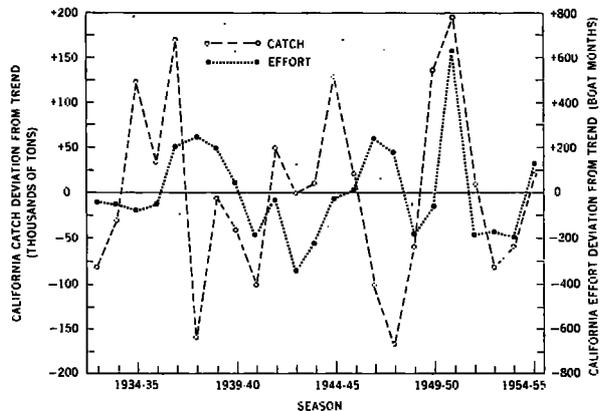


FIGURE 22.—Deviations from trend of California catch and effort, 1932-33 through 1954-55 seasons.

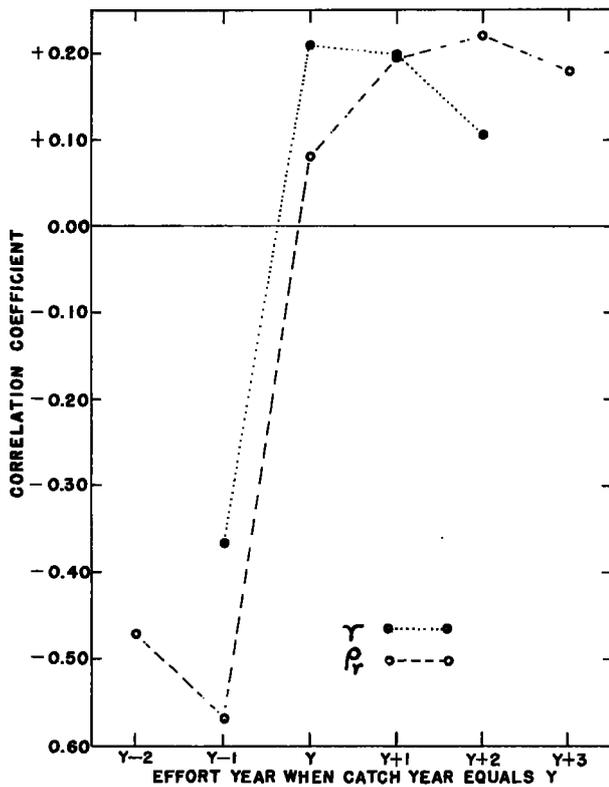


FIGURE 23.—Correlation and rank correlation between deviations from trend of California catch and effort 1932-33 through 1954-55 seasons.

It is also noteworthy that the 1934-35 effort of 715 boat-months yielded the second highest catch of the 23-year period despite the fact that effort did not drop below the 1934-35 figure until 1951-52 and averaged 54 percent higher during these 16 years. The high negative correlations between effort in one year and catch the following year may mean that high effort in one year will reduce the catch in the following year or it may only be a manifestation of the cyclical nature of the data.

Two-annulus sardines are not fully available to the fishery. This may be seen from the following 28-year average (geometric mean) survival rates for sardines based on all ports:

Percent	From annul—	to annul—
109.....	2	8
46.....	3	4
37.....	4	5
30.....	5	6
22.....	6	7
10.....	7	8

A survival rate of 109 percent would be impossible if the fishery sampled the 2-annulus fish

equally as well as the older fish. There may also be some selectivity of larger fish by fishermen.

Table 5 presents correlation coefficients obtained from direct correlations of various pairs of parameters based on the San Pedro sardine fishery for the 14-year period 1937-38 and 1950-51. These parameters exhibit negligible trend over this period.

TABLE 5.—Correlation coefficients¹ for various pairs of parameters, San Pedro sardines 1937-38 through 1950-51 seasons

	Spawning-stock size index	Effort	Catch
Percent of year class taken as 2-annulus fish.....	-0.773	-0.007	+0.137
Effort.....	-.342		+.309
Spawning-stock size index.....		-.342	-.031

¹ Probability levels: N=14 n=12 P=0.1 0.01 0.001
r=0.458 .661 .780

There is an excellent negative correlation between spawning stock size index and the percent of a year class taken as 2-annulus fish. None of the other pairs of parameters involved yields a significant correlation for this period of years.

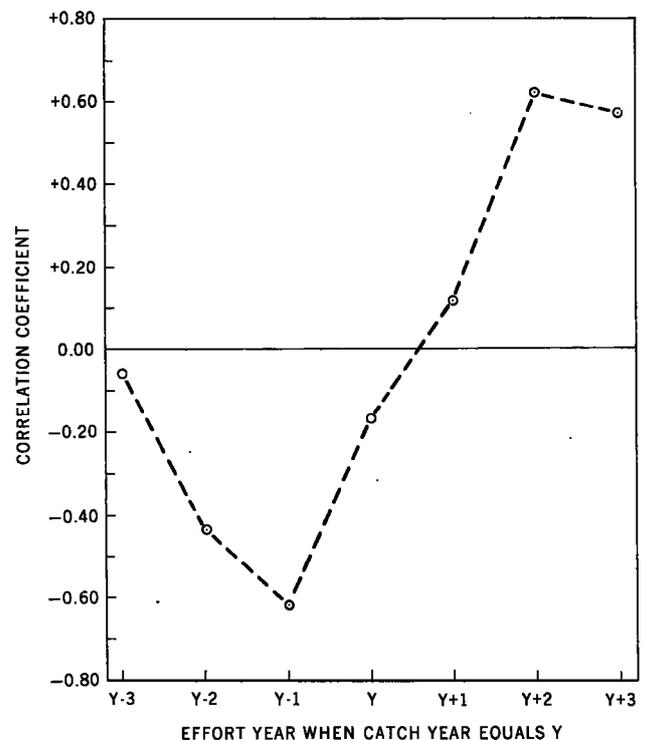


FIGURE 24.—Correlations between deviations from trend of California catch in year, *y*, and effort deviations from trend in year, *y*, the preceding 3 years and the succeeding 3 years.

These data indicate that catch was maintained relatively high during periods of low spawning-stock size by directing more fishing effort against the 2-annulus fish which were entering the fishery at that time.

A measure of survival or mortality may be obtained by comparing the number of sardines having three or more annuli caught in one season with the number of sardines having four or more annuli caught in the following season. This measure includes the effect of changing effort and availability. This is shown by the fact that in some years survivals in excess of 100 percent (or negative mortalities) may be obtained.

Survival data, computed as above, are presented in table 6 and figure 25 for all ports and for San Pedro only. Logarithmic second degree parabolic trend line values fitted to these data are also plotted. The apparent high survival values during 3 of the first 4 years are probably caused by increasing effort as the fishery was developing. Following that period, effort appears to be saturated with respect to population size and its effects become secondary. In theory effort should affect survival rates both absolutely and relatively. A high effort should increase total mortality thus decreasing survival, and a low effort should con-

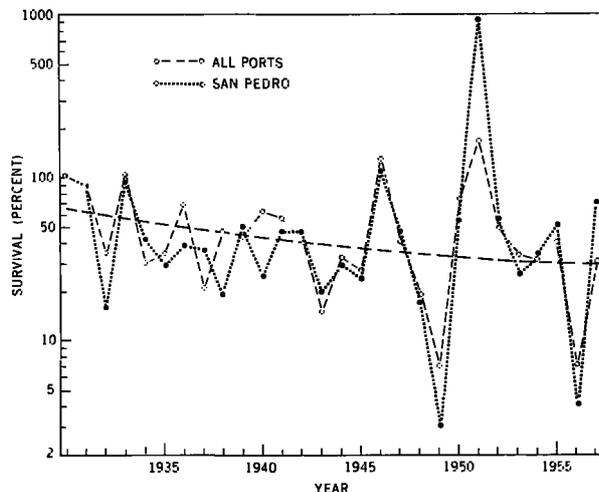


FIGURE 25.—Apparent survival trends for all ports and San Pedro only, 1933 through 1960.

versely increase survival. Also a change from a lower effort to a higher effort should cause apparent survival to increase. These relationships are not apparent in the survival data.

In addition to being affected by the increasing effort during the early years, the trend lines are also influenced by the changing age composition of the population. In the earlier years a greater proportion of the population was made up of the

TABLE 6.—Sardine survival as measured by 4-annulus and older fish caught in one year expressed as a percent of 3-annulus and older fish caught the preceding year

Season		All ports				San Pedro			
		Population size (millions of fish)		Survival (percent)		Population size (millions of fish)		Survival (percent)	
3-annulus and older	4-annulus and older	3-annulus and older	4-annulus and older	Observed	Computed	3-annulus and older	4-annulus and older	Observed	Computed
1932-33	1933-34	1,401	1,459	104	65.1	473	489	103	56.1
1933-34	1934-35	1,769	1,532	87	62.1	578	509	88	52.9
1934-35	1935-36	2,807	981	35	59.3	377	142	16	50.0
1935-36	1936-37	2,829	2,915	103	56.7	719	678	94	47.4
1936-37	1937-38	3,861	1,151	30	54.3	861	369	43	45.1
1937-38	1938-39	1,672	645	39	52.0	510	149	29	43.1
1938-39	1939-40	1,890	604	68	50.0	206	78	38	41.3
1939-40	1940-41	1,875	399	21	48.2	244	88	36	39.7
1940-41	1941-42	1,544	792	47	46.2	409	78	19	38.4
1941-42	1942-43	2,373	1,075	45	44.6	543	269	50	37.2
1942-43	1943-44	2,981	1,622	62	43.1	941	237	25	36.1
1943-44	1944-45	3,893	1,627	56	41.6	587	276	47	35.2
1944-45	1945-46	2,384	948	40	40.3	797	370	46	34.5
1945-46	1946-47	1,819	270	15	39.1	740	151	20	33.9
1946-47	1947-48	654	210	32	37.9	471	137	29	33.4
1947-48	1948-49	404	109	27	36.9	261	69	24	33.1
1948-49	1949-50	287	380	128	35.9	215	233	108	32.8
1949-50	1950-51	1,210	495	41	35.0	771	364	47	32.7
1950-51	1951-52	1,530	285	19	34.2	1,229	204	17	32.7
1951-52	1952-53	1,017	87	7	33.4	707	20	3	32.8
1952-53	1953-54	89	66	74	32.0	23	12	52	33.0
1953-54	1954-55	108	194	170	32.0	18	148	925	33.4
1954-55	1955-56	409	199	49	31.5	339	135	55	33.9
1955-56	1956-57	467	157	34	30.9	437	110	25	34.5
1956-57	1957-58	247	78	32	30.4	60	54	31	35.2
1957-58	1958-59	192	67	41	30.0	109	60	51	36.1
1958-59	1959-60	168	22	7	28.6	233	9	4	37.1
1959-60	1960-61	181	56	31	23.3	56	40	71	38.3

longer lived northern fish. As an example, the geometric mean of survival for the 7 years 1942-48 was 54 percent in the Pacific Northwest and 32 percent in San Pedro. Aside from the effects of changing population composition, effort, and availability, survival probably remained relatively unchanged over the 28-year period.

Although not measurable, the effects of availability may be seen in the increasingly large fluctuations in survival toward the end of the 28-year period in figure 25. It appears that availability has had its greatest effect on the northern periphery of the sardine range, and considerably influenced the catch in British Columbia and the Pacific Northwest throughout the existence of the fisheries in these areas. Population size, however, also exerted great influence and was undoubtedly related to availability in this area. Certainly population size was the primary factor influencing the fisheries when all ports are considered. In more recent years the reduction of the range of the sardine has caused the effects of availability to be felt much farther to the south, and the relatively larger proportion of the population affected has caused the greater fluctuation in apparent survival. In at least a few of these later years availability has probably been the dominant factor affecting the fishery, although population size and availability are probably to a certain extent themselves related. Nevertheless, over the period of years treated in this paper, population size has been, without any doubt, the primary and dominating factor influencing the success of the fishery.

SUMMARY

1. For the 26-year period (1932-1957) an excellent negative correlation exists between anomalies of spawning-stock size and year-class size for the Pacific sardine.

2. This correlation may be demonstrated by correlating deviations from trends of the two parameters or by directly correlating the parameters for three (all ports) or two (San Pedro only) periods of no no trend separated by fishery failures and a reduction in sardine range.

3. The data indicate that the good negative correlation existing between spawning-stock size and year-class size is not a secondary result of year classes occurring in cycles which generate cycles of population size several years later.

4. The indices of year-class size and spawning-stock size are based on catch, which is determined primarily by actual population size. Catch may also be influenced by fishing effort and availability. During the period of study effort seems to have been near saturation, and changes in effort had little effect on catch. On the other hand, catch appeared to have considerable effect on the amount of effort expended, especially in the two immediately following seasons, with large catches causing increased effort and small catches causing decreased effort. Availability seems to have been secondary to population size in determining catch, although the effects of availability as evidenced by apparent total mortality rates appeared to increase during the latter half of the 26-year period.

LITERATURE CITED

- CLARK, FRANCES N., AND JOHN C. MARR.
1955. Part II: Population dynamics of the Pacific sardine. California Department of Fish and Game, Marine Research Committee, Progress Report California Cooperative Fisheries Investigations, 1 July 1953 to 31 March 1955, pp. 11-48.
- DAUGHERTY, ANITA E., AND ROBERT S. WOLF.
1960. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1957-58. California Fish and Game, vol. 46, No. 2, pp. 189-194.
- ECKLES, HOWARD H.
1954. Age composition of the commercial catch of Pacific sardines, 1932-38. In Kenneth H. Mosher and Howard H. Eckles, Age determination of Pacific sardines from otoliths, pp. 24-40. U.S. Fish and Wildlife Service, Research Report 37.
- FELIN, FRANCES E., RAY ANAS, ANITA E. DAUGHERTY, AND LEO PINKAS.
1950. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1949-50. California Fish and Game, vol. 36, No. 3, pp. 241-249.
1951. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1950-51. California Fish and Game, vol. 37, No. 3, pp. 339-349.
- FELIN, FRANCES E., JOHN MACGREGOR, ANITA E. DAUGHERTY, AND DANIEL J. MILLER.
1953. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1952-53. California Fish and Game, vol. 39, No. 3, pp. 409-417.
1954. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1953-54. California Fish and Game, vol. 40, No. 4, pp. 423-431.
1955. Age and length composition of the sardine catch off the Pacific coast of the United States and

- Mexico in 1954-55. California Fish and Game, vol. 41, No. 4, pp. 285-293.
- FELIN, FRANCES E., AND JULIUS B. PHILLIPS.
1948. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada, 1941-42 through 1946-47. California Division Fish and Game, Fish Bulletin No. 69, 122 pp.
- FELIN, FRANCES E., JULIUS B. PHILLIPS, AND ANITA E. DAUGHERTY.
1949. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1948-49. California Fish and Game, vol. 35, No. 3, pp. 165-183.
- FELIN, FRANCES E., ROBERT S. WOLF, ANITA E. DAUGHERTY, AND DANIEL J. MILLER.
1958. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1955-56. California Department Fish and Game, Fish Bulletin No. 106, pp. 7-12.
- HERRINGTON, WILLIAM C.
1948. Limiting factors for fish populations: some theories and an example. A symposium on fish populations. Bulletin of the Bingham Oceanographic Collection, vol. XI, art. 4, pp. 229-283.
- MARR, JOHN C.
1960. The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard). Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, vol. 3, pp. 667-791.
- MOSHER, KENNETH H., FRANCES E. FELIN, AND JULIUS B. PHILLIPS.
1949. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1947-48. California Fish and Game, vol. 35, No. 1, pp. 15-40.
- RICKER, WILLIAM E.
1954. Stock and recruitment. Journal Fisheries Research Board of Canada, vol. 11, No. 5, pp. 559-623.
- WOLF, ROBERT S.
1961. Age composition of the Pacific sardine 1932-60. U.S. Fish and Wildlife Service, Research Report 53, 36 pp.
- WOLF, ROBERT S. AND ANITA E. DAUGHERTY.
1961. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1958-59. California Fish and Game, vol. 47, No. 3, pp. 273-285.
- WOLF, ROBERT S., JOHN S. MACGREGOR, ANITA E. DAUGHERTY, AND DANIEL J. MILLER.
1958. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1956-57. California Department Fish and Game, Fish Bulletin No. 106, pp. 13-17.

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LIFE HISTORY OF LAKE HERRING IN LAKE SUPERIOR

BY WILLIAM R. DRYER AND JOSEPH BEIL, *Fishery Biologists (Research)*
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ABSTRACT

The average annual commercial catch of lake herring (*Coregonus artedii*) in U.S. waters of Lake Superior was nearly 12 million pounds in 1929-61. This production contributed 62.4 percent of the total U.S. take of lake herring for the Great Lakes. About 90 percent of the annual catch is taken from small-mesh gill nets during the November-December spawning season.

The life-history studies were based on 12,187 fish collected in 1950-62; past growth was computed for 3,779 specimens collected from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich.

Age group IV dominated the catch in each year's collection at each port, followed by age groups III and V. The average age of the lake herring in the commercial samples was 3.9 years at Bayfield, Portage Entry, and Marquette, and 4.1 years at Duluth. With few exceptions, the mean age of the females exceeded that of the males.

The strength of the year classes varied considerably at each port but generally declined over the 1946-55 period. Fluctuations were similar at Bayfield and Marquette, but at neither port resembled closely the fluctuations at Portage Entry. Year classes 1954 and 1955 were, however, well below average at all three ports.

Females were larger than males (largest difference was 0.6 inch) at all ports except Marquette where the males held a slight advantage. With only one exception, the average lengths of the age groups were larger in 1956-59 than in 1950-55. The largest increase from the earlier to the later period was 1.1 inches for the V-group males at Portage Entry. In general, the average size of the lake herring increased from the western to the eastern part of the lake.

The weight of the lake herring in the combined samples increased as the 3.170 power of the length.

Lake herring of corresponding lengths were heavier in 1956-61 than in 1950-55 (greatest increase was 8.8 percent at Bayfield). Port-to-port differences in average weight among fish of the same length in 1950-55 showed a west-to-east trend toward increased weight.

The calculated lengths and weights of fish from Duluth were smallest, followed by those from Bayfield, Portage Entry, and Marquette. With only one exception, the calculated lengths and weights of lake herring taken in 1956-59 were greater than those taken in 1950-55.

The trends in annual fluctuations of growth in length and weight were closely correlated among the three ports. Growth was generally below average in 1945-53 and above average in 1954-59.

The percentage of females equalled or exceeded that of the males in all age groups above I. The percentage of females, all age groups combined, was 68.5. The first mature males appeared in the 8.5- to 8.9-inch group; the first mature females were in the 9.5- to 9.9-inch group. All males were mature at lengths greater than 11.4 inches, and all females at lengths greater than 11.9 inches. The youngest mature lake herring belonged to age group II, and all fish older than age group III were mature. Spawning of Lake Superior lake herring normally is at its peak during the last week in November and the first week in December. The average number of eggs produced by female Lake Superior lake herring was 6,351.

Crustacea were the most common food and were found in 83 percent of the 146 stomachs examined.

The distribution of lake herring may be influenced by temperature, abundance of plankton, and spawning. The fish are most common near the surface in early summer, migrate to deeper water as the surface water warms, and are randomly distributed between the surface and about 20 fathoms in the late fall.

The lake herring, *Coregonus artedii* LeSueur, occurs in all of the Great Lakes and in the deeper

inland waters of the St. Lawrence River, Hudson River, and Mississippi River drainages (Hubbs and Lagler, 1947). The name "lake herring"

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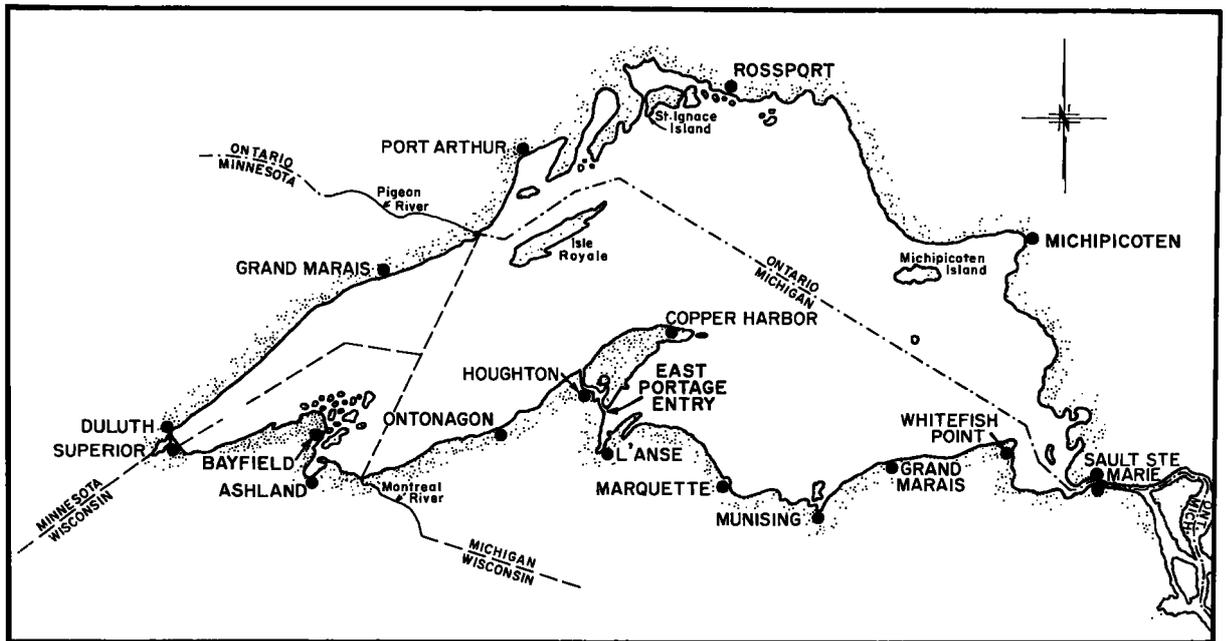


FIGURE 1.—Map of Lake Superior.

undoubtedly originates from the resemblance and analogous ecological position to the Atlantic marine herring, *Clupea harengus*. Both are pelagic and feed largely on plankton. They are the basis of considerable commercial fishing and also serve as forage for the more valuable food fishes—the marine forms for cod and other predators, and the fresh-water forms for the once-abundant lake trout.

The lake herring did not gain high importance in the Great Lakes fisheries until the early 1900's when it assumed first position in the total Great Lakes production; it has held this rank to the present time. The average production in U.S. waters in 1929–61, the most recent years for which dependable statistics are available for all Great Lakes, was nearly 19 million pounds. The catch of 24,371,000 pounds in 1948 was the highest recorded in that period, but Lake Erie alone produced greater catches before the collapse of the fishery there in 1925. Production in the Great Lakes in most recent years has not equalled that of the earlier years, but continues to be substantial (nearly 21 million pounds, for example, in 1954).

The lake herring (usually known as cisco in Lake Erie and in small lakes) is a member of an extremely complex genus. The coregonines have

confused taxonomists for many decades, and even though researchers have added greatly to the amount of data available, the group is still not well understood. The confusion stems from the difficulty in describing a group which varies widely in size, shape, and systematic characters, and in which the morphology is affected by the environment. The deepwater members of the genus, known collectively as chubs, are often difficult and sometimes impossible to identify by species at the smaller sizes. The separation of lake herring from chubs, however, rarely causes difficulty.

Numerous papers have been published on the age, growth, and ecology of *C. artedii* of the smaller lakes but the only major publications on the species in the Great Lakes have been those of Van Oosten (1929), Scott (1951), and Smith (1956). This paper is the first contribution to the life history of the lake herring in Lake Superior.

MATERIALS AND METHODS

The studies of the Lake Superior lake herring were based on 12,187 specimens collected from commercial and experimental gill nets fished at various locations and dates during 1950–62. The main study of age and growth was based on 3,779

TABLE 1.—Ports and dates of collection of Lake Superior lake herring used in study of age and growth

Date	Port	Gill net mesh size	Number of fish	Date	Port	Gill net mesh size	Number of fish
1950				1956			
Dec. 4	Bayfield	(1)	103	Nov. 19	Bayfield	2 $\frac{3}{4}$	63
Dec. 5	Portage Entry	(1)	96	Dec. 5	Marquette	2 $\frac{3}{4}$	83
Dec. 15	Marquette	2 $\frac{1}{4}$	68	Dec. 10	Portage Entry	2 $\frac{3}{4}$	100
1951				1957			
Nov. 20	Marquette	2 $\frac{3}{4}$	106	Nov. 25	Portage Entry	2 $\frac{3}{4}$	106
Nov. 27	Bayfield	2 $\frac{3}{4}$	147	Nov. 26	Marquette	2 $\frac{3}{4}$	81
Nov. 27	Portage Entry	2 $\frac{3}{4}$	123	Nov. 27	Bayfield	2 $\frac{1}{4}$	105
1952				Dec. 3	Duluth	(1)	47
Nov. 11	Bayfield	2 $\frac{3}{4}$	125	Dec. 4	Bayfield	2 $\frac{1}{4}$	92
Nov. 24	Portage Entry	2 $\frac{3}{4}$	106	Dec. 6	Duluth	(1)	43
Dec. 11	Marquette	2 $\frac{3}{4}$	101	Dec. 9	Portage Entry	2 $\frac{1}{4}$	103
1953				Dec. 9	Marquette	2 $\frac{1}{4}$	78
Nov. 20	Marquette	2 $\frac{3}{4}$	84	1958			
Dec. 1	Portage Entry	2 $\frac{3}{4}$	91	Nov. 25	Portage Entry	2 $\frac{1}{4}$	118
1954				Dec. 1	Marquette	2 $\frac{3}{4}$	117
Dec. 1	Portage Entry	2 $\frac{1}{4}$	96	Dec. 3	Duluth	2 $\frac{1}{4}$ -2 $\frac{3}{4}$	122
Dec. 6	Bayfield	2 $\frac{1}{4}$	161	Dec. 10	Bayfield	2 $\frac{1}{4}$	116
Dec. 10	Marquette	2 $\frac{1}{4}$	102	1959			
1955				Nov. 24	Duluth	2 $\frac{3}{4}$	113
Dec. 2	Portage Entry	2 $\frac{3}{4}$	85	Dec. 1	Portage Entry	2 $\frac{3}{4}$ -2 $\frac{1}{2}$	125
Dec. 5	Marquette	4 $\frac{1}{2}$	95	Dec. 1	Marquette	2 $\frac{1}{4}$	123
1956				Dec. 8	Bayfield	(1)	110
Nov. 6	Marquette	2 $\frac{3}{4}$	72	Total			3,779
Nov. 11	Portage Entry	2 $\frac{3}{4}$	143				

¹ Mesh size unknown.

fish from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich., (fig. 1) during the fall spawning seasons of 1950-59 (table 1). The mesh sizes of the commercial gill nets ranged from 2 $\frac{1}{4}$ to 2 $\frac{3}{4}$ inches, extension measure (the sample collected at Marquette in 1955 came from 4 $\frac{1}{2}$ -inch-mesh trout nets). The 2 $\frac{3}{4}$ -inch-mesh gill nets were by far the most common in the fishery. Scale samples and data on length, weight, sex, and state of gonads were obtained from each fish.

The remainder of the samples came from experimental gill nets fished from the Bureau's research vessel *Siscowet* (fig. 2) in western Lake Superior (table 2), from special collections during the 1961 spawning run at Bayfield, and from the summer lake herring fishery at Marquette. The numbers of fish employed in the individual phases of the life-history study varied according to the appropriate materials available or the number of specimens required. The numbers and sources of the fish used for each particular study are listed in the text.

All collections used in this report represent the entire catch or net-run samples.

Total length (tip of the snout to the end of the tail, lobes compressed) was recorded to the nearest 0.1 inch. Weights were measured on a spring scale and recorded to the nearest 0.1 ounce. All lengths are given in inches, and weights in ounces.

Whenever possible, the scales for the study of age and growth were removed from the left side of the body at a point midway between the lateral

TABLE 2.—Lake herring taken in experimental gill nets by the M/V *Siscowet* in western Lake Superior, 1958-61

Date	Number of fish	Date	Number of fish
1958		1960	
June	323	April	66
July	62	May	57
August	45	June	20
September	774	July	53
October	53	September	176
November	208	October	217
December	80	November	269
		December	621
1959		1961	
April	6	May	2
May	23	June	5
June	9	July	6
July	289	September	120
August	4	October	10
September	32	November	245
October	177	December	74
November	886	Total	5,184
December	272		



FIGURE 2.—M/V *Siscowet*.

line and the middle of the base of the dorsal fin. Scales were not always available from this area, however, particularly on fish which had been choked through the gill nets, thus leaving them devoid of scales in the midriff. Under these circumstances, the scales were removed from wherever they could be found, usually from a point posterior to the dorsal fin.

Plastic impressions of scales were made in cellulose acetate (Smith, 1954) and were magnified 43 diameters by means of a microprojector (Moffett, 1952). Diameters of scales and growth fields were measured through the focus along a line that roughly bisected the anterior field, and were recorded to the nearest millimeter.

Some difficulty was encountered in distinguishing accessory marks or false annuli from the true annuli. If doubt as to true age was great, the

specimen was excluded from the analysis. It is felt that these few exclusions (about 3 percent) made the age determinations reasonably dependable.

Age groups are designated by Roman numerals corresponding to the number of annuli. All the fish were considered to have passed into the next age group on January 1. For fish of all spawning-run collections, the numbers of completed growing seasons ran one greater than the indicated ages. The annulus formation offered no difficulties in age determinations since the samples for the age and growth studies were all collected during the fall spawning run, whereas the annulus is laid down in the early summer.

Calculations from scale measurements of lengths at time of completion of earlier annuli were made by direct proportion. The validity of this

method was demonstrated for Saginaw Bay (Lake Huron) lake herring by Van Oosten (1929) and for Green Bay (Lake Michigan) lake herring by Smith (1956). Materials available in the present study were unsuitable for the determination of the body-scale relation for lake herring of Lake Superior.

An instructive discussion of the various phases of this paper requires a preliminary statement on the probable extent to which various sources of bias affect the data. The major bias to the data from the spawning-run samples can be traced to four sources: gear selection; segregation on the basis of maturity; selective fishing mortality; and time of capture within the spawning season. These sources may act independently or collectively to prejudice estimates of age composition, relative strength of the year classes, size at capture, growth, sex composition, and annual fluctuations in size and growth. The first two factors have so much in common that certain of their effects cannot be separated, and together they make possible the selective fishing that leads to the progressive change in the actual growth of the survivors.

Bias from gear selection affects estimates of age composition through failure of the gear to take representative samples of the younger age groups which actually may be present on the spawning grounds. The selection of only the larger members of the younger age groups causes overestimates of average size and calculated lengths. The possibility of selecting the small members of the older age groups also exists, but the scarcity of old fish and the reduction of growth with age probably make this selection insignificant. Changes from cotton to nylon twine, in mesh sizes, and subtle changes in the hang of the net may bias comparisons among samples, especially those dealing with changes in the average size, growth, and weight. During 1950-55 the 2½-inch-mesh net was the most common, although samples were collected from 2½-inch-mesh nets in Marquette in 1950 and 1954 and at Portage Entry in 1954. One sample was collected from 2¼-inch-mesh nets at Bayfield in 1954. In the years following 1955, the fishery adjusted the mesh size to conform with the increased size of the fish at all ports except Bayfield (comparable data are not available for Duluth). At Portage Entry, the 2¼- and 2½-inch-mesh nets were in common use, and at

Marquette the mesh sizes ranged from 2½-inch in 1956 to 2½-inch mesh in 1958, 1960, and 1961. At Bayfield, despite the increased size of the fish, the mesh sizes actually decreased during 1956-61 from 2½- in 1956 to 2¼-inch mesh in 1961.

Successively larger meshes would be expected to capture fish of larger size, and the shorter fish captured should have a greater relative girth (and hence, be heavier than fish of the same length captured in nets with smaller meshes). Deason and Hile (1947) found that *C. kiyi* of the same length captured in nets of successively larger meshes had successively greater values of the coefficient of condition, *K*.

Other questions arise relating to comparisons among samples taken from different makes of twine. The mesh sizes recorded in the data were those ordered by the fishermen and not necessarily the actual size as fished. Different twine companies supply different mesh sizes on identical orders; some produce mesh sizes which are scant whereas others give accurate meshes. Also, lots of twine of the same general material (e.g., cotton, linen, or nylon) have different shrinkage under use. When the fisherman receives the twine he may hang the net on the one-half basis (i.e., 4 feet of twine, flat mesh, hung on 2 feet of maitre) or tighter, such as two-third basis (6 feet of twine on 4 feet of maitre). The selective action of the gill nets may vary according to their hang—a tightly hung net has a lesser tangling action and hence may be more selective than one hung loosely.

Undoubtedly the most severe source of bias in the spawning-run collections was segregation on the basis of maturity. Since only mature individuals were found on the spawning grounds, I-group fish were entirely lacking and age groups II and III were poorly represented. Age group IV was the first age at which all of the lake herring were mature; consequently, fish of this age group were persistently dominant in the samples. Only the faster growing of the younger age groups were mature. Bias from segregation according to maturity is made more complicated by sex differences in attainment of maturity. Since females mature at a greater size and age than do males, overestimates of growth and underestimates of numbers among younger fish are more severe for them. Data on sex ratio by age are impaired correspondingly.

The production of about 90 percent of the annual catch under the conditions just described leads to selective fishing mortality according to growth rate and sex. This selective destruction modifies the growth and sex ratio of a year class as it passes through the fishery. At the younger ages males are subjected to greater mortality than females, and the faster growing fish of both sexes are eliminated. The survivors of a year class have slower growth, and fewer males than would be characteristic of a year class which had not been subjected to a selective fishery or to no fishery at all. In some situations the longer exposure of males to selective fishing could make them appear to grow more slowly than females whether or not the sexes actually grew at different rates. The selective destruction probably does not end until all of the fish are mature and fully vulnerable to the gear.

Records of age composition and hence also judgments of year-class strength may be affected by the time of capture within the spawning season. Collections made in the early days of the season often had an unduly high percentage of fish in the younger age groups (the early-maturing males of the population reach the spawning grounds first). Conversely, samples collected during the last few days of the season frequently included disproportionately large numbers of fish in the older age groups (see section on reproduction). This source of bias is most damaging at the extremes of the season—the time of capture is of little consequence during the main season.

COMMERCIAL FISHERY FOR LAKE HERRING

The lake herring has been the principal species in the commercial production in U.S. waters of Lake Superior since 1908 (Koelz, 1926). Between 1891 and 1907 the lake trout occupied first place in poundage produced, and in the years prior to 1891 the whitefish was the principal species taken.

The statistical records of lake herring production in Lake Superior for 1929–61 (table 3) are from Lake Fish issued annually by the Bureau of Commercial Fisheries and those for Ontario are issued by the Province.

The first published record of lake herring production in Lake Superior is for 1867 in Ontario. The first record of production in the U.S. waters of

Lake Superior is for 1879, but in 1879–1928 the statistics often included the catch of small chubs and in some years the catch of round whitefish (*Prosopium cylindraceum*). Only since about 1929 can the records for lake herring production in the U.S. waters of Lake Superior be termed reasonably dependable.

TABLE 3.—Production (thousands of pounds) of lake herring in Lake Superior, 1929–61

Year	United States				Canada	Grand total
	Minnesota	Wisconsin	Michigan	Total	Ontario	
1929.....	8,571	2,625	1,516	12,712	3,529	15,241
1930.....	8,368	705	2,341	11,414	2,745	14,159
1931.....	5,363	662	886	6,912	1,396	8,308
1932.....	5,123	362	540	6,026	962	6,988
1933.....	5,203	650	941	6,794	1,744	8,538
1934.....	8,017	2,946	2,068	13,031	2,157	15,188
1935.....	7,911	2,422	2,782	13,115	1,506	14,621
1936.....	5,243	2,866	3,657	11,767	2,789	14,546
1937.....	5,623	2,991	3,170	11,784	2,378	14,162
1938.....	5,715	2,485	2,394	10,594	1,917	12,511
1939.....	6,590	3,119	3,357	13,066	1,435	14,501
1940.....	7,381	4,909	4,213	16,503	1,201	17,703
1941.....	5,724	6,160	5,954	17,838	1,433	19,271
1942.....	4,697	5,035	5,113	14,844	1,393	16,237
1943.....	5,079	4,435	4,360	13,874	1,209	15,084
1944.....	5,069	4,712	4,446	14,227	1,481	15,708
1945.....	4,398	6,538	3,109	14,045	1,708	15,753
1946.....	3,443	6,342	3,357	13,142	1,611	14,753
1947.....	2,904	4,641	3,263	10,808	1,017	11,825
1948.....	3,890	6,291	4,524	14,705	1,285	15,991
1949.....	4,054	5,028	4,122	13,204	1,255	14,459
1950.....	2,489	3,953	1,715	8,158	505	8,663
1951.....	2,249	5,347	2,829	10,424	763	11,187
1952.....	2,683	5,890	3,448	12,021	993	13,014
1953.....	2,667	5,356	2,415	10,439	745	11,184
1954.....	2,854	5,575	3,393	11,823	920	12,743
1955.....	2,332	4,359	3,443	10,134	708	10,842
1956.....	2,600	4,158	3,719	10,478	821	11,299
1957.....	3,177	3,162	5,017	11,355	1,696	13,051
1958.....	2,870	2,496	4,850	10,216	1,744	11,960
1959.....	2,408	2,862	6,242	11,512	2,833	14,345
1960 ¹	1,863	2,255	6,693	10,806	2,117	12,923
1961 ¹	1,580	2,559	7,306	11,445	1,505	12,950

¹ Materials supplied for this report in advance of general release for all species.

Lake Superior contributed an average of 62.4 percent to the total U.S. production of lake herring for the Great Lakes in 1929–59. (This percentage unquestionably was much lower before the collapse of the highly productive Lake Erie cisco fishery in 1925.) The annual percentage contribution ranged from 39.7 percent in 1931 to 92.0 percent in 1959. The high figure for 1959 did not reflect a particularly great yield in Lake Superior but rather a very low catch of lake herring in the other Great Lakes.

In the U.S. waters of Lake Superior the catch of lake herring was 12.7 million pounds in 1929, dropped to 6 million pounds in 1932, and reached nearly 18 million pounds in 1941, the highest production recorded. Since 1934 the take has exceeded 10 million pounds in all years but one (1950).

Although the catch of lake herring has contributed nearly three-fourths (74.2 percent) to the 1929-59 total U.S. production of Lake Superior, the value of the lake herring represented less than one-third (30.4 percent) of the total. The annual percentage contribution to the total value of the fishery ranged from 17.7 percent (\$67,000) in 1932 to 56.9 percent (\$854,000) in 1941. In recent years the lake herring has contributed a relatively high percentage to the total value of the fishery due to the drastic decline of the high-priced lake trout.

Reasons for the relatively low value of the lake herring stem from strongly seasonal production, capture and handling procedures, and technological problems. On the average, about 90 percent of the annual production occurs during the November-December spawning run when the market is soon glutted. Individual catches, often running as large as 10 tons, are piled in the gill net tugs and brought to shore where they are picked from the nets in warm sheds. Little care is taken in picking the fish from the nets. The rough treatment of this highly palatable but delicate fish often produces an inferior product hardly fit for human consumption. Even those fish which are removed carefully from the nets and well iced soon become soft and unappetizing. Frozen lake herring readily dehydrate and suffer objectionable oxidation of the fat.

In the early years, nearly all of the lake herring were salted; large quantities were shipped to economically depressed areas in the east and southeast. With the advent of mink farming in the early 1940's, a large percentage of the lake herring was sold for mink food. The 1961 lake herring production at Bayfield, Wis., was divided about equally between salt herring and mink food.

The distribution of the catch of lake herring among the different states has shifted markedly during the period for which sound statistics are available. Minnesota dominated the catch in 1929-40, Wisconsin held the lead in 1941-56 (exception was 1942 when Michigan occupied first place), and Michigan had the largest catch in 1957-61.

The 1929-61 average annual production of lake herring from Canadian waters of Lake Superior was 1,527,000 pounds, only 11 percent of the lake's total. The catch exceeded 2 million pounds in only 7 years and was below 1 million in 8 years.

TABLE 4.—Average catch (pounds) of Lake Superior lake herring per 1,000 feet of gill nets lifted in November-December 1929-59

[Number of feet of nets lifted (in thousands of feet) is in parentheses]

Year	Minnesota	Wisconsin	Michigan ¹	Year	Minnesota	Wisconsin	Michigan ¹
1929			303 (3, 235)	1948			279 (13, 815)
1930			248 (5, 656)	1949	268 (8, 906)	688 (7, 086)	330 (11, 128)
1931			170 (8, 830)	1950	286 (5, 240)	490	224 (6, 714)
1932			175 (2, 421)	1951	352 (4, 100)	745 (7, 100)	395 (6, 783)
1933			186 (3, 549)	1952	348 (5, 343)	785 (7, 566)	445 (6, 293)
1934			194 (7, 326)	1953	444 (3, 217)	670 (7, 901)	396 (4, 995)
1935			205 (8, 709)	1954	320 (4, 697)	542 (10, 217)	449 (6, 699)
1936			236 (12, 182)	1955	303 (4, 439)	641 (6, 749)	469 (5, 812)
1937			155 (15, 831)	1956	330 (3, 996)	665 (6, 101)	409 (6, 267)
1938			165 (11, 901)	1957	317 (4, 944)	483 (6, 370)	419 (9, 811)
1939			164 (18, 110)	1958	301 (4, 038)	472 (5, 172)	356 (9, 738)
1940			294 (13, 092)	1959	218 (4, 940)	424 (6, 590)	295 (14, 517)
1941			266 (17, 909)	1960	190 (3, 076)	548 (3, 825)	299 (13, 033)
1942			230 (16, 676)	1961	192 (3, 780)	715 (3, 331)	345 (11, 739)
1943			206 (15, 735)				
1944			232 (13, 210)	Average 1949- 61			
1945			216 (13, 006)		298 (4, 669)	604 (6, 501)	372 (8, 733)
1946			232 (9, 854)	1929- 61			
1947			173 (15, 900)				278 (10, 317)

¹Based on the November-December catch per unit effort for statistical districts 1-4 and 6. To obtain the grand averages in the column, the catch per unit effort in each district was weighted by the percentage contribution of the district to the total State of Michigan catch in 1929-43.

Although recent production of lake herring in U.S. waters is not significantly below that of the 1929-61 mean of 11,794,000 pounds, some evidence exists that the abundance has declined in certain areas of the lake, particularly in Minnesota. The catch per unit effort during the 2-month spawning season in Minnesota (table 4) reached a peak of 444 pounds per 1,000 linear feet of net lifted in 1953, but the trend was downward after that year and the 1960-61 catch per unit effort (mean of 191 pounds) was the lowest for the 13-year period. Much of the decline in Minnesota can be traced to the near collapse of the fishery in the Duluth area, which in the years prior to 1955, contributed the major portion of Minnesota's production. The average annual catch per unit effort at Duluth in 1951-53 was over 300 pounds. An erratic decline in abundance after 1953 reduced the catch per unit effort to only 68.5 pounds in 1960 (the catch per unit effort increased slightly to 91.7 pounds in 1961).

TABLE 5.—Average catch of Lake Superior lake herring per 1,000 linear feet of gill nets lifted in November-December, 1950-59, according to weight and number of fish

Year	Minnesota ¹		Wisconsin ¹		Portage Entry		Marquette	
	Number of pounds	Number of fish	Number of pounds	Number of fish	Number of pounds	Number of fish	Number of pounds	Number of fish
1950			490	1,307	200	471	265	643
1951			745	2,055	426	1,082	325	722
1952			765	1,826	462	1,001	472	967
1953					421	999	320	656
1954			542	1,262	504	1,320	213	425
1955					519	1,154	273	588
1956			685	1,565	451	949	242	471
1957	317	757	453	991	453	928	330	468
1958	301	669	472	995	381	664	269	439
1959	218	425	424	807	305	554	267	442
1960	190	380	548	913	313	538	271	434
1961			715	1,395	334	534	431	651
Average: 1950-55			636	1,613	422	1,005	311	667
1956-61			551	1,111	372	695	302	484
Percentage decrease			13.4	31.1	11.8	30.8	2.9	27.4

¹ Data were lacking to calculate the numerical catch per unit effort for Minnesota in 1950-56 and for Wisconsin in 1953 and 1955.

Some evidence of declining abundance exists also in Wisconsin waters where the catch per unit effort during the 2-month spawning season declined from a mean of 649 pounds per 1,000 feet of gill nets lifted in 1949-55 to 551 pounds in 1956-61. The catch per unit effort in 1961 (715 pounds), however, was the highest since 1952 (765 pounds). On the other hand, little evidence of a decline exists in those Michigan waters in which substantial catches were made each year since 1929. The average catch per 1,000 feet of gill nets in 1956-61 (354 pounds) was slightly below that of 1949-55 (387 pounds), but far above the 1929-61 mean of 278 pounds.

A measure of abundance according to numbers of fish caught per unit effort, rather than pounds of fish, may better describe changes in population density. Since the average size of the lake herring captured was greater in 1956-61 than in 1950-55, fewer individuals were required to reach the same weight in the later period. The data are inadequate to make comparisons between the early and late periods at Duluth since samples were taken only in 1957-60. The catch per unit effort in pounds at Bayfield declined 13.4 percent from 1950-55 to 1956-61 (table 5). The catch per unit effort in numbers,¹ on the other hand, declined 31.1 percent (from 1,613 in 1950-55 to 1,111 in 1956-61). The decrease in catch per unit

¹ The numerical catch per unit effort was based on the catch per unit effort in pounds divided by the average weight of the fish in the sample.

effort according to weight from the early to the later period was 11.8 percent at Portage Entry and 2.9 percent at Marquette. The number of fish caught per 1,000 feet of gill nets lifted decreased 30.8 percent at Portage Entry and 27.4 percent at Marquette.

Fishing effort, based on the number of linear feet of gill nets (in units of 1,000 feet) lifted during the 2-month spawning season, varied from state to state and year to year (table 4). Fishing effort in Minnesota ranged from 3,076 units in 1960 to 8,906 units in 1949 (the 1949-61 mean was 4,669). The fishing effort in Wisconsin exceeded that of Minnesota in all years except two (1949 and 1961). The number of units exceeded 10,000 in 1954, and the 1949-61 mean was 6,501. Fishing effort in Michigan² exceeded 10,000 units lifted in 1936-49 (exception in 1946 when the value was 9,854 units) and in 1959-61. Over 18,000 units of gill nets were lifted during the 2 spawning months in 1939. The 1949-61 mean was 8,733 units, well below the 1929-61 average of 10,317.

The interpretation of data on catch per unit effort for lake herring in terms of actual availability is difficult because of the recent change-over from cotton to nylon gill nets. This change took place much later and at a slower pace in Lake Superior than did the changeover to nylon trout nets. Not until 1958 or 1959 were the majority of Wisconsin lake herring fishermen using nylon nets, and a few fishermen were still fishing cotton nets in 1961. Since the cotton lake herring nets were commonly used only once a year, during the fall spawning season, they lasted many years. The fishermen were reluctant to replace perfectly good cotton nets with new, expensive nylon.

Extensive observations on the relative efficiency of cotton and nylon lake herring nets have not been made. The Bureau's research vessel *Cisco* provided comparisons between the catch of chubs in nylon and linen gill nets in Lake Michigan. Nylon gill nets took 2.2 times as many chubs as linen nets of corresponding mesh fished in the same gang. The Bureau vessel *Siscowet* obtained only one comparison between catches of lake herring in nylon and cotton nets. In this experiment the nylon nets took 4.3 times as many lake herring as did cotton nets fished in the same gang.

² Total November-December effort for statistical districts 1-4 and 6.

Since the conversion to nylon nets has taken place slowly over the past 5 to 8 years and dependable conversion factors on the relative efficiency of the two types of nets for taking lake herring are unavailable, it appears impossible to undertake any adjustment in the statistics. Fishing intensity, therefore, may have been underestimated and the availability or abundance, based on the catch per unit effort, may have been to the same degree overestimated more and more as nylon nets replaced cotton nets.

ANNULUS FORMATION AND PROGRESS OF THE SEASON'S GROWTH

Smith (1956) determined that some lake herring started new growth in Green Bay as early as May 8 in 1950, and that annulus formation was completed by July 13. Van Oosten (1929) suggested that annulus formation occurred during the winter for the lake herring of Saginaw Bay.

Information on the time of annulus formation is scarce from Lake Superior since lake herring were difficult to catch during the spring and early summer. The only reliable data came from Marquette where an early-summer lake herring fishery developed in 1961 and continued in 1962.

The earliest collection was made on May 3, 1962 (table 6), and included several fish which had already begun new growth. As late as July 27 (a full 2 weeks after annulus formation was completed in Green Bay), a few individuals still gave no indication of new growth. New growth had started on all of the lake herring collected on August 21, 1961, and on all fish collected later that season.

Among the best represented age groups (IV-VI), the younger fish started new growth earlier than did the older ones. On June 28, for example, 94 percent of the IV-group and 86 percent of the

TABLE 6.—Percentage of lake herring with completed annuli collected at Marquette during period of annulus formation
[Number of fish in parentheses]

Date	Percentage with completed annuli in age group						Ages combined
	III	IV	V	VI	VII	VIII	
1962							
May 3.	17 (46)	11 (101)	8 (109)	0 (70)	5 (22)	0 (4)	8 (352)
1961							
June 28.	50 (4)	94 (16)	86 (20)	65 (17)	64 (11)	20 (5)	73 (73)
July 27.	88 (8)	100 (21)	96 (25)	88 (25)	60 (5)	75 (4)	91 (88)
Aug. 28.	100 (14)	100 (26)	100 (27)	100 (12)	100 (6)	-----	100 (85)

V-group fish had a completed annulus as contrasted with a percentage of 65 for age group VI. On July 27, the percentages were 100 and 96 for age groups-IV and V but only 88 percent for VI-group fish.

The period of annulus formation for lake herring in Lake Superior exceeds 8 weeks. Extreme care is needed in age determination for fish captured during the spring and early summer.

The data on the amount and percentage of the season's growth were taken from samples collected at Marquette during the summer of 1961 and in the spring of 1962 (table 7). Collections were not available in 1961 until late June when the summer fishery started. Since the summer fishery ended in late September, the estimate of full season's growth was based on samples of the same year class collected in May 1962. Special arrangements were made to obtain these samples before the regular summer fishery began in late June.

The records of table 7 exhibit some irregularities in trend which probably can be attributed to the small numbers of fish on which certain estimates were based. Ten of 29 estimates were based on fewer than 10 fish. The most reliable data are those for age groups IV, V, and VI, where all 15 percentages are based on more than 10 fish and 12 on 20 or more.

Despite the irregularities in the data, a general idea of the progress of the season's growth can be formed from the weighted means of the percentages of growth completed for the different dates (fig. 3).

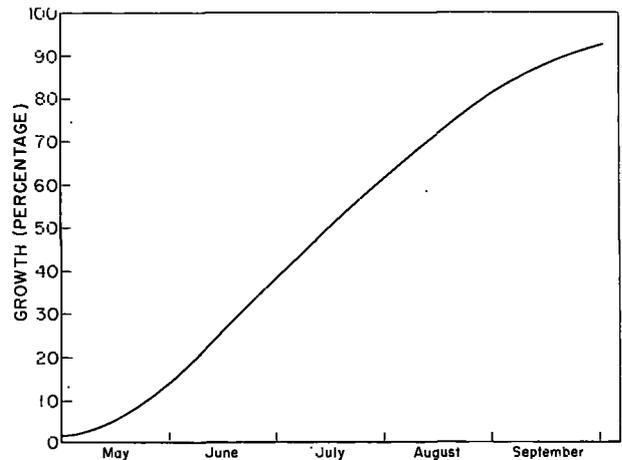


FIGURE 3.—Percentage of season's growth completed at time of capture, age groups combined. The curve was drawn freehand on the basis of data of table 7.

TABLE 7.—Amount of season's growth in length (inches) completed by age groups on various dates of capture

[The full season's growth of fish caught in 1961 determined from samples of the same year class collected on May 3, 1962]

Age group and item	Date of collection					Full-season growth in 1961
	May 3, 1962 ¹	June 28, 1961	July 27, 1961	August 21, 1961	September 25, 1961	
Age group III:						
Current-season growth.....	0.08	0.19	0.76	1.16	1.09	1.58
Percentage completed.....	5.1	12.0	48.1	73.4	69.0	100.0
Number of fish.....	46	4	8	14	5	77
Age group IV:						
Current-season growth.....	0.04	0.47	0.84	1.07	1.15	1.28
Percentage completed.....	3.1	36.7	65.6	83.6	89.8	100.0
Number of fish.....	101	16	21	26	20	184
Age group V:						
Current-season growth.....	0.02	0.35	0.68	0.83	0.99	0.96
Percentage completed.....	2.1	36.5	70.8	86.5	103.1	100.0
Number of fish.....	109	20	25	27	26	207
Age group VI:						
Current-season growth.....	0.00	0.42	0.51	0.63	0.82	0.89
Percentage completed.....	0.0	47.2	57.3	70.8	92.1	100.0
Number of fish.....	70	17	25	12	14	138
Age group VII:						
Current-season growth.....	0.01	0.42	0.33	0.56	0.49	0.79
Percentage completed.....	1.3	53.2	41.8	70.9	62.0	100.0
Number of fish.....	22	11	5	6	5	49
Age group VIII:						
Current-season growth.....	0.00	0.04	0.39	-----	0.85	0.85
Percentage completed.....	0.0	4.7	45.9	-----	100.0	100.0
Number of fish.....	4	5	4	-----	2	15
Average percentage:²						
All age groups.....	2.3	38.0	60.9	80.1	92.0	100.0
Age groups III-V.....	3.0	34.1	65.4	82.6	94.5	100.0
Age groups VI-VIII.....	0.3	42.8	53.7	70.8	85.8	100.0

¹ Current-season growth made in 1962; percentage computed from full-season growth of fish of same age in 1961.

² Weighted means.

The following percentages were obtained from the curve in the same figure:

Period of growth	Percentage of season's growth completed	
	During period	At end of period
Before May.....	2.3	2.3
May.....	11.5	13.8
June.....	25.0	38.8
July.....	22.5	61.3
August.....	20.0	81.3
September.....	11.2	92.5
After September.....	7.5	100.0

The greatest amount of growth in any single month took place in June (25.0 percent) and by the end of August, 81.3 percent of the season's growth was completed. Over two-thirds of the season's growth was in June-August and 90 percent in May-September.

Growth of Green Bay lake herring started sometime in May and ended in October (Smith, 1956). The greatest amount of growth took place in July. Hile (1936) found that growth of lake herring (ciscoes) in northeastern Wisconsin was complete by the end of July in Trout Lake, near the end of August in Muskellunge Lake, in early September in Sliver Lake, and in early October in Clear Lake. Differences in the length of the

growing season contributed importantly to differences of growth rate in the four populations..

Growth of the related *C. kiyi* of northern Lake Michigan (Deason and Hile, 1947) was 39 percent completed by June 14, 80 percent by July 9, and 100 percent completed by September 7.

AGE COMPOSITION AND YEAR-CLASS STRENGTH

AGE COMPOSITION

The age composition of the spawning-run samples varied relatively little from year to year and port to port. Age group IV dominated the catch in each year's collection at each port. Indeed, the contribution of the IV group (table 8) exceeded 50 percent in all but 8 collections (Duluth, 1957 and 1959; Bayfield, 1958; Portage Entry, 1955 and 1958; and Marquette, 1955, 1956, and 1959). The highest percentage of IV-group fish was 68.1 (Bayfield, 1957) and the lowest was 37.0 percent (Bayfield, 1958). The average percentage for the IV group for the combined collections was 53.2.

Fish of age group III were second in abundance in 16 of the 31 collections. The percentage contribution ranged from 11.0 (Bayfield, 1959) to 40.6 (Portage Entry, 1954) and averaged 24.8. The V

TABLE 8.—Age composition of Lake Superior lake herring according to port and year of capture

[Averages are unweighted]

Port and year of capture	Number of fish	Percentage age group						Average age
		II	III	IV	V	VI	VII	
Duluth:								
1957	90	5.6	15.6	42.2	34.4	2.2		Years 4.1
1958	122	2.5	31.1	50.8	15.6			3.8
1959	113	0.9	21.2	37.1	24.8	14.2	1.8	4.4
Average		3.0	22.6	43.4	24.9	5.5	0.6	4.1
Bayfield:								
1950	103		37.9	61.1	1.0			3.6
1951	147		28.5	60.6	12.9			3.8
1952	125		19.2	55.2	22.4	3.2		4.1
1954	161		18.8	66.5	16.1	0.6		4.0
1956	93	2.2	16.1	58.0	23.7			4.0
1957	197	3.0	20.8	68.1	8.1			3.8
1958	116	5.2	24.1	37.0	27.6	5.2	0.9	4.0
1959	110	2.7	11.0	50.1	24.5	1.8	0.9	4.2
Average		1.6	21.6	58.3	17.0	1.3	0.2	3.9
Portage Entry:								
1950	96		31.2	61.5	7.3			3.7
1951	123	0.8	18.7	56.1	22.8	1.6		4.1
1952	106	0.9	20.8	54.8	22.6	0.9		4.0
1953	91	3.3	39.6	53.8	3.3			3.6
1954	96	4.2	40.6	52.1	3.1			3.5
1955	85		20.0	43.5	34.1	2.4		4.2
1956	243	2.1	35.8	56.3	5.8			3.6
1957	209	3.8	22.5	58.9	14.8			3.8
1958	118	0.8	22.0	39.9	36.5	0.3		4.1
1959	125	1.6	14.4	54.4	28.0	1.6		4.1
Average		1.8	26.6	53.1	17.8	0.7		3.9
Marquette:								
1950	68	1.5	22.1	63.2	13.2			3.9
1951	106	0.9	19.8	59.5	19.8			4.0
1952	101		20.8	53.4	23.8	2.0		4.1
1953	84		38.1	52.4	8.3	1.2		3.7
1954	102	1.0	19.6	57.8	20.6	1.0		4.0
1955	95	2.1	21.1	41.0	34.7	1.1		4.1
1956	155	3.9	27.1	44.5	21.9	2.6		3.9
1957	159	4.4	28.9	55.4	9.4	1.9		3.8
1958	117	6.0	31.6	52.1	10.3			3.7
1959	123	1.6	34.1	43.2	19.5	1.6		3.9
Average		2.1	26.3	52.3	18.2	1.1		3.9
Grand total or average	3,779	2.0	24.8	53.2	18.4	1.5	0.1	3.9

group ranked second in 14 collections; it ranged from 1.0 percent (Bayfield, 1950) to 36.5 percent (Portage Entry, 1958), and averaged 18.4 percent for the combined collections. Age groups III and V were equally represented in the 1951 Marquette collection. Other age groups were sparsely represented or entirely lacking. The youngest fish were members of the II group (mean percentage contribution, 2.0). The VI group appeared in 18 collections (mean percentage, 1.5) but VII-group fish (the oldest in the samples) were taken only at Duluth in 1959 and at Bayfield in 1958 and 1959. The mean age ranged from 3.5 years in 1954 at Portage Entry to 4.4 years at Duluth in 1959. The mean ages of the combined years' collections from the several ports differed little—4.1 years at Duluth and 3.9 years at Bayfield, Portage Entry,

and Marquette. The average age of fish taken in the 1950–55 period of relatively slow growth differed little from that of the faster growing fish captured in 1956–59.

The records of age composition according to sex (table 9) show a higher percentage contribution for females than for males in all age groups above III (exceptions were the VII group at Duluth and the IV group at Marquette). The differences in percentage contribution of the sexes were greatest at Duluth; the percentage of males in the III group was twice that of the females, and the percentage of females was slightly larger than that of the males in age group IV. The percentage of females was twice that of males in age group V and nearly four times in the VI group.

TABLE 9.—Age composition of Lake Superior lake herring according to sex and port, 1950–59

Port and sex	Number of fish	Percentage in age group						Average age
		II	III	IV	V	VI	VII	
Duluth:								
Males	135	6.7	33.3	42.3	14.8	2.2	0.7	Years 3.8
Females	190		16.3	44.8	30.5	7.9	0.5	4.3
Bayfield:								
Males	452	2.9	26.5	55.5	14.2	0.9		3.8
Females	600	0.7	17.5	62.2	17.8	1.5	0.3	4.0
Portage Entry:								
Males	584	3.1	30.7	50.3	15.4	0.5		3.8
Females	708	1.0	23.4	57.0	17.9	0.7		3.9
Marquette:								
Males	701	2.1	27.5	52.2	17.3	0.9		3.9
Females	409	2.9	23.2	50.6	19.3	2.0		3.9

With few exceptions the average age of the females exceeded that of the males in each of the collections (table 10). The difference between the mean ages of the sexes among the combined collections from each port ranged from nil at Marquette to 0.5 year at Duluth.

TABLE 10.—Average age of Lake Superior lake herring according to port, year of capture, and sex

Year of capture	Duluth		Bayfield		Portage Entry		Marquette	
	Males	Females	Males	Females	Males	Females	Males	Females
1950			3.6	3.6	3.8	3.7	3.8	4.1
1951			3.8	3.9	4.0	4.3	4.0	4.1
1952			4.3	4.0	3.8	4.1	4.1	4.0
1953					3.5	3.7	3.8	3.7
1954			3.9	4.1	3.4	3.9	4.0	4.0
1955					4.1	4.3	4.1	4.3
1956			4.0	4.7	3.5	3.7	3.8	4.0
1957	4.0	4.2	3.5	3.9	3.8	3.9	3.6	3.9
1958	3.5	4.0	3.8	4.6	4.2	4.1	3.7	3.7
1959	3.9	4.7	3.7	4.3	3.9	4.2	3.7	4.1
All years	3.8	4.3	3.8	4.0	3.8	3.9	3.9	3.9

YEAR-CLASS STRENGTH

Fluctuations in the strength of year classes of fish have been the subject of extensive research since Hjort (1914) demonstrated the significance of year-class abundance in the fluctuations of productivity of major marine fisheries. The literature in this field is so widely known and has been summarized so frequently that a review of it would not be appropriate in this paper. Even a listing of studies of year classes in the Great Lakes is not required in view of El-Zarka's (1959) broad coverage of the subject.

The evaluation of the relative strength of year classes usually has been based on data on the percentage age composition of samples in a series of years. On occasion, the records have permitted only the identification of certain year classes of unusual strength or weakness (Van Oosten and Hile, 1949—Lake Erie whitefish; Jobes, 1952—Lake Erie yellow perch). In other circumstances it has been possible to arrange year classes ordinarily (Hile, 1941—Nebish Lake rock bass) or from a series of comparisons to set up a system of "ranks" (Hile, 1954—Saginaw Bay walleye). El-Zarka (1959—Saginaw Bay yellow perch) attempted to improve the precision of estimates of year-class strength by subjecting his data on percentage age composition to an analysis of year-to-year change similar to the one used by Hile (1941) for the study of annual fluctuations of growth rate.

Instructive as these uses of data on age composition may be, much more effective judgments can be made of the strength of year classes if catch-effort data are available on the fishery from which samples were obtained. Records of catch per unit of fishing effort make it possible to estimate the availability of each age group in terms of numbers of fish. The study of fluctuations in the strength of year classes of lake herring in Lake Superior accordingly has been based on the application of age-composition data for spawning-run samples to statistics on the catch (in pounds) per 1,000 linear feet of small-mesh gill nets during the spawning months of November and December. The procedures followed are similar to those employed by Pycha (1961) in his study of the year classes of walleye in northern Green Bay, Lake Michigan. El-Zarka (1959) had recognized the value of this approach but

was unable to use it because of the small numbers of legal-sized fish in certain of his samples.

The application of data on age composition to statistics on catch per unit effort is illustrated best by a hypothetical example. Let it be assumed that a sample containing 223 lake herring weighed 69.1 pounds and that the catch of lake herring of the same port in the same year was 341 pounds per 1,000 feet of gill net lifted in November and December. It is then computed that 1,000 feet of commercial nets took $341/69.1=4.935$ times as many lake herring as were in the sample. Numbers per unit effort for individual age groups are then calculated by multiplying the number in the age group by the ratio 4.935; for example, an age group that contributed 43 fish to the sample was produced in the commercial fishery at the rate of $43 \times 4.935=189$ individuals per 1,000 feet of net. It was by this procedure that the records of table 11 were obtained. Data are given only for age groups III, IV, and V since other age groups were poorly represented or lacking in the samples.

Numbers of fish caught per unit effort were estimated for certain age groups as indicated by footnote in table 11. All figures for the III groups of the 1946 year class and the V groups of the 1955 year class were estimated; at Bayfield, additional estimates were needed to fill gaps created by the lack of collections in 1953 and 1955. These estimations required first the determination of the ratios of the average numbers of fish in different age groups from all available samples at a port; the appropriate ratios were then applied to available data on year classes to obtain estimates for missing data. The actual computation for age group III of the 1946 year class at Bayfield illustrates the procedure. From all available Bayfield samples it was determined that the average number of lake herring in age group III amounted to 0.378 times the average number in age group IV and 1.317 times the average number in age group V. The following two estimates then were made of the number per unit effort for the missing III group of the 1946 year class; $0.378 \times 799=302$; $1.317 \times 265=349$. The mean of the two estimates, 326, was entered in table 11. All other estimates were obtained similarly.

The relations among the successive samples of the same year class off a port varied widely in samples from all three ports (table 11). The

TABLE 11.—Numbers of lake herring caught per lift of 1,000 linear feet of small-mesh gill nets by year class and age group, off three Lake Superior ports

[Based on samples from commercial landings during the spawning season and on catch-effort statistics for November and December]

Port and age group	Year class										Average
	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	
Bayfield:											
III.....	1 328	495	545	351	1 317	212	1 224	252	206	240	317
IV.....	799	1,245	1,008	1 816	839	1 926	908	675	368	478	806
V.....	265	409	1 352	203	1 241	371	80	274	198	1 160	255
Total.....	1,390	2,149	1,905	1,370	1,397	1,509	1,212	1,201	772	878	1,378
Portage Entry:											
III.....	1 280	147	202	208	392	594	231	340	209	146	275
IV.....	290	607	549	533	637	502	534	547	265	301	477
V.....	247	226	33	38	393	55	137	243	155	1 94	162
Total.....	817	980	784	779	1,422	1,151	902	1,130	629	541	914
Marquette:											
III.....	1 199	142	143	201	250	83	124	128	135	139	154
IV.....	406	430	517	344	246	242	210	259	229	191	308
V.....	143	230	54	88	204	103	44	45	86	1 84	108
Total.....	748	802	714	633	700	428	378	432	450	414	570

1 Estimated by procedure explained in text.

records for the year classes in the Portage Entry samples illustrate this variability. The strongest year class (1950) and the third strongest (1953) held their ranks by reason of catches well above the 10-year average (given in right-hand column of table 11) at all three ages; similarly, the weakest year class (1955) yielded catches well below average as the III group and the IV group (V group estimated), and the next to the weakest (1954) was taken in below-average numbers at all three ages (though near average as age group V). The next to strongest year class (1951), on the contrary, held that position because of tremendous numbers caught as age group III (over twice the mean of 275); its representation was only moderately above average as age group IV and was extremely low as age group V. The 1947 year class held a rank above average only because of a strong upward trend of the catches; the numbers were far below average as age group III, above average as age group IV, and highest (relatively) as age group V. The catches of the remaining year classes from Portage Entry can be described best as variable but without clear trend. Two examples should illustrate the situation. The 1947 year class was weakly represented as age group III, but catches as age groups IV and V were sufficient to bring the total above average. In the 1952 year class, the poor catches as age groups III and V were counterbalanced by the good catch as age group IV to bring the total near the mean.

Numerous causes can be advanced for the discrepancies among successive samples of certain year classes, but no clear demonstration or evaluation can be offered for any of them. Random error unquestionably played a role because none of the annual samples was truly large and some were undesirably small (table 1). Major sources of bias were weather, nature of previous fishing on the year class, and changes of gear specifications.

The shortness of the spawning season in late November and early December makes the success of fishing highly sensitive to weather. Near the height of spawning, a storm that is severe enough to damage gear and disperse the schools depresses the catch per unit effort and causes underestimates of the strength of year classes represented in the year's sample. Conversely, exceptionally calm, favorable weather can make the catch per unit effort higher than normal. Should the weather, by mischance, cause the catch per unit effort to be abnormally high or low in 2 or all of the 3 years in which a year class is present in numbers, a severe misjudgment must result. It was not possible to relate weather conditions to the behavior of estimates of year-class strength at successive ages. Storms cannot be classified satisfactorily as to the expected effect on catch per unit effort, and furthermore the effects of a single storm are not uniform for all gear in an area. It is only to be hoped that biases from weather conditions were not cumulative for many year classes and that for most they were compensatory.

Intensity of fishing or fishing conditions that influence the vulnerability of a year class in its first year or years of exploitation can influence later estimates of its strength. If, for example, a year class is highly vulnerable to the nets and fished heavily as age group III, the original numbers may be so reduced that catches as age groups IV and V are relatively low. If both age groups III and IV are removed in large numbers, the return per unit effort as the V group may be extremely small. Low vulnerability and low removal at the earlier ages should have the reverse influence. Effects of earlier fishing against year classes may well have contributed to the discrepancies among age groups and to the upward or downward trends described for the Portage Entry samples and present in those from the other two ports.

As was pointed out in the section on materials and methods, many fishermen increased the mesh size of lake herring gill nets during the years of sampling. A second change of gear was the gradual conversion from cotton to nylon twine. The change of mesh size was an adjustment to the increase in the mean size of the lake herring and tended to maintain the capacity of the gear to take fish in constant relation to the true abundance of lake herring on the grounds. Fishermen who did not increase mesh size as fish size increased probably lowered the relative efficiency of their nets. The conversion from cotton to nylon almost certainly increased the catching power of the nets. It is not possible, however, to offer quantitative estimates of the effects of either the increases of mesh size or the change in netting material.

Other possible sources of bias to the samples could be stated but the chance that any of them were significant is too small to justify even a listing.

Even though the discrepancies that appear in the data for certain year classes at each port can be explained logically, the explanations do not weaken the necessary conclusion that certain of the estimates of year-class strength are less precise than might be wished. The method which appears least biased for judging the strength of each year class is one based on the number of fish caught per unit of effort for the three age groups combined.

The apparent strength of the year classes (see year-class totals of table 11) varied considerably but not excessively at each port. The richest year class at Bayfield (1947—2,149 fish at three

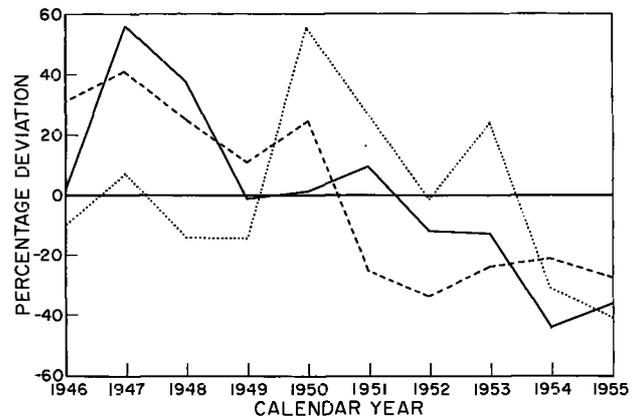


FIGURE 4.—Fluctuations in the relative strength of the year-classes 1946–55 of lake herring from Bayfield (solid line); Portage Entry (dotted line); and Marquette (dashes).

ages) was 2.78 times as strong as the weakest (1954—772 fish). The strongest year class at Portage Entry (1950) yielded catches that were 2.63 times those of the weakest (1955), and at Marquette the catches of the 1947 year class were 2.12 times those of the 1952 year class. These 2.12- to 2.78-fold fluctuations may appear substantial but they are trivial in comparison with the 88.5-fold fluctuation of year-class strength determined by Pycha (1961) for the Green Bay walleye.

The year-to-year fluctuations of year-class strength at each port are grasped best from the data of table 12 (see also fig. 4) in which each year-class total of table 11 is expressed as a percentage deviation from the mean for the 10 year classes. It is obvious at once that fluctuations at Bayfield and Marquette had many

TABLE 12.—Fluctuations of year-class strength of lake herring off three Lake Superior ports

[Percentage deviations computed from year-class totals of table 11]

Year class	Percentage deviation from average for port		
	Bayfield	Portage Entry	Marquette
1946	0.8	-10.6	31.3
1947	55.9	7.3	40.7
1948	38.2	-14.2	25.3
1949	-6	-14.7	11.1
1950	1.4	55.7	22.8
1951	9.5	26.0	-24.9
1952	-12.1	-1.3	-33.7
1953	-12.8	23.7	-24.2
1954	-44.0	-31.1	-21.0
1955	-36.3	-40.8	-27.4

similarities but exhibited only limited agreement with those off Portage Entry.

The deviations from average at Bayfield and Marquette were on the same side of the average for 8 of 10 year classes. Year classes off the two ports agreed particularly well in 1947 (the best year class at each port) and 1948 when year classes were strong and in 1952-55 when all four year classes were decidedly below average. Agreement was poor in 1946, 1949, and 1950 which produced year classes near average at Bayfield and above average at Marquette; the 1951 year class produced the worst disagreement—9.5 percent above average at Bayfield and 24.9 percent below at Marquette.

The closeness of the agreement between year-class fluctuations at Bayfield and Marquette is brought out by the coefficient of correlation ($r=0.726$) between the deviations from average. This value of the coefficient is significant at the 2-percent probability level ($r=0.716$ at $p=0.02$; $df=8$).

The data for Portage Entry agreed clearly with those for Bayfield and Marquette in 1954 and 1955 when the year classes were decidedly weak off all three ports but showed most limited agreement in other years.

Data for Bayfield and Portage Entry agreed in some measure in 1947 and 1951 when year classes were above average at both ports. Year classes of 1946, 1949, 1950, and 1952 were near average at one of the two ports but departed from average by at least 10.6 percent and as

much as 55.7 percent at the other. Major disagreements between Bayfield and Portage Entry were provided by the year classes of 1948 and 1953.

The only consequential agreement between records for Portage Entry and Marquette, aside from the previously mentioned 1954 and 1955 year classes, was provided by the year classes of 1947 and 1950. The agreement for 1952 was unimportant, and disagreements were major for the year classes of 1946, 1948, 1949, 1951, and 1953.

No attempt has been made yet to inquire into the factors of year-class fluctuation in Lake Superior stocks of lake herring or into the reasons for the broad similarities of these fluctuations at Bayfield and Marquette and the apparently independent fluctuations at Portage Entry. A longer series of data is needed.

SIZE AT CAPTURE

LENGTH AND WEIGHT OF THE AGE GROUPS

Data on length and weight of the age groups (table 13) provide comparisons by sex, port, and two periods of capture (1950-55 and 1956-59). The females were longer than the males in 20 of 24 comparisons at Duluth, Bayfield, and Portage Entry, and the males held an advantage (7 of 10 comparisons) at Marquette. Among the best represented age groups (III-V), sex differences in average length were small. The largest advantage for the females was 0.6 inch (V groups in the Duluth collections); the largest for the males was 0.2 inch at Marquette (III group in the 1950-55 and the IV group in the 1956-59 samples)

TABLE 13.—Average total lengths and weights of the age groups of male and female lake herring according to port and period of capture

Age group and sex	Duluth		Bayfield				Portage Entry				Marquette			
	1957-59		1950-54		1956-59		1950-55		1956-59		1950-55		1956-59	
	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight
II: Males.....	Inches 11.3	Ounces 6.3			Inches 11.7	Ounces 7.0	Inches 11.3	Ounces 6.3	Inches 11.9	Ounces 7.4	Inches 11.7	Ounces 7.0	Inches 12.6	Ounces 8.8
Females.....					Inches 11.8	Ounces 7.2	Inches 11.5	Ounces 6.7	Inches 12.0	Ounces 7.6	Inches 11.3	Ounces 6.3	Inches 12.3	Ounces 8.2
III: Males.....	11.3	6.3	11.0	5.8	11.8	7.2	11.4	6.5	12.0	7.6	11.7	7.0	12.7	9.0
Females.....	11.9	7.4	11.3	6.3	11.9	7.4	11.5	6.7	12.0	7.6	11.9	7.4	12.7	9.0
IV: Males.....	11.9	7.4	11.1	6.0	11.8	7.2	11.4	6.5	12.1	7.8	11.9	7.4	12.9	9.6
Females.....	12.1	7.8	11.5	6.7	12.2	8.0	11.8	7.2	12.3	8.2	12.0	7.6	12.7	9.0
V: Males.....	11.6	6.8	11.5	6.7	11.9	7.4	11.5	6.7	12.6	8.8	12.2	8.0	12.9	9.6
Females.....	12.2	8.0	11.8	7.2	12.4	8.4	11.8	7.2	12.7	9.0	12.1	7.8	12.8	9.8
VI: Males.....	12.3	8.2	12.8	9.3	12.8	9.3	11.1	6.0	11.6	6.8	12.8	9.3	14.0	12.3
Females.....	12.8	9.3	12.5	8.6	12.7	9.0	11.6	6.8	12.8	9.3	11.7	7.0	13.2	10.3
VII: Males.....	15.6	17.2												
Females.....	12.4	8.4			12.8	9.3								

It is difficult, if not impossible, to distinguish possible true sex differences in the growth of Lake Superior lake herring from the effect of bias from segregation by size and maturity and the resulting selective action of the fishery on the population. Since male lake herring mature at a slightly younger age than do females, a substantially larger percentage of males than females were represented in age groups II and III at all ports except Marquette (table 9). The intensive lake herring fishery at the ports west of Marquette selectively destroyed these early-maturing, fast-growing males in the younger age groups, leaving the slower growing, late-maturing members of the sex to represent the older age groups. This phenomenon may well lead to low estimates of size for males in the older age groups. Since the lake herring from Marquette grew faster than those from the other ports, proportionately larger numbers of mature females were represented in the younger age groups. The sex ratio, therefore, was more nearly equal in age groups II and III and the fishery which has never been intensive at Marquette, was not particularly selective toward the males.

A detailed discussion of table 13 is not desirable as more discriminating information is given in the section on calculated growth. Most of the lake herring, regardless of age, fell within the 11- to 13-inch range and weighed 6 to 10 ounces. The small difference in size among the age groups is surely a result of the highly selective gill nets, segregation by maturity, and of selective fishing mortality.

With only one exception (that of the VI-group males in the 1956-59 Bayfield collections), the average size of the age groups was larger in 1956-59 than in 1950-55. Among the best represented age groups (III-V), the increase in length from the early to the late period ranged from 0.4 inch to 1.1 inches (11.5 to 11.9 inches for the V-group males at Bayfield and 11.5 to 12.6 inches for the V-group males at Portage Entry). In general, the average size of the lake herring increased from the western to the eastern part of the lake. Lake herring of age groups III-V from the 1956-59 Marquette collections were 0.6 to 1.4 inches longer and 1.3 to 2.7 ounces heavier than fish of the same age from Duluth.

LENGTH DISTRIBUTION OF THE SAMPLES

The length-frequency records for the samples (table 14), by port and period of capture, indicate

generally compact distributions. The range in length from the shortest to the longest fish was greatest (6.9 inches) in the Duluth samples and smallest (3.9 inches) in the 1950-55 Portage Entry collections. The Duluth samples were represented by both the shortest (9.0 inches) and the longest (15.9 inches) fish taken in all of the collections.

TABLE 14.—Length distribution of Lake Superior lake herring according to port for the periods 1950-55 and 1956-59

[Asterisks indicate modes]

Total length	Duluth	Bayfield		Portage Entry		Marquette	
	1957-59	1950-54 ¹	1956-59	1950-55	1956-59	1950-55	1956-59
<i>Inches</i>							
9.0-9.4	1						
9.5-9.9	4	3					
10.0-10.4	12	21	1	5	1	1	5
10.5-10.9	13	106	18	61	13	2	5
11.0-11.4	43	*198	58	180	60	15	11
11.5-11.9	61	180	155	*235	183	91	46
12.0-12.4	*114	53	*167	102	*201	143	116
12.5-12.9	55	17	89	11	139	*195	*148
13.0-13.4	19	6	21	2	66	91	141
13.5-13.9	1	1	6	1	24	13	71
14.0-14.4	1		1		7	3	12
14.5-14.9						2	2
15.0-15.4							
15.5-15.9	1				1		2
Number of fish	325	535	516	597	695	556	554
Average length	11.9	11.3	12.0	11.6	12.2	11.9	12.8
Percentage over 11.9 inches	58.8	14.4	55.0	19.4	68.0	80.4	88.8

¹ Samples were not collected in 1953 and 1955.

The length composition clearly changed from 1950-55 to 1956-59 at two of the three ports. From the earlier to the later period, the modal length increased 1.0 inch at Bayfield (from 11.0-11.4 to 12.0-12.4 inches) and 0.5 inch at Portage Entry (11.5-11.9 to 12.0-12.4 inches). The mean length increased 0.7 inch (from 11.3 to 12.0 inches) at Bayfield and 0.6 inch (11.6 to 12.2 inches) at Portage Entry. The mode at Marquette (12.5-12.9 inches) was the same for the two periods but the mean length increased 0.7 inch (11.9 to 12.8 inches). Port-to-port differences of modal length were greatest in the 1950-55 samples; the mode was 11.0-11.4 inches at Bayfield, 11.5-11.9 inches at Portage Entry, and 12.5-12.9 inches at Marquette. The average lengths increased from 11.3 inches at Bayfield to 11.6 at Portage Entry and 11.9 at Marquette.

The percentage of fish longer than 11.9 inches varied with differences in modal and mean lengths. The percentage of lake herring 12.0 inches long or longer in the 1950-55 collections was 14.4 at Bayfield, 19.4 at Portage Entry, and 80.4 at

Marquette. The percentages were higher in 1956-59 at all ports—58.5 percent at Duluth (no earlier data), 55.0 percent at Bayfield, 63.0 percent at Portage Entry, and 88.8 percent at Marquette.

LENGTH DISTRIBUTION OF THE AGE GROUPS

The records on the length-frequency distributions of the age groups have been limited to one example, that of the 1957 Marquette collection (table 15). It is not believed that the additional information to be gained would warrant the large expansion of tabular material to show the length distributions of the age groups for each year or period at each port. The 1957 Marquette sample was selected because it illustrates the general characteristics of all the samples.

TABLE 15.—Length distribution of the age groups of Lake Superior lake herring captured at Marquette, 1957

Total length	Age group				
	II	III	IV	V	VI
<i>Inches</i>					
11.0-11.4			1	1	
11.5-11.9	1	3	7		
12.0-12.4	1	14	16	5	1
12.5-12.9	3	16	24	3	
13.0-13.4	2	9	31	4	1
13.5-13.9		4	8	2	
14.0-14.4			1		
14.5-14.9					
15.0-15.4					
15.5-15.9					1
Total	7	46	88	15	3
Average length	12.6	12.7	12.8	12.7	13.6

Typical of the length distributions of the age groups of Lake Superior lake herring are the small ranges of length and the extensive overlap of the age groups. The range in length of the age groups of the 1957 Marquette sample was only 1.9 inches for age group II to 3.9 inches for the VI-group fish. Despite the small range, overlap was extensive. The length interval of 12.0-13.4 inches was represented by all five age groups.

LENGTH-WEIGHT RELATION

GENERAL RELATION

The data on general length-weight relation of the Lake Superior lake herring (table 16) were based on fish from all of the collections regardless of port, year, or season of capture, type of gear, sex, or state of maturity. The length-weight relation does vary according to port and year of capture, and between ripe and fully spent females, but it was held that the best estimate of the general

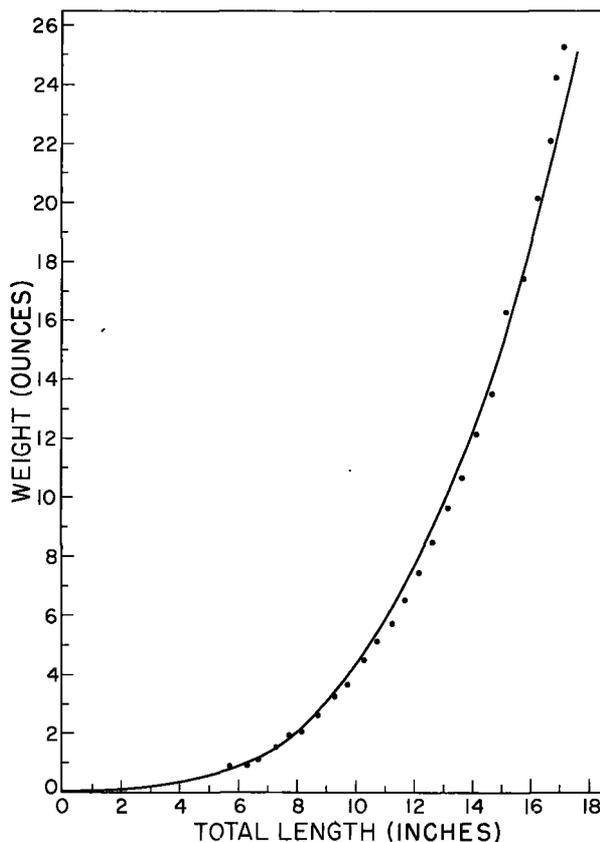


FIGURE 5.—Length-weight relation of Lake Superior lake herring. The curve represents the calculated weights and the dots the empirical weights.

relation is one based on all available fish. The empirical weights at different lengths are given graphically by dots in figure 5. The curve is a graph of the following equation derived by fitting a straight line (by least squares) to the logarithms of the average lengths and weights:

$$\log W = -2.54688 + 3.17008 \log L,$$

where W = weight in ounces
and L = total length in inches.

Although the calculated weights were higher than the empirical weights for fish between 9.2 and 15.2 inches long, the agreement between the empirical and calculated values was acceptable. The largest disagreement was at 17.55 inches where the empirical weight (28.50 ounces) was 3.52 ounces above the calculated weight (24.98 ounces); only 2 fish were weighed, however, at

TABLE 16.—Length-weight relation of Lake Superior lake herring of the combined collections, 1950-59

Number of fish	Total length <i>Inches</i>	Weight	
		Empirical <i>Ounces</i>	Calculated <i>Ounces</i>
12	5.73	0.83	0.72
20	6.27	.97	1.96
11	6.53	1.14	1.14
13	7.24	1.53	1.51
24	7.72	1.86	1.85
20	8.18	2.13	2.22
25	8.70	2.69	2.70
25	9.22	3.26	3.25
29	9.70	3.66	3.81
72	10.28	4.54	4.58
444	10.76	5.11	5.30
1,210	11.23	5.76	6.07
1,890	11.68	6.51	6.87
2,068	12.19	7.42	7.87
1,314	12.68	8.41	8.92
682	13.17	9.66	10.05
294	13.65	10.68	11.26
118	14.17	12.18	12.68
101	14.67	13.56	14.15
72	15.20	16.22	15.84
47	15.68	17.51	17.41
35	16.22	20.74	19.46
23	16.66	22.15	21.18
11	17.18	25.26	23.35
2	17.55	28.50	24.98

this interval. Most disagreements were less than 0.5 ounce.

INCREASE OF WEIGHT FROM 1950-55 TO 1956-61

The annual data on the length-weight relation of Lake Superior lake herring have been combined for 1950-55 and 1956-61. This arbitrary division seems to be best for showing the long-term changes in weight for the 12-year period. Year-to-year differences in 1950-55 were without trend at each of the ports, but weights of fish of the same length showed a definite upward trend from 1956 through 1961. The data of table 17 are based entirely on records of weights of spawning-run male lake herring. Although the weights of the females exhibited trends similar to those of the males, these trends were often obscured by sample differences in the proportions of ripe, partially spent, or spent fish. Weight differences between fully ripe and spent females are considered too severe for the data to be included in this study. Deason and Hile (1947), for example, demonstrated that the loss of weight of the female *C. kiyi* at spawning amounted to 11.8 percent, whereas the loss of weight of males was altogether unimportant (mean percentage loss, 1.6).

The differences of weight in the two collecting periods were strongly consistent. Among comparisons of length intervals represented by 10 or more fish in each period, lake herring captured in 1956-61 were without exception heavier than those of the same length taken in 1950-55 (table 17).

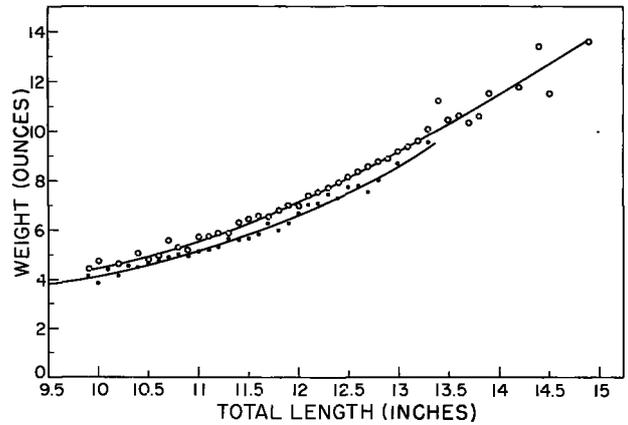


FIGURE 6.—Weights of Bayfield lake herring captured in 1950-54 (solid dots) and in 1956-61 (open dots). The curves were fitted by inspection.

The percentage increase in weight, length for length, ranged from 4.1 to 13.4 at Bayfield (fig. 6). The percentage increases in weight at the other ports ranged from 2.3 to 6.9 at Portage Entry and from 2.7 to 9.7 at Marquette. The average percentage increase in weight was greatest at Bayfield (8.8 percent), followed by Marquette (5.2 percent), and Portage Entry (4.4 percent). When the numbers of fish were small, lake herring caught in 1950-55 occasionally were heavier than those of the same length taken in 1956-61, but even here the 1956-61 fish were heavier in the great majority of the comparisons.

Despite the fact that mesh sizes of the commercial gill nets were frequently larger in 1956-61 than in 1950-55, lake herring of the same length were heavier during the later period regardless of the mesh size of the net from which they were taken.

Port-to-port differences in average weights among fish of the same length in 1950-55 showed a west-to-east trend toward increased weight. Comparisons of weights for length intervals represented by 5 or more fish from each port revealed the Marquette lake herring to be the heaviest in 9 of 14 comparisons, fish from Portage Entry ranked second in 9 of 14 comparisons, and the Bayfield lake herring were lightest in 13 of 14 comparisons. In 1956-61, the Marquette lake herring were heaviest in 7 of 11 comparisons, but port-to-port differences in weight among fish from Duluth, Bayfield, and Portage Entry were small and without trend.

TABLE 17.—Weights of spawning-run male lake herring taken in Lake Superior during 1950–55 and 1956–61

Total length <i>Inches</i>	Duluth		Bayfield				Portage Entry				Marquette			
	1956-60 ¹		1950-54 ²		1956-61		1950-55		1956-61		1950-54 ³		1956-61	
	Number of fish	Average weight <i>Ounces</i>	Number of fish	Average weight <i>Ounces</i>	Number of fish	Average weight <i>Ounces</i>	Number of fish	Average weight <i>Ounces</i>	Number of fish	Average weight <i>Ounces</i>	Number of fish	Average weight <i>Ounces</i>	Number of fish	Average weight <i>Ounces</i>
9.5	1	3.80	1	3.90										
9.6	1	3.90												
9.7	2	4.25												
9.8														
9.9	1	4.50	4	4.15	1	4.40	1	4.0			1	3.89		
10.0			1	3.84	1	4.70					1	4.08		
10.1	3	4.27	3	4.41										
10.2	2	4.35	7	4.19	1	4.60	2	4.53	1	4.70				
10.3	2	4.70	4	4.52			1	4.30			1	4.36		
10.4	7	4.66	11	4.49	2	5.00	4	4.77						
10.5			16	4.70	2	4.75	4	4.79			13	4.78		
10.6	3	5.23	21	4.78	3	4.93	7	4.89			1	4.87		
10.7	2	5.25	34	4.85	4	5.58	16	5.05	3	4.87	8	5.31	1	5.30
10.8	7	5.14	49	4.95	6	5.28	18	5.19	3	5.37	9	5.13	1	5.90
10.9	4	5.38	45	4.97	5	5.16	23	5.26	3	5.27	4	5.62	1	5.50
11.0	7	5.36	48	5.17	8	5.74	32	5.32	8	5.54	11	5.23	1	5.20
11.1	8	5.85	38	5.21	5	5.62	35	5.48	7	5.60	18	5.69	1	6.30
11.2	10	5.70	48	5.36	19	5.81	41	5.66	11	6.05	31	5.76		
11.3	6	6.20	38	5.61	24	5.84	57	5.78	9	5.73	44	5.81	3	6.63
11.4	9	6.14	21	5.64	19	6.22	50	5.91	9	6.11	61	6.02	3	6.63
11.5	13	6.29	23	5.66	23	6.40	55	6.14	5	6.24	77	6.14		
11.6	12	6.41	15	5.89	34	6.51	53	6.18	21	6.47	65	6.13	4	6.42
11.7	8	6.75	10	6.26	22	6.56	64	6.36	28	6.68	80	6.37	5	7.06
11.8	10	6.87	10	5.99	39	6.79	33	6.46	24	6.71	100	6.48	7	8.02
11.9	15	7.09	4	6.28	29	6.93	38	6.70	19	6.88	90	6.77	4	6.86
12.0	13	7.07	5	6.65	34	6.99	54	6.83	21	6.98	123	6.89	13	7.66
12.1	16	7.17	12	7.00	32	7.38	32	7.04	12	7.23	102	7.07	18	7.70
12.2	12	7.08	2	7.02	29	7.43	33	7.09	14	7.42	92	7.26	18	7.63
12.3	9	7.49	5	7.47	21	7.66	18	7.27	12	7.77	72	7.47	19	7.96
12.4	5	7.82	1	7.23	36	7.93	12	7.47	14	7.76	86	7.59	19	7.94
12.5	10	7.98	1	7.72	24	8.10	8	7.46	11	8.06	69	7.71	22	8.08
12.6	9	8.46	2	7.78	27	8.31	4	7.74	11	8.36	69	8.01	24	8.24
12.7	7	8.67	2	7.53	19	8.53	4	7.99	13	8.12	56	8.24	26	8.46
12.8	4	8.15	1	8.01	18	8.77	3	8.25	8	8.35	33	8.32	28	8.59
12.9	5	8.92			11	8.88			5	8.72	27	8.69	24	9.11
13.0	4	8.80	1	8.61	9	9.14	1	8.25	7	9.14	9	8.95	32	9.06
13.1	3	9.30			14	9.34			6	9.43	14	9.09	28	9.48
13.2	2	8.85			7	9.69			5	9.84	7	9.16	28	9.56
13.3	3	9.27	1	9.52	4	10.08			3	10.13	3	9.71	26	9.69
13.4	1	7.20			1	11.20			5	9.62	4	9.52	24	10.05
13.5					6	10.37			1	10.20	2	10.14	24	10.14
13.6	4	9.65			2	10.58	1	11.57	10	10.25			26	10.06
13.7					4	10.30			3	10.27	1	12.35	11	10.54
13.8					1	10.60			2	10.45	1	10.51	12	10.90
13.9					1	11.50			1	11.50	1	11.61	11	10.87
14.0									2	10.75			9	10.67
14.1									3	11.10	1	9.88	3	11.23
14.2					1	11.80							4	13.12
14.3											1	12.70	3	11.60
14.4					1	13.40			1	13.80			3	12.53
14.5					1	11.50			1	11.30			3	11.67
14.6													1	13.10
14.7													3	12.67
14.8													1	14.50
14.9					2	13.60					1	16.58		
15.5													1	17.99
15.8											1	17.81	1	15.40

¹ Samples were not collected in 1961. ² Samples were not collected in 1953 and 1955. ³ Appropriate samples were not available for 1955.

CALCULATED GROWTH GROWTH IN LENGTH

The growth rate of the Lake Superior lake herring varied considerably but in general tended to be faster in the later collections. A division in the data accordingly was made to separate a period of relatively slow growth (1950–55) from a period of more rapid growth (1956–59). A detailed discussion of annual fluctuations in growth is presented in a later section.

The calculated lengths of the sexes (data not given here) revealed slightly higher values for the females at Duluth, Bayfield, and Portage Entry, and greater lengths for the males at Marquette. The differences were small, never exceeding 0.6 inch. True sex differences in growth rate have been observed in only one stock of lake herring, that of Clear Lake in northeastern Wisconsin, where Hile (1936) demonstrated that the calculated lengths of the females were up to 0.3 inch longer than those of the males.

TABLE 18.—Calculated total length of lake herring taken at Duluth in 1957–59

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	8
II.....	9	Inches 4.8	Inches 8.5	Inches 11.3	Inches 11.5	Inches 12.0	Inches 12.0	Inches 12.7	Inches 14.0
III.....	76	4.8	7.4	9.9	10.7	11.1	12.0	12.7	14.0
IV.....	142	4.2	6.8	8.9	9.8	10.9	11.9	12.7	14.0
V.....	78	3.9	6.3	8.1	9.7	10.8	12.3	13.3	14.0
VI.....	18	4.1	6.5	8.2	9.6	10.8	12.3	13.3	14.0
VII.....	2	3.9	6.6	8.3	9.6	10.8	12.3	13.3	14.0
Grand average ²		4.3	6.8	9.0	10.6	11.6	12.5	13.3	14.0
Number of fish.....		325	325	325	316	240	98	20	2

¹ Average length at capture following completion of current-season growth.
² Based on the successive addition of mean increments beyond the fifth year of life.

Since it appears impossible to distinguish true sex differences in growth of Lake Superior lake herring from the effect of bias through the selective action of the fishery on a population segregated by maturity, the sexes have been combined for the study of calculated growth.

The major difficulties in the estimation of growth of Lake Superior lake herring arise from the systematic decline in calculated growth rate with an increase in age. These discrepancies were similar in the data for all of the collections at each port (tables 18 through 24). The situation is described best by a few examples. First-year calculated lengths of lake herring from Duluth decreased from 4.8 inches for the II group to 3.9 inches for age group V (table 18); at Bayfield, the decrease was from 5.6 inches for the II group to 4.3 inches for the VI group in the 1956–59 collections (table 20). Second-year calculated lengths decreased from 9.6 inches (II group) to 5.7 inches (VI group) in the 1956–59 Portage Entry samples (table 22)

TABLE 19.—Calculated total length of lake herring taken at Bayfield in 1950–54¹

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
III.....	129	Inches 4.8	Inches 7.6	Inches 9.4	Inches 11.2	Inches 11.3	Inches 11.7	Inches 12.6
IV.....	328	4.5	7.0	8.7	10.4	11.0	11.7	12.6
V.....	74	4.4	6.7	8.4	9.8	10.8	11.8	12.6
VI.....	5	4.5	6.7	8.4	9.7	10.8	11.8	12.6
Grand average ²		4.6	7.1	8.8	10.5	11.2	11.9	12.7
Number of fish.....		536	536	536	536	407	79	5

¹ Samples were not collected in 1953.
² Average length at capture following completion of current-season growth.
³ Based on the successive addition of mean increments beyond the fifth year of life.

and from 9.8 inches for age group II to 6.5 inches for age-group VI in the 1956–59 Marquette collections (table 24). A detailed review of the comments of other investigators on this kind of disagreement is not considered necessary here since systematic discrepancies of this type have been observed repeatedly among the lake herring and other species and have been discussed at length in the literature. Most investigators agree that the high calculated lengths of the younger age groups and the low values for the older fish can be traced to two major sources of bias: gear selection of the larger fish in the younger age groups and the progressive destruction of the faster growing fish by the fishery. These sources of bias, combined with segregation by maturity of the spawning-run samples, undoubtedly account for the discrepancies among the calculated growth histories of Lake Superior lake herring.

The two major sources of bias to estimates of growth are to some degree compensating. The best estimates of general growth are held, therefore, to be those based on records from all the fish from each of the spawning-run collections. Fish collected by the *Siscowet* and from the summer commercial fishery have been omitted from the study to permit comparisons among the spawning-run collections at the various ports.

The extent of the variation of growth of Lake Superior lake herring according to port and period of capture is seen best from the summary in table 25. The fish from Bayfield were the slowest growing in the 1950–55 samples, and those from Marquette had the fastest growth (fig. 7). Portage Entry lake herring grew faster than the Bayfield fish but more slowly than those from Marquette. First-year calculated lengths ranged from

TABLE 20.—Calculated total length of lake herring taken at Bayfield in 1958-59

Age group	Number of fish	Calculated length at end of year of life							
		1	2	3	4	5	6	7	8
II	17	Inches 5.6	Inches 9.2	Inches 11.7	Inches	Inches	Inches	Inches	Inches
III	96	4.9	7.8	10.2	11.8				
IV	296	4.7	7.4	9.2	10.9	12.0			
V	97	4.6	6.9	8.6	10.1	11.3	12.2		
VI	6	4.3	6.6	8.4	9.8	11.0	11.8	12.7	
VII	2	4.8	6.4	7.8	9.0	10.2	11.3	12.3	12.8
Grand average ²		4.7	7.4	9.4	10.9	11.8	12.7	13.6	14.1
Number of fish		514	514	514	497	401	105	8	(2)

¹ Average length at capture following completion of current-season growth.
² Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 21.—Calculated total length of lake herring taken at Portage Entry, 1950-55

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
II	9	Inches 5.6	Inches 8.7	Inches 11.4	Inches	Inches	Inches	Inches
III	167	5.0	7.6	9.8	11.4			
IV	322	4.8	7.2	9.0	10.6	11.6		
V	94	4.6	6.7	8.3	9.9	10.9	11.7	
VI	5	4.3	5.7	6.9	8.3	9.8	10.7	11.4
Grand average ²		4.8	7.2	9.1	10.7	11.4	12.2	12.9
Number of fish		597	597	597	588	421	99	5

¹ Average length at capture following completion of current-season growth.
² Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 22.—Calculated total length of lake herring taken at Portage Entry, 1956-59

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
II	16	Inches 5.6	Inches 9.6	Inches 11.9	Inches	Inches	Inches	Inches
III	178	4.9	7.9	10.2	12.0			
IV	375	4.6	7.2	9.1	11.0	12.2		
V	123	4.6	6.8	8.6	10.4	11.7	12.7	
VI	3	3.5	5.7	7.2	8.9	10.6	11.8	12.2
Grand average ²		4.7	7.4	9.4	11.1	12.1	13.1	13.5
Number of fish		695	695	695	679	501	126	3

¹ Average length at capture following completion of current-season growth.
² Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 23.—Calculated total length of lake herring taken at Marquette 1950-55

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
II	5	Inches 5.5	Inches 9.6	Inches 11.6	Inches	Inches	Inches	Inches
III	129	5.1	8.0	10.2	11.8			
IV	302	4.7	7.5	9.4	10.9	11.9		
V	115	4.5	7.2	8.8	10.3	11.4	12.2	
VI	5	4.4	6.8	8.5	9.9	10.9	11.9	12.6
Grand average ²		4.8	7.6	9.5	11.0	11.8	12.6	13.3
Number of fish		556	556	556	551	422	120	5

¹ Average length at capture following completion of current-season growth.
² Based on the successive addition of mean increments beyond the fifth year of life.

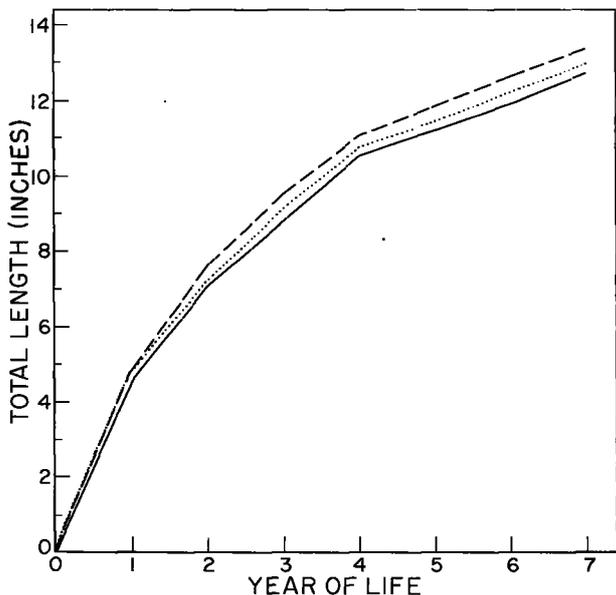


FIGURE 7.—General growth of Lake Superior lake herring of the 1950-55 collections from Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

4.6 inches at Bayfield to 4.8 inches at Portage Entry and Marquette. At the end of 4 years of life the calculated lengths were 10.5 inches at Bayfield, 10.7 inches at Portage Entry, and 11.0 inches at Marquette. Sixth-year calculated lengths were 11.9 inches at Bayfield, 12.2 inches at Portage Entry, and 12.6 inches at Marquette.

TABLE 24.—Calculated total length of lake herring taken at Marquette, 1956–59

Age group	Number of fish	Calculated length at end of year of life						
		1	2	3	4	5	6	7
II.....	22	5.3	9.8	12.5				
III.....	187	5.5	8.6	10.9	12.7			
IV.....	271	4.8	7.6	9.7	11.5	12.8		
V.....	85	4.6	7.2	8.9	10.6	11.8	12.8	
VI.....	9	4.5	6.5	8.1	9.9	11.2	12.3	13.4
Grand average ¹		5.0	7.9	10.0	11.7	12.5	13.5	14.6
Number of fish.....		554	554	554	532	365	94	9

¹ Average length at capture following completion of current-season growth.
² Based on the successive addition of mean increments beyond the fifth year of life.

TABLE 25.—Calculated total length¹ of Lake Superior lake herring according to port for the years 1950–55 and 1956–59

Year of life	Duluth	Bayfield		Portage Entry		Marquette	
	1957–59	1950–54 ²	1956–59	1950–55	1956–59	1950–55	1956–59
1.....	4.3	4.6	4.7	4.8	4.7	4.8	5.0
2.....	6.8	7.1	7.4	7.2	7.4	7.6	7.9
3.....	9.0	8.8	9.4	9.1	9.4	9.5	10.0
4.....	10.6	10.5	10.9	10.7	11.1	11.0	11.7
5.....	11.6	11.2	11.8	11.4	12.1	11.8	12.5
6.....	12.5	11.9	12.7	12.2	13.1	12.6	13.5
7.....	13.3	12.7	13.6	12.9	13.5	13.3	14.6
8.....	14.0		14.1				

¹ Calculated lengths beyond the fifth year of life are based on the successive addition of mean increments.
² Samples were not collected in 1953 and 1955.

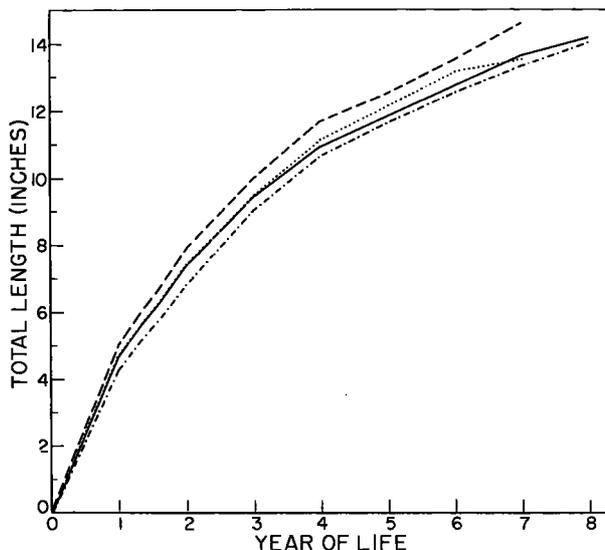


FIGURE 8.—General growth in length of Lake Superior lake herring of the 1956–59 collections from Duluth (dots and dashes), Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

Growth in 1956–59 also increased from the western to eastern ports (fig. 8). The lake herring from Duluth grew 4.3 inches in the first year, those from Bayfield and Portage Entry grew 4.7 inches, and the Marquette fish grew 5.0 inches. In the fourth year of life the calculated lengths of lake herring were 10.6 inches at Duluth, 10.9 inches at Bayfield, 11.1 inches at Portage Entry, and 11.7 inches at Marquette. At the end of 6 years of life the calculated lengths were 12.5 inches at Duluth, 12.7 inches at Bayfield, 13.1 inches at Portage Entry, and 13.5 inches at Marquette.

Dryer (1963) found a similar west-to-east change in the growth of whitefish of Lake Superior. The slowest growing stocks were those from Bayfield; the growth rate increased to the east where the fastest growing fish were from Whitefish Bay. Smith (1956) observed that lake herring from northern Green Bay grew less in their first year than did those from southern Green Bay but grew faster than the southern fish in subsequent years. By the end of the fourth year the differences in size had largely disappeared.

With only one exception (that of the first-year calculated length of the Portage Entry fish) the calculated lengths of lake herring taken at all ports in 1956–59 were greater than those of the 1950–55 collections (fig. 9). The fish taken in the later period at Bayfield were 0.1 inch longer in the first year, 0.6 inch longer in the third, and 0.8 inch longer in the sixth year of life. At Portage Entry the first-year calculated length (4.7 inches) of the 1956–59 fish was 0.1 inch less than that of the 1950–55 samples, but beginning in the second year of life the calculated lengths of the fish taken in the later period were without exception the longer (the largest difference was 0.9 inch in the sixth year of life). Lake herring taken in the later period at Marquette ranged from 0.2 inch longer in the first to 1.3 inches longer in the seventh year of life.

GROWTH IN WEIGHT

The weights in table 26 were computed from the general length-weight equation given on page 509 and correspond exactly with the lengths of table 25. Questions relating to the reliability of the calculated lengths apply, therefore, to the calculated weights.

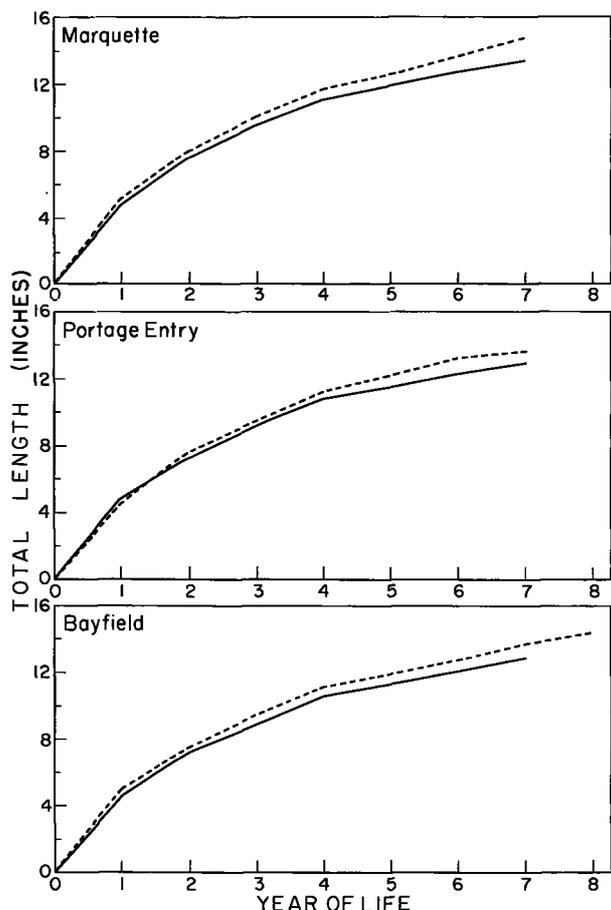


FIGURE 9.—General growth in length of Lake Superior lake herring from Bayfield, Portage Entry, and Marquette. Growth in 1950-55, solid line; in 1956-59, broken line.

TABLE 26.—Calculated weight of Lake Superior lake herring according to port for the years 1950-55 and 1956-59

[Weights were computed from the calculated lengths of table 25 by means of the general length-weight equation. Increments in parentheses.]

Year of life	Duluth		Bayfield		Portage Entry		Marquette	
	1957-59	1950-54 ¹	1956-59	1950-55	1956-59	1950-55	1956-59	
1.....	Ounces 0.40 (0.40)	Ounces 0.43 (0.43)	Ounces 0.52 (0.52)	Ounces 0.58 (0.58)	Ounces 0.52 (0.52)	Ounces 0.58 (0.58)	Ounces 0.60 (0.60)	
2.....	1.22 (0.82)	1.40 (0.97)	1.60 (1.08)	1.43 (0.85)	1.60 (1.08)	1.78 (1.20)	2.00 (1.40)	
3.....	3.04 (1.82)	2.82 (1.42)	3.58 (1.98)	3.18 (1.75)	3.58 (1.98)	3.64 (1.88)	4.33 (2.33)	
4.....	5.20 (2.16)	5.05 (2.23)	5.68 (2.10)	5.30 (2.12)	6.00 (2.42)	5.80 (2.16)	7.02 (2.69)	
5.....	6.84 (1.64)	6.16 (1.11)	7.20 (1.52)	6.49 (1.19)	7.80 (1.80)	7.20 (1.40)	8.61 (1.59)	
6.....	8.61 (1.77)	7.40 (1.24)	9.10 (1.90)	8.00 (1.51)	10.10 (2.30)	8.84 (1.64)	11.10 (2.49)	
7.....	10.60 (1.99)	9.10 (1.70)	11.37 (2.27)	9.60 (1.60)	11.10 (1.00)	10.60 (1.76)	13.98 (2.88)	
8.....	12.38 (1.78)		12.69 (1.32)					

¹ Samples were not collected in 1953 and 1955.

The calculated weights of lake herring from the various ports differed little at the end of the first year (from 0.4 ounce at Duluth to 0.6 ounce in the 1956-59 Marquette samples), but in subsequent years of life differences among ports and between periods of capture were sometimes considerable.

In 1950-55 the lake herring from Bayfield had the slowest growth in weight (fig. 10). The fish

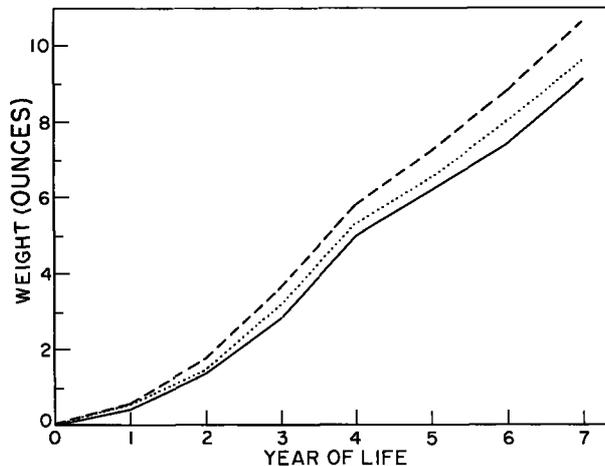


FIGURE 10.—General growth in weight of Lake Superior lake herring in 1950-55 at Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

reached 1.4 ounces during the second year of life, and by the seventh year they were 9.1 ounces. Portage Entry fish grew slightly faster than those from Bayfield, reaching 9.6 ounces at the end of 7 years of life. Growth at Marquette was similar to that of fish from the other ports during the first year but was faster in subsequent years; at the end of 7 years the lake herring from Marquette were 1 ounce heavier than those from Portage Entry and 1.5 ounces heavier than the Bayfield fish.

Growth in weight was faster during 1956-59 than in 1950-55 at all ports. At the end of 6 years of life, for example, the fish from Bayfield were 1.7 ounces heavier in 1956-59 (9.1 ounces) than in 1950-55 (7.4 ounces). At Portage Entry the VI-group fish were 2.1 ounces heavier (increase from 8.0 to 10.1 ounces) and at Marquette they were 2.3 ounces heavier (increase from 8.8 to 11.1 ounces).

Port-to-port differences of growth in weight had a general west-to-east trend toward faster growth during 1956-59 also (fig. 11). Duluth lake herring

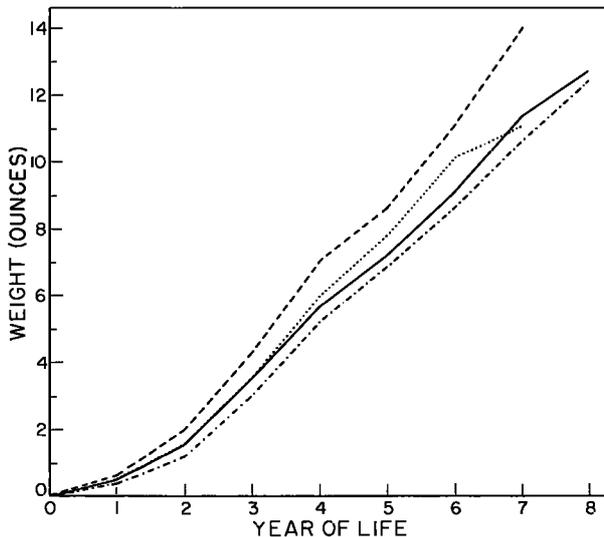


FIGURE 11.—General growth in weight of Lake Superior lake herring in 1956–59 at Duluth (dots and dashes), Bayfield (solid line), Portage Entry (dotted line), and Marquette (dashes).

weighed 0.4 ounce in the first year, those from Bayfield and Portage Entry grew 0.5 ounce, and at Marquette they grew 0.6 ounce. At the end of 7 years the fish weighed 10.6 ounces at Duluth, 11.4 ounces at Bayfield, 11.1 ounces at Portage Entry, and 14.0 ounces at Marquette.

The second-year increments of weight were more than twice that of the first year's growth at all of the ports except Portage Entry in 1950–55, and third-year growth was double the second-year increments at Duluth and at Portage Entry in 1950–55. The increments in weight reached a peak in the fourth year of life at all ports except Bayfield in 1956–59 and Marquette where the annual increments were highest in the seventh year of life. The largest increment in weight (2.9 ounces) was in the seventh year of life at Marquette in 1956–59.

ANNUAL FLUCTUATIONS IN GROWTH FLUCTUATIONS OF GROWTH IN LENGTH

Voluminous data and discussions have been published on the extent of annual fluctuations of growth and on the various factors affecting the growth of fish. Temperature and population densities probably have been most commonly considered but the results have been varied and often inconclusive. A discussion of this vast literature

need not be undertaken here. Excellent reviews and references to publications on factors of growth have been given by Hile (1936), Van Oosten (1944), and Watt (1956).

The number of studies on factors affecting the growth of lake herring has not been large. Hile (1936), who considered the possible influence of air temperature and population density on the growth of cisco populations in northeastern Wisconsin, concluded that the failure of variations of both factors to operate in the same direction in the same years may obscure the effect of each of them. Van Oosten (1929), Carlander (1945), and Smith (1956) found no correlation between annual fluctuations in growth of lake herring and air temperatures.

The data on annual fluctuations of growth in length of Lake Superior lake herring are separated according to port (tables 27, 28, and 29). Data are given only for age groups III, IV, and V; other groups were not adequately represented. The Duluth samples have been omitted since the collections, available only for 1957–59, cover too few years for a satisfactory study of annual fluctuations.

The growth increments are arranged in the following manner: the columns show the growth for different years of life in a particular calendar year; the horizontal rows show growth in a particular year of life in the different calendar years; and the diagonal rows show the growth history of an age group belonging to a year class that can be identified by the calendar year in which the first-year growth was made. The data for different age groups had to be kept separate because of the systematic discrepancies described in the section on calculated growth in length.

Although examination of the growth increments of lake herring from the various ports reveals strong though irregular trends toward improved growth in the later years, a procedure based on the actual percentage change from one calendar year to the next offers a more precise estimate of growth fluctuations. This method was described in detail by Hile (1941).

The largest annual fluctuations in growth occurred at Bayfield (table 30). Growth was poorest in 1945 and 1946 when the percentage deviations from the 15-year (1945–59) mean were –14.7 and –23.5 percent. Growth improved irregularly to 12.0 percent above average in 1951

TABLE 27.—Annual increments of growth in length of Lake Superior lake herring captured at Bayfield, 1950-59

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches
6						0.7	0.7	0.7				0.7	1.0	1.0	1.2
5					1.6	1.0	1.1		1.4		1.1	1.4	1.2	1.6	
4				2.0	1.3	1.6		1.4		1.5	1.8	1.4	1.3		
3			1.0	1.3	1.5		1.5		1.6	1.7	1.8	1.5			
2		1.3	2.1	2.8		1.3		2.4	2.1	2.3	2.0				
1	4.7	4.3	4.6		4.7		4.5	3.9	4.6	4.5					
Number of fish	(1)	(19)	(28)		(26)		(22)	(16)	(32)	(27)					
Age group IV:						0.9	1.0	1.0		1.0		1.0	1.1	1.2	1.1
5					1.6	1.5	1.9		1.9		1.9	1.9	1.6	1.9	
4				1.7	1.8	1.6		1.9		1.9	1.9	2.2	1.3		
3			2.4	2.4	2.6		2.3		2.4	2.5	2.5	3.4			
2		4.7	4.4	4.6		4.7		4.7	4.6	4.6	4.7				
1		(63)	(89)	(89)		(107)		(54)	(134)	(43)	(65)				
Number of fish															
Age group III:						1.7	2.1	1.5		1.4		1.6	1.6	1.3	1.4
4					2.0	1.9	2.5		2.3		2.4	2.4	2.4	2.8	
3				2.5	2.6	2.4		2.8		2.7	3.2	2.8	2.9		
2			4.9	4.6	5.0		4.9		4.8	4.7	5.4	5.3			
1			(39)	(39)	(24)		(27)		(15)	(41)	(28)	(12)			
Number of fish															

TABLE 28.—Annual increments of growth in length of Lake Superior lake herring captured at Portage Entry, 1950-59

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches
6						0.7	0.7	0.7	1.0	0.9	0.8	0.9	1.0	1.0	1.1
5					1.3	1.0	1.0	1.0	1.0	1.3	1.5	1.3	1.4	1.3	
4				1.3	1.5	1.4	1.7	1.8	1.7	1.8	1.7	1.8	1.8		
3			1.8	1.6	1.9	1.6	1.9	1.5	1.8	1.8	1.8	1.7			
2		2.2	2.2	2.2	1.9	2.0	2.1	2.1	2.2	2.3	2.3				
1	4.4	4.5	4.7	4.7	4.3	4.6	4.5	4.3	4.7	4.8					
Number of fish	(7)	(28)	(24)	(3)	(3)	(29)	(14)	(31)	(43)	(35)					
Age group IV:						1.1	.9	.9	1.1	1.0	.6	1.2	1.3	1.2	1.2
5					1.4	1.6	1.6	1.7	1.6	1.7	1.8	1.9	2.0	1.9	
4				1.9	1.9	1.9	1.8	1.9	1.9	1.9	2.0	2.1	2.2		
3			2.8	2.5	2.6	2.2	2.1	2.3	2.6	2.6	2.9	2.6			
2		4.6	4.6	4.7	4.9	5.2	5.5	4.6	4.5	4.7	4.5				
1		(59)	(69)	(58)	(49)	(50)	(37)	(137)	(123)	(47)	(88)				
Number of fish															
Age group III:						1.6	1.9	1.7	1.7	1.6	1.8	1.9	1.9	1.5	1.8
4					2.2	2.0	2.2	2.2	2.1	2.1	2.3	2.3	2.3	2.5	
3				2.9	2.7	2.5	2.6	2.5	3.0	2.9	3.0	3.9	2.5		
2			4.9	4.8	5.0	5.1	5.3	4.9	4.8	5.0	5.0	5.2			
1			(30)	(23)	(22)	(36)	(39)	(17)	(87)	(47)	(26)	(18)			
Number of fish															

TABLE 29.—Annual increments of growth in length of Lake Superior lake herring captured at Marquette, 1950-59

Age groups and years of life	Increment of total length in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches
6						1.0	0.7	0.9	0.9	0.9	0.7	0.9	1.1	1.2	1.1
5					0.9	1.1	1.0	1.3	1.3	1.1	1.1	1.3	1.6	1.2	
4				1.1	1.5	1.6	1.5	1.6	1.7	1.6	1.8	1.7	1.7		
3			2.0	1.4	1.6	1.6	1.7	1.7	1.8	1.6	2.0	1.8			
2		2.5	2.9	2.8	2.7	2.7	2.4	2.7	2.6	2.2	2.6				
1	4.5	4.5	4.4	4.4	4.4	4.6	4.8	4.4	4.4	4.9					
Number of fish	(9)	(21)	(24)	(7)	(21)	(33)	(34)	(15)	(12)	(24)					
Age group IV:						1.0	1.1	1.2	1.0	1.0	1.0	1.1	1.3	1.5	1.3
5					1.6	1.4	1.6	1.7	1.8	1.8	1.8	1.8	2.0	1.9	
4				1.8	2.0	2.0	2.0	1.9	2.0	2.1	2.1	2.2	2.1		
3			2.7	2.8	2.8	2.7	2.7	3.3	2.7	2.8	2.9	2.9			
2		4.6	4.7	4.6	4.8	4.8	4.9	4.9	4.9	4.6	4.8				
1		(43)	(63)	(54)	(44)	(59)	(39)	(89)	(88)	(61)	(53)				
Number of fish															
Age group III:						1.6	1.5	1.5	1.8	1.7	1.6	1.8	1.8	1.9	1.9
4					2.4	2.0	2.4	2.2	2.1	1.9	2.2	2.5	2.6	2.2	
3				2.9	3.4	2.8	2.8	3.1	4.0	4.2	4.1	4.5	3.6		
2			4.7	5.0	5.3	5.3	5.5	4.8	5.0	5.0	4.9	5.4			
1			(15)	(21)	(21)	(32)	(20)	(20)	(42)	(46)	(37)	(42)			
Number of fish															

but then fell to -3.6 percent in 1952. Beginning in 1953, growth improved progressively (exception in 1957) to 1959 when a maximum value of 16.3 percent above average was reached.

Growth at Portage Entry remained below average in 1945-53 (percentage range, from -0.4 to -5.2) and was above average in 1954-59 (exception in 1958). Growth improved steadily from 1952 to 1956 when the value of 8.9 percent above average was reached. The percentage declined in 1957 and 1958 but recovered to 8.7 percent in 1959.

TABLE 30.—Percentage deviation of growth in length of Lake Superior lake herring from the 1945-59 mean

Year	Percentage deviation at			Year	Percentage deviation at		
	Bayfield	Portage Entry	Marquette		Bayfield	Portage Entry	Marquette
1945.....	-14.7	-4.4	-9.3	1953.....	-0.9	-0.7	3.1
1946.....	-23.5	-2.3	-9.3	1954.....	.1	1.2	-1.5
1947.....	-6.1	-5	-6.0	1955.....	6.3	2.5	4.8
1948.....	-2	-2.8	-7.9	1956.....	7.7	8.9	11.2
1949.....	1.8	-2.5	-1.8	1957.....	1.0	3.4	11.2
1950.....	-6.8	-4.1	-7	1958.....	10.6	-1.8	6.2
1951.....	12.0	-4	-7	1959.....	16.3	8.7	-5
1952.....	-3.6	-5.2	-1.8				

The percentages of departure from average growth at Marquette fell below the mean in 1945-52 (range, -0.7 to -9.3) and were above average in 1953-58. The maximum value of 11.2 percent occurred in 1956 and 1957, after which the growth rate declined to -0.5 percent in 1959.

With few exceptions, the percentage deviations of growth in length of Lake Superior lake herring at all ports were below average in 1945-53 and above average in 1954-59 (fig. 12). Improvement in growth was especially marked in 1953-56.

To obtain a better measure of the similarity of the long-term changes of growth at the three localities, coefficients of correlation were calculated for the actual annual deviations from average. The coefficients are as follows:

Ports	r
Bayfield-Portage Entry.....	0.595
Bayfield-Marquette.....	.618
Portage Entry-Marquette.....	.601

The coefficients between annual fluctuations in growth were significant at a probability level between 2 and 1 percent (absolute values of *r* at

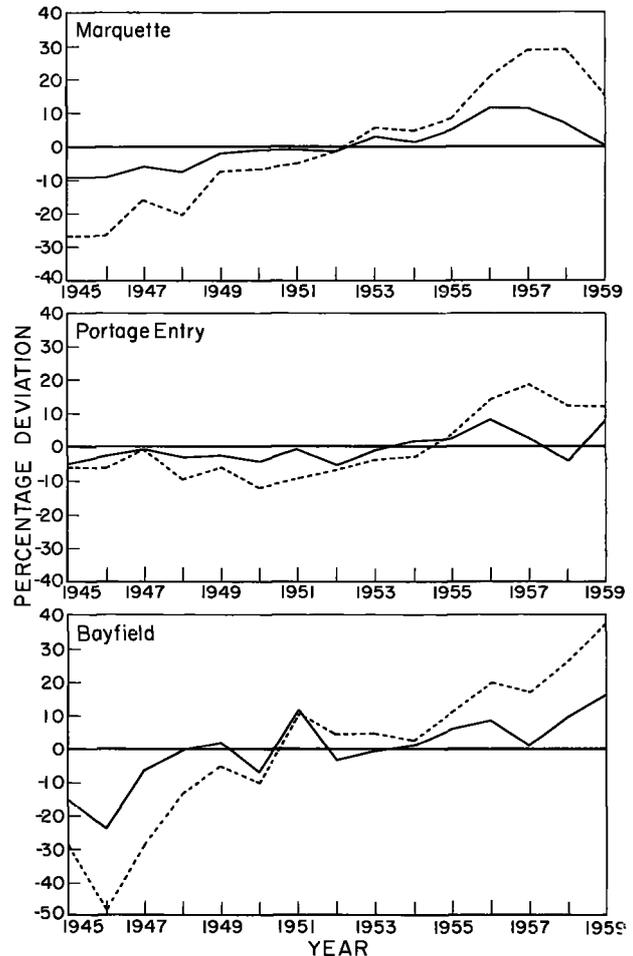


FIGURE 12.—Annual fluctuations of growth in length (solid line) and weight (broken line), of Lake Superior lake herring from Bayfield, Portage Entry, and Marquette.

the 2- and 1-percent levels of significance are 0.592 and 0.641). Conditions as a whole are apparently undergoing a progressive change favorable to improved growth at the three ports. Temperature alone was not responsible for the growth fluctuations of Lake Superior lake herring. Meteorological conditions should operate similarly over the entire lake and hence should have similar effects on trends in the growth at all three ports. The temperature records give no evidence, however, for a major upward trend since 1954.

The inverse relation which appears to exist between the upward trend in improved growth and the downward trend in abundance of lake herring at the various ports suggests that the decrease in population density may have contributed to the

change. A statistically significant correlation between growth (in both length and weight) and abundance could not be established, however. The number of years covered by the data may have been inadequate for a sound statistical analysis. Data on fluctuations of both growth and of abundance in terms of numbers of fish were available only for the 10 years 1950-59. Data on both growth and abundance in terms of pounds of fish were available for 15 years (1945-59) in Michigan waters only.

FLUCTUATIONS OF GROWTH IN WEIGHT

The annual increments of growth in weight (tables 31, 32, and 33) are arranged in the same manner as those of length in tables 27, 28, and 29. Since the calculated weights were based on the calculated lengths, the trends in annual fluctua-

tions of growth in weight for Lake Superior lake herring were similar to those of growth in length (fig. 11). Growth in weight was below average at Bayfield in 1945-50, at Portage Entry in 1945-54, and at Marquette in 1945-52. Growth was above average at all of the ports after 1954.

The correlation between annual fluctuations of growth in weight of Lake Superior lake herring at the three ports was even closer than that for length. The values of *r* follow:

Ports		
Bayfield-Portage Entry.....		0.651
Bayfield-Marquette.....		.889
Portage Entry-Marquette.....		.823

The coefficients were well beyond the 1-percent level of probability, and 2 were beyond the 0.1-percent level.

TABLE 31.—Annual increments of growth in weight of Lake Superior lake herring captured at Bayfield, 1950-59

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:															
6.....						1.1	1.0	1.4		1.0		1.2	1.7	1.9	2.2
5.....					2.2	1.3	1.8				1.7	2.1	1.8	2.2	
4.....				1.6	1.2	2.0		1.2		1.8	1.8	1.8	1.3		
3.....			0.5	.7	1.4		.8		1.2	.9	1.4	1.0			
2.....			.7	1.1		.4		.8	.6	.8	.6				
1.....	0.5	0.4	.5		.5		.5	.3	.5	.5					
Number of fish.....	(1)	(19)	(28)		(26)		(22)	(16)	(32)	(27)					
Age group IV:						1.4	1.5	1.7		1.7		1.7	2.0	2.1	2.1
4.....					2.1	1.9	2.5		2.6		2.7	2.6	2.3	2.8	
3.....				1.4	1.4	1.3		1.6		1.6	1.6	2.0	1.4		
2.....			.9	.8	1.0		.8		.9	.9	.9	1.6			
1.....		.5	.4	.5		.5		.5	.5	.5	.5				
Number of fish.....		(63)	(89)	(69)		(107)		(54)	(124)	(43)	(65)				
Age group III:						2.5	3.0	2.2		2.1		2.5	2.6	2.2	2.6
4.....					1.9	1.8	2.6		2.5		2.5	2.8	3.0	3.6	
3.....				1.0	.9	1.0		1.2		1.2	1.5	1.5	1.5		
2.....										1.2	1.5	1.5	1.5		
1.....			.6	.5	.6		.6		.5	.5	.7	.7			
Number of fish.....			(39)	(39)	(24)		(27)		(15)	(41)	(28)	(12)			

TABLE 32.—Annual increments of growth in weight of Lake Superior lake herring captured at Portage Entry, 1950-59

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Age group V:															
6.....						1.2	1.3	1.7		1.6	1.5	1.8	1.8	2.2	2.4
5.....					1.8	1.5	1.5	1.5	1.9	1.9	2.4	2.1	2.4	2.2	
4.....				1.6	1.7	1.8	2.0	2.1	2.0	2.2	2.0	2.4	2.4		
3.....			1.2	1.1	1.5	1.0	1.2	1.0	1.2	1.2	1.5	1.4			
2.....			.8	.8	.7	.6	.7	.8	.7	.8	.9				
1.....	0.4	0.8	.5	.4	.4	.5	.4	.4	.5	.5	.5				
Number of fish.....	(7)	(28)	(24)	(3)	(3)	(29)	(14)	(31)	(43)	(35)					
Age group IV:						1.9	1.4	1.5	1.8	1.7	1.2	2.2	2.4	2.6	2.2
4.....					1.9	2.2	2.3	2.3	2.2	2.5	2.4	2.6	3.1	2.8	
3.....				1.8	1.6	1.8	1.5	1.8	2.0	1.7	1.8	2.1	2.0		
2.....			1.1	.9	1.0	.8	.9	1.2	1.0	.9	1.3	.9			
1.....		.5	.5	.5	.6	.6	.7	.5	.5	.5	.5				
Number of fish.....		(59)	(69)	(58)	(49)	(50)	(37)	(187)	(123)	(47)	(68)				
Age group III:						2.5	2.8	2.6	2.6	2.4	2.9	3.1	3.2	2.8	3.0
4.....					2.4	2.0	2.2	2.4	2.3	2.3	2.5	2.7	3.2	2.8	
3.....				1.3	1.2	1.1	1.2	1.2	1.4	1.3	1.5	2.3	1.2		
2.....															
1.....			.6	.5	.6	.6	.7	.6	.5	.6	.6	.6			
Number of fish.....			(30)	(28)	(22)	(36)	(39)	(17)	(87)	(47)	(26)	(18)			

TABLE 33.—Annual increments of growth in weight of Lake Superior lake herring captured at Marquette, 1950-59

Age groups and years of life	Increment of weight in calendar years														
	1945	1946	1947	1948	1949	1950	1951	1952	1943	1954	1955	1956	1957	1958	1959
Age group V:	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces
6.....					1.3	1.8	1.3	1.7	1.7	1.8	1.4	2.0	2.3	2.6	2.6
5.....					1.3	1.7	1.6	2.1	2.1	1.7	1.9	3.1	2.6	2.2	
4.....				1.5	2.0	2.1	1.9	2.0	2.2	2.3	2.3	2.2	2.4		
3.....			1.7	1.2	1.3	1.3	1.5	1.4	1.7	1.3	1.4	1.7			
2.....		0.8	1.1	1.1	1.0	1.0	.8	1.2	.9	.8	1.1				
1.....	0.5	.5	.4	.4	.4	.5	.5	.4	.4	.6					
Number of fish.....	(9)	(21)	(24)	(7)	(21)	(33)	(34)	(15)	(12)	(24)					
Age group IV:						1.7	1.9	2.2	1.8	1.8	1.8	2.1	2.8	3.3	2.8
5.....					2.1	2.0	2.3	3.5	2.6	2.5	2.8	2.8	3.1	3.0	
4.....					1.7	2.0	1.9	1.9	1.9	2.1	2.2	2.2	2.2		
3.....			1.0	1.2	1.1	1.2	1.2	.8	1.2	1.2	1.2	1.3			
2.....		.5	.5	.5	.5	.5	.6	.6	.6	.5	.5				
1.....		(43)	(53)	(54)	(44)	(59)	(39)	(59)	(88)	(61)	(53)				
Number of fish.....															
Age group III:						2.5	2.5	2.6	3.1	3.1	2.9	3.8	4.0	4.5	3.8
4.....					2.5	2.5	2.9	2.6	2.7	2.5	3.2	3.6	4.0	3.2	
3.....					1.3	1.8	1.4	1.9	2.3	2.7	2.6	3.0	2.3		
2.....			.5	.6	.7	.7	.5	.6	.6	.6	.6	.7			
1.....			(15)	(21)	(21)	(32)	(20)	(20)	(42)	(46)	(37)	(42)			
Number of fish.....															

The range of the percentage fluctuations of growth in weight (table 34) was much greater at each port than was that of growth in length (table 30). This difference is largely due to the nature of the length-weight relation, namely, the increase of weight approximately as the cube of the length. Consequently, the increment of weight corresponding to a particular increment of length depends not only on the amount of growth in length but also on the length of the fish at the time the growth is made. For example, a lake herring that weighs 2 ounces at a length of 8 inches will weigh 4.3 ounces upon reaching a length of 10 inches, a gain of 2.3 ounces. A 10-inch fish that experiences the same 2-inch growth (from 10 to 12 inches) increases its weight from 4.3 to 7.6 ounces, a gain of 3.3 ounces. Both the large size of the fish and the large increments of length contributed to the excellent growth in weight in the more recent years.

The curves of fluctuations of growth in length and weight are further affected by differences with respect to the years of life that exerted greatest influence on the year-to-year percentage changes. Under the procedure of Hile (1941) for estimates of growth fluctuations, the earlier years of life dominated the estimates of fluctuations of growth in length by reason of their larger increments. The data on weight, on the other hand, were least affected at lower ages since the increments of weight were smallest during the earlier years of life. In the later years of life, the weight increments were large when those of length were small.

Similar discrepancies between estimates of fluctuations of growth in length and weight were

found by Hile (1954) for walleye and by El-Zarka (1959) for yellow perch in Saginaw Bay.

TABLE 34.—Percentage deviation of growth in weight of Lake Superior lake herring from the 1945-59 mean

Year	Percentage deviation at			Year	Percentage deviation at		
	Bay-field	Portage Entry	Marquette		Bay-field	Portage Entry	Marquette
1945.....	-28.3	-6.0	-26.8	1953.....	4.6	-3.4	5.4
1946.....	-48.4	-6.0	-26.8	1954.....	2.2	-2.5	4.2
1947.....	-28.3	-.4	-16.4	1955.....	11.5	3.8	8.1
1948.....	-13.6	-9.3	-20.3	1956.....	19.9	15.2	20.5
1949.....	-5.7	-6.0	-7.6	1957.....	16.5	17.1	28.3
1950.....	-9.9	-12.0	-7.0	1958.....	26.4	13.7	28.3
1951.....	11.5	-9.5	-5.7	1959.....	37.0	12.7	16.0
1952.....	4.6	-6.6	-.2				

REPRODUCTION

SEX COMPOSITION

Segregation by maturity in the spawning run, in combination with sex differences in age at first maturity and sex differences in the time of arrival of fish on the grounds, limited the use of spawning-run samples for the study of sex composition. The collections from Bayfield in 1959 and 1961 offer examples of the effects of time of capture within the spawning period. A net-run sample collected on November 19, 1959, contained only 3 percent females, and a later sample from the same area on December 8 included 82 percent females. In 1961, net-run samples of lake herring were collected each day the nets were lifted during 15 days of the spawning season (table 35). The number of females exceeded that of the males in all but the first and third days of collection. Had the

production of spawning-run fish begun earlier in the season,³ the percentage of males undoubtedly would have been higher during the first few days. The percentage of females increased steadily after November 23 (exceptions on November 27 and 28) to December 3, when they contributed 93 percent to the total. The advantage of the females decreased slightly in the last 2 days of the season.

Smith (1956) was able to demonstrate differences in the sex ratio according to age, year of collection, depth, season, and gear of capture. His samples from pound nets contained a higher percentage of females in February than during other months; the percentage of females in the samples decreased during 1949-52; the percentage of females decreased with an increase in age in pound net collections and increased with increase in age in gill net collections; in October, females were relatively more plentiful in the deeper than in shallow water.

TABLE 35.—Changes in the sex ratio of Lake Superior lake herring during the 1961 spawning season at Bayfield

[The age groups have been combined]

Date	Number of males	Number of females	Percentage of females
Nov. 20.....	85	67	44.1
22.....	87	123	58.6
23.....	80	75	48.4
24.....	57	97	63.0
25.....	57	156	73.2
26.....	50	150	75.0
27.....	41	97	70.3
28.....	53	147	73.5
29.....	38	155	80.3
30.....	28	122	81.3
Dec. 1.....	26	132	83.5
2.....	21	129	86.0
3.....	10	132	93.0
4.....	19	144	88.3
6.....	23	123	84.2
Combined samples.....	675	1,849	73.3

Comparable data from Lake Superior did not disclose differences in the sex ratio according to season (with the exception of the spawning season), geographical location, or depth. Since all of the samples came from gill nets, sex data for fish from different gears could not be compared.

The data on sex composition of Lake Superior lake herring were collected during the summer (no fish collected later than September 27 were used in the study of the sex ratio) at: Two Harbors, Minn; Bayfield, Wis.; and Marquette, Mich. The samples for the various dates at these ports

³ The fishermen did not start intensive fishing until they could be assured of good catches.

were so similar that the collections have been combined (table 36).

The number of females equalled or exceeded that of the males in each age group except the I group (only 1 fish). In the later years, the advantage of the females increased from 52.3 percent for age group III to 81.8 percent for group VII (the percentage dropped to 71.4 percent for age group VIII). For all age groups combined, the percentage of females was 68.5.

TABLE 36.—Sex composition of age groups of Lake Superior lake herring

[Based on summer collections]

Age group	Number of males	Number of females	Percentage of females
I.....	1	0.0
II.....	20	20	50.0
III.....	68	69	52.3
IV.....	56	146	72.3
V.....	51	154	75.1
VI.....	37	87	70.2
VII.....	8	36	81.8
VIII.....	4	10	71.4
Combined samples.....	240	522	68.5

AGE AND SIZE AT MATURITY

Variation is considerable in the age and size at maturity among different populations of lake herring. Most of the lake herring are mature at age group II in the lakes of northeastern Wisconsin (Hile, 1936), Saginaw Bay (Van Oosten, 1929), Green Bay (Smith, 1956), and Lake Erie (Clemens, 1922); at age group III in Lake Ontario (Stone, 1938), Blind Lake, Mich. (Cooper, 1937), Lake Oconomowoc, Wis. (Cahn, 1927), and Lake Superior; and at age group IV in Hudson Bay (Dymond, 1933) and Manitoba Lakes (Bajkov, 1930). Differences in the age and size at maturity often can be correlated with the growth rates of the stocks; fish which have particularly slow growth may mature at a higher age but at a length below that of faster growing specimens (Alm, 1959). This phenomenon was demonstrated among various stocks of whitefish in Lake Superior (Dryer, 1963), but a similar correlation does not appear to exist among all populations of lake herring. Indeed, lake herring from Trout, Silver, and Muskellunge Lakes in northeastern Wisconsin (Hile, 1936) are among the slowest growing for which growth data have been published, but these fish matured at a younger age than those from the faster growing stocks of Lakes Superior and Ontario.

The limited data on the age and size at maturity for Lake Superior lake herring (tables 37 and 38) came from records of nonspawning-run samples. Nearly all of the fish taken in the spawning-run samples were mature. The youngest mature lake herring in Lake Superior belonged to age group II (table 37), and all fish older than the III group were mature. The percentage maturity was higher for males than for females in age groups II and III. All lake herring shorter than 8.5 inches were immature, and all fish longer than 11.9 inches were mature (table 38). The first mature male appeared in the 8.5- to 8.9-inch group and all the males were mature at lengths greater than 11.4 inches. The first mature females appeared in the 9.5- to 9.9-inch group and all were mature at lengths greater than 11.9 inches.

SPAWNING

Spawning of the lake herring in the Great Lakes region takes place some time between mid-November and mid-December. Most investigators agree that water temperature is the main factor influencing the onset of spawning. Various observations and experiments (Cahn, 1927; Pritchard, 1930; Stone, 1938; Brown and Moffett, 1942; Smith, 1956) have shown that spawning does not occur until water temperatures drop below 39.0° F. (3.9° C.).

The earliest spent lake herring from Lake Superior was caught on November 12 in Keweenaw Bay in 1951, and ripe fish were observed as late as December 20 in the Apostle Islands area in 1960. The bulk of the spawning normally takes place during the last week of November and the first week of December. Water temperatures during this time ranged from 40° F. to 37° F. (4.4° C. to 2.8° C.).

Prespawning fish appear on shallow (3 to 6 fathoms) reefs in the Apostle Islands in mid-October. Lake herring are fished commercially

TABLE 37.—Relation between age and sexual maturity of Lake Superior lake herring

[All fish younger than age group II were immature; all fish older than age group III were mature]

Age group and sex	Number immature	Number mature	Percentage mature
Males:			
II.....	9	7	44
III.....	5	22	81
Females:			
II.....	14	5	26
III.....	6	20	77

TABLE 38.—Relation between length and sexual maturity of Lake Superior lake herring

[All fish shorter than 8.5 inches were immature; all fish longer than 11.9 inches were mature]

Total length (inches)	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Percentage mature
<i>Inches</i>						
8.5-8.9.....	1	1	50	-----	-----	-----
9.0-9.4.....	4	4	50	4	-----	0
9.5-9.9.....	4	4	50	3	1	25
10.0-10.4.....	3	6	67	6	3	33
10.5-10.9.....	-----	6	100	2	8	80
11.0-11.4.....	1	4	80	2	10	83
11.5-11.9.....	-----	6	100	1	6	86

on these reefs from mid-October to late November, but the catches rarely include spent fish. The fishermen follow the lake herring off the reefs into about 20 fathoms where large-scale spawning first occurs. As the spawning season progresses, the fishermen move into deeper water and the last large catches are taken from water 60 to 70 fathoms deep. Koelz (1929) stated that spawning lake herring at Marquette were first found in 8 or 9 fathoms but later moved out to 14 or even 20.

Scanning with the fish magnifier of the depth recorder aboard the *Siscowet* during the 1961 spawning season in the Apostle Islands region, confirmed earlier suggestions (Smith, 1956) that the lake herring are pelagic spawners. Night scanning during the peak of the season revealed a heavy concentration of fish (presumably lake herring) at 5 to 15 fathoms below the surface in water 35 fathoms deep. A midwater trawl towed 10 fathoms below the surface took small numbers of lake herring and a 5-foot nylon-cloth, 1/8-inch-mesh net (usually used for the collection of larval fish) towed at 20 fathoms caught small numbers of lake herring eggs. The eggs undoubtedly were drifting toward the bottom after release from the fish. Additional evidence of pelagic spawning comes from the north shore of Lake Superior where commercial gill nets floated 7 fathoms below the surface in 80 fathoms of water take large numbers of spawning lake herring.

These findings do not prove that lake herring are exclusively pelagic spawners. Most of the commercial production from the south shore of the lake comes from nets set on the bottom. The fish move to the bottom sometime during the night; spawning may continue there.

Evidence from Lake Superior supports earlier findings that spawning lake herring show no preference for a particular bottom type.

FECUNDITY

Fecundity studies of lake herring by earlier authors demonstrated that the number of eggs varied widely according to stock and individuals within a stock. Smith's (1956) detailed account of these findings revealed, in general, that the number of eggs tended to increase with length and weight of the female, but the number of eggs per ounce of body weight decreased with increase in length. The average diameters of eggs from Green Bay lake herring showed no change with increase in length of the female, and the egg diameter and the total number of eggs per individual fish were not correlated.

The fecundity of Lake Superior lake herring was investigated from 30 fully ripe females collected in 1950-54 at Marquette and Portage Entry. The formalin-preserved ovaries were broken up thoroughly and the connective tissue removed. The eggs were then set aside to dry at room temperature for 24 hours or until all signs of moisture had disappeared. A sample of 500 eggs was removed and weighed to the nearest 0.0001 g., and the total number of eggs was computed from their total weight (determined to the nearest 0.0001 g.) and the sample weight.

The dependability of this method was tested by making 14 estimates from 500-egg samples of one pair of ovaries for which an actual count was made. The actual number of eggs counted was 7,523, and the estimates ranged from 7,407 to 7,609. The extreme percentage errors were -1.54 and 1.14. The mean of the absolute values of the percentage errors was 0.63.

The fecundity data for Lake Superior lake herring exhibited identical trends to those described by earlier investigators. The number of eggs tended to increase with fish length, and the number of eggs per ounce of body weight to decrease with increase in length (table 39). The average number of eggs ranged from 4,314 for fish in the 10.6- to 10.8-inch size group to 10,250 for a 14.0-inch fish. The average for the entire sample was 6,351 eggs. The average number of eggs per ounce of body weight ranged from 1,006 for fish in the 10.9- to 11.1-inch size group to 746 for those in the 12.4- to 12.6-inch group. The average number of eggs per ounce of fish for the entire sample was 842.

Comparable data from Lake Superior and Green Bay (Smith, 1956) reveal that the Lake Superior

lake herring typically produce fewer eggs per individual fish and fewer eggs per ounce of fish weight (table 40). The production of eggs from individual Green Bay lake herring was larger for each length interval for which comparable data were available (exception at 11.5 to 11.7 inches). The number of eggs per ounce of fish was also higher for Green Bay lake herring in 4 of 6 comparisons. The unweighted means for each sample showed that Green Bay lake herring produced over 1,000 more eggs per individual fish and nearly 100 more eggs per ounce of fish.

The egg diameters of Lake Superior lake herring were measured for only one 11.4-inch female.

TABLE 39.—Relation between the length of Lake Superior lake herring and the total number of eggs and the number per ounce of weight

[Number of fish in parentheses]

Total length (Inches)	Number of eggs per fish		Average number of eggs per ounce of fish
	Average	Range	
10.6-10.8.....	4,314 (2)	3,834-4,704	828
10.9-11.1.....	5,802 (4)	3,728-9,417	1,006
11.2-11.4.....	5,354 (4)	4,515-6,922	896
11.5-11.7.....	6,719 (7)	4,712-8,579	978
11.8-12.0.....	5,425 (4)	4,735-5,912	787
12.1-12.3.....	6,075 (3)	5,310-7,514	792
12.4-12.6.....	5,495 (2)	5,305-5,684	746
12.7-12.9.....	7,726 (3)	6,970-8,685	793
13.9-14.1.....	10,250 (1)	-----	754
All lengths.....	6,351 (30)	3,728-10,250	842 (30)

TABLE 40.—Number of eggs per fish and per ounce of weight produced by lake herring of Green Bay (Lake Michigan), and Lake Superior

[The data for Green Bay are from Smith (1956). Number of fish in parentheses]

Total length (Inches)	Average number of eggs per fish		Average number of eggs per ounce of fish	
	Green Bay	Lake Superior	Green Bay	Lake Superior
10.6-10.8.....	6,662 (15)	4,314 (2)	1,156 (16)	828 (2)
10.9-11.1.....	6,079 (16)	5,802 (4)	976 (15)	1,006 (4)
11.2-11.4.....	5,790 (14)	5,354 (4)	918 (11)	896 (4)
11.5-11.7.....	6,140 (11)	6,719 (7)	851 (9)	978 (4)
11.8-12.0.....	7,663 (4)	5,425 (4)	986 (3)	787 (4)
12.1-12.3.....	8,109 (1)	6,075 (3)	977 (1)	973 (3)
All lengths ¹	6,741	5,615	977	881

¹ Unweighted means.

The mean diameter of 48 eggs was 1.88 mm., exactly that found by Smith (1956) from 20 specimens taken in November in Green Bay.

FOOD HABITS

Stomach contents were examined from 146 lake herring collected on various dates in 1950-60 at Bayfield, Wis., and Marquette, Mich. (table 41).

Crustacea, found in 83 percent of the stomachs examined were by far the most common food of lake herring. Copepods (*Diaptomus*, *Epischura*, and *Limnocalanus*) were found in all of the stomachs of small lake herring (5.6-6.4 inches) in the May sample, in 93 percent of the stomachs of the June-July and September-October collections, and in 66 percent of the stomachs of the December sample. The total frequency of occurrence for copepods was 71 percent. Cladocera (*Daphnia*) ranked second (36 percent), and Mysidacea (*Mysis relicta*), important only in the December sample, were in 19 percent of the total stomachs examined.

Insects were not found in the May or December collections but were in 61 percent of the June-July samples and in 23 percent of the September-October collections. Of the insects that were

TABLE 41.—Food in stomachs of Lake Superior lake herring collected at Bayfield and Marquette, 1950-60

Item	Percentage occurrence in seasonal samples				All dates
	May 3, 1960	June 6- July 30, 1959	Sept. 17, 1958 Sept. 30- Oct. 2, 1959	Dec. 5, 1950	
Number of stomachs	5	43	43	55	146
Length of fish ¹	5.6-6.4	4.3-13.0	5.3-16.5	11.0-12.9	5.6-16.5
Food item:					
Crustacea (total)	100	93	93	66	83
Copepoda	100	84	58	10	71
Cladocera		44	74	2	36
Mysidacea		9	5	40	19
Amphipoda				2	2
Unidentified remains		12	19	33	21
Insecta (total)		61	23		25
Formicidae		7			2
Diptera		7	5		4
Lepidoptera		2			1
Homoptera		2			1
Hymenoptera ²		2			1
Hemiptera		2			1
Thysanoptera		2			
Unidentified remains		33			15
Pelecypoda			19		1
Rotatoria		2	2		3
Hydracarina			2		1
Fish remains				6	1
Fish eggs				2	1
Chlorophyta	40	72		4	23
Diatoms		35	7		24
Unidentified debris		7	12	35	19

¹ Total length, inches.
² Exclusive of the ants.

positively identified, Formicidae and Diptera were most common.

Fish eggs (lake herring) were found in 62 percent of the stomachs in the December sample. Although the lake herring is known to prey on its own eggs, a question arises as to whether lake herring eggs are a preferred food or if they are eaten incidentally with plankton. Since the major foods of the lake herring are pelagic, the eggs may simply be eaten as they drift toward the bottom after being released by pelagic spawners. Some eggs could, of course, have been taken from the bottom. The consumption of fingernail clams and water mites, though rare, gives evidence of occasional bottom feeding.

The common food found in the lake herring stomachs during various seasons of the year gives strong support to the belief that the lake herring is primarily pelagic.

DISTRIBUTION

The seasonal distribution of the lake herring has been a subject of considerable speculation among fishermen as well as researchers. That the fish disappear in Lake Superior during the summer cannot be disputed. Prior to 1960 the only summer fishery for lake herring on the lake existed along the north shore and at Isle Royale where floated nets yielded small catches.

A small summer lake herring fishery developed in 1960-62 at Marquette where bottom nets set at about 20 fathoms produced some good catches.

Koelz (1929) caught only a few stragglers in his experimental nets at depths of 10 to 100 fathoms during the summer in Lake Superior and reported that fishermen believed they had seen schools of lake herring near the surface in the open lake at that season.

In the course of the 1958-61 studies of fish populations in western Lake Superior by the research vessel *Siscowet*, special cruises collected information on the seasonal changes in the areal and depth distribution of the lake herring. Experimental fishing was carried out in several locations among the Apostle Islands with standard gill nets (300 feet each of 2- to 2¼-inch mesh), bull nets (gill nets 300 feet long, 100 meshes deep, with mesh sizes of 2½ and 2½ inches), and bottom and midwater trawls. The bottom trawls were a semiballoon type with a 31-foot headrope, 2½-

TABLE 42.—Number of lake herring caught per 1,000 linear feet of 2- to 2¼-inch-mesh gill nets set on the bottom at various depths in western Lake Superior, 1958-61

[Number of lifts in parentheses]

Time period and item	Depth of water (fathoms)									
	<10	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	
April 27-June 30										
Number of fish.....	5	8	12	11	0	4	2	0	3	
	(3)	(11)	(21)	(6)	(2)	(15)	(4)	(4)	(4)	
July 1-Sept. 13										
Number of fish.....	0	8	10	1	3	3	7	-----	2	
	(2)	(22)	(21)	(5)	(14)	(6)	(1)	-----	(2)	
Sept. 14-Oct. 14										
Number of fish.....	13	35	4	2	0	0	0	7	-----	
	(3)	(16)	(18)	(3)	(4)	(1)	(2)	(2)	-----	
Oct. 15-Nov. 15										
Number of fish.....	85	0	4	23	-----	19	-----	-----	-----	
	(22)	(2)	(3)	(1)	-----	(4)	-----	-----	-----	
Nov. 16-Dec. 20										
Number of fish.....	287	330	42	98	201	284	280	-----	66	
	(7)	(2)	(3)	(3)	(2)	(7)	(3)	-----	(4)	

inch-mesh body, and ½-inch-mesh cod end. The midwater trawl was converted from a bottom trawl to full-balloon type and was equipped with trawl plane floats. The standard gill nets were fished on the bottom at depths of 2 to 89 fathoms, and the bull nets were floated at different depths below the surface or set obliquely from the surface to the bottom. The floating and "oblique" nets were suspended at the desired distance below the surface from a series of floats. A limited amount of drift-netting (nets attached to unanchored boat, allowed to drift freely) was carried out in various parts of the open lake but few lake herring were captured. The bottom trawls were fished at 5 to 60 fathoms, and the midwater trawl was employed when pelagic schools of fish were observed on the sensitive echo-sounder aboard the vessel. The data gained from this experimental fishing failed by far to bring out clearly the movements and distribution of the lake herring, but they did add

materially to the hitherto negligible information on the subject.

Some explanations are required to permit an instructive account of the depth distribution of lake herring in Lake Superior from the records of tables 42 and 43. The time covered may be subdivided according to seasonal thermal conditions and the spawning season. Prior to July 1, the water of western Lake Superior was generally homothermous although surface temperatures occasionally reached 50° F. in late June. The surface water began to warm fairly rapidly in early July, and a pronounced thermocline soon developed. This condition persisted until about mid-September when the early fall storms mixed the water and the depth of the epilimnion increased to 80-100 feet. By mid-November (the beginning of the spawning season) the water was again almost homothermous at temperatures of about 43° F.

The depths listed in table 42 are the depths of water in fathoms where the nets were set; the nets fished 1 fathom of water immediately above the bottom. In table 43, the listed depths show the range and mean (in fathoms) that the bull nets were fished below the surface. The change of catch with the depth the nets were fished below the surface did not vary with the maximum depth of the water.

The catch of lake herring from gill nets set on the bottom was small at all depths and periods except during the spawning season (table 42). During April 27-June 30, the largest catch was only 12 fish per 1,000 linear feet (taken at 20-29 fathoms). At no depths below 39 fathoms did the catch exceed four fish. Between July 1 and

TABLE 43.—Number of lake herring caught per 1,000 linear feet of 2¾- and 2½-inch-mesh bull nets fished at various depths below the surface in western Lake Superior, 1958-60

[Number of lifts in parentheses. Temperatures ° F.]

Time period and item	Depth of water fished (fathoms)—range and mean (in parentheses)								
	<6.5 (3.3)	3.3-9.8 (6.6)	6.7-13.2 (10.0)	10.0-16.5 (13.3)	13.3-19.8 (16.6)	16.7-23.2 (20.0)	20.0-26.5 (23.3)	23.3-29.8 (26.6)	26.7-33.2 (30.0)
May 17-June 30:									
Number of fish.....	51	29	20	-----	-----	-----	-----	-----	-----
Average temperature.....	46°	42°	39°	-----	-----	-----	-----	-----	-----
	(4)	(4)	(1)	-----	-----	-----	-----	-----	-----
July 1-Sept. 13:									
Number of fish.....	19	27	25	23	7	2	4	4	0
Average temperature.....	87°	56°	45°	42°	41°	39°	39°	39°	39°
	(13)	(9)	(7)	(7)	(5)	(4)	(6)	(4)	(3)
Sept. 14-Oct. 5:									
Number of fish.....	140	127	133	110	104	50	12	17	2
Average temperature.....	55°	55°	55°	52°	47°	45°	44°	42°	44°
	(6)	(13)	(8)	(9)	(9)	(6)	(6)	(4)	(3)

September 13, few lake herring were captured, all at depths below 10 fathoms. The data suggest a widely scattered distribution between 10 and 69 fathoms during this period. In the early fall (September 14–October 14), most of the lake herring were taken in the 10- to 19-fathom stratum; they disappeared almost entirely at depths below 39 fathoms (exception was the catch of 7 fish per 1,000 linear feet of net at 70–79 fathoms). The prespawning fish began to concentrate on shallow reefs in October 15–November 15. Small-mesh gill nets set on the lake trout spawning reefs (3 to 6 fathoms) during mid-October often caught large numbers of lake herring which were nearly ripe. The period November 16–December 20 (which includes the lake herring spawning season) yielded relatively large numbers of lake herring at all depths. (The small numbers of fish taken at 20–39 fathoms is misleading because these sets were made for another species on grounds not frequented by lake herring.)

Water temperatures on the bottom were relatively low during all seasons. The highest temperature (53.5° F.) was recorded at 15 fathoms on September 30, and the lowest (34.9° F.) was at 24 fathoms on December 13.

Because the small catches of lake herring in the bottom nets suggest a pelagic life for the species, a better description of their depth distribution should be obtained from the records of catches from floating and "oblique" sets of bull nets (table 43). During May 17–June 30, the lake herring were most abundant (51 per 1,000 linear feet) at depths less than 7 fathoms. The catch of 29 fish at 3–10 fathoms and 20 fish at 7–13 fathoms suggested a decrease in abundance with an increase in depth. The average water temperature during this period ranged from 46° F. at 3 fathoms to 39° F. at 10 fathoms. No sets were made below 13 fathoms during the period. From July 1 to September 13 the largest numbers of lake herring were caught at 3–17 fathoms. The decrease in the number of fish between the surface and 7 fathoms may be the result of relatively high water temperatures in the surface layers (67° F.). Good catches of lake herring were rare in water warmer than 60° F. Lake herring were scarce below 17 fathoms. Since the lake herring are principally plankton feeders during the summer and the heaviest concentration of plankton occurs in the upper water levels, their depth distribution

may be determined by the abundance of food at various depths. On July 9, 1959, the *Siscowet* collected several plankton samples with a series of Clarke-Bumpus plankton samplers towed at 2, 7, and 20 fathoms below the surface. The concentration of plankton at 2 fathoms was extremely heavy; it was much lighter at 7 fathoms, and at 20 fathoms practically no plankters were captured.

The best catches in the bull nets were made during September 14–October 5. At this time the fish were abundant at depths to 20 fathoms (140 fish per 1,000 linear feet at 0–7 fathoms to 104 fish at 13–20 fathoms). The increase in the catch in the shallowest water followed a decrease in average water temperature to 55° F. The fish at this time apparently were moving toward the inshore areas prior to the late-fall spawning.

The catch of lake herring in bottom trawls was practically nil regardless of season, depth, or temperature of water. The midwater trawl towed 10 fathoms below the surface at night during the spawning season took only small numbers of lake herring.

The data from the catches of bottom nets and bull nets suggest that the vertical distribution of the lake herring may be influenced by temperature, abundance of plankton, and spawning. Very little is known of the horizontal movements of the species, although the available evidence indicates a random areal distribution in the inshore areas during April–June, a wide scattering during the summer (possibly small scattered schools in the open lake), an inshore movement in early fall when the fish begin to form larger schools in advance of spawning, and finally, the spawning season when they can be caught at widely varied depths and locations. Our recorded catches were affected, to be sure, by changes in activity as well as numbers. Heightened activity was probably an important factor in the fall catches, especially in the spawning season.

SUMMARY

1. The lake herring has been the principal species in the commercial production of Lake Superior since 1908. The 1929–61 average annual catch in U.S. waters was nearly 12 million pounds, 62.4 percent of the total U.S. production of lake herring for the Great Lakes. Minnesota dominated the catch in 1929–40, Wisconsin held the

lead in 1941-56 (exception in 1942), and Michigan had the largest catch in 1942 and 1957-61.

2. Small-mesh gill nets ($2\frac{1}{4}$ - to $2\frac{3}{8}$ -inch mesh) are the principal gear for catching lake herring in Lake Superior. On the average, about 90 percent of the annual production is landed during the spawning season in November and December.

3. Although recent production of lake herring in U.S. waters is not significantly below the 1929-61 mean, evidence exists that abundance has declined in certain areas of the lake. The decline from 1950-55 to 1956-61 in numbers of fish caught per unit effort of fishing was 31 percent at Bayfield and Portage Entry, and 27 percent at Marquette.

4. The life-history studies were based on 12,187 lake herring collected from commercial and experimental gill nets fished at various locations in Lake Superior in 1950-62. Individual growth histories were computed for 3,779 specimens collected from commercial landings at: Duluth, Minn.; Bayfield, Wis.; and Portage Entry and Marquette, Mich., during the fall spawning seasons of 1950-59. Growth was computed from scale measurements by direct proportion. Fish used in other phases of the study came from experimental gill nets and from the summer commercial lake herring fishery.

5. Some fish had begun new growth by May 3, although annulus formation was not complete until mid-August. Over 90 percent of the season's growth was complete by the end of September.

6. The age composition and mean age of the commercial samples varied moderately by year of capture and port. Age group IV dominated the catch each year at each port and contributed 53.2 percent of the total, followed by age group III (24.8 percent) and age group V (18.4 percent). The remaining age groups (II, VI, and VII) combined, contributed only 3.6 percent. The mean age of all the years' collections was 3.9 at Bayfield, Portage Entry, and Marquette, and 4.1 at Duluth. With few exceptions the average age of the females exceeded that of the males. The differences between the mean ages of the sexes did not exceed 0.5 year.

7. Although estimates of year-class strength were affected by several sources of bias, a ranking was nevertheless made on the basis of the number of fish of various ages taken per unit effort of fishing. The strength of the year classes declined irregularly at all of the ports during the period

(1946-55) for which data were available. The values (given as percentage deviations from the mean) ranged from 55.9 in 1947 to -44.0 in 1954 at Bayfield, from 55.7 in 1950 to -40.8 in 1955 at Portage Entry, and from 40.7 in 1947 to -33.7 in 1952 at Marquette. Fluctuations of year-class strength were similar at Marquette and Bayfield. Only the 1947 and 1950 year classes showed better than average strength at each port. Year classes 1954 and 1955 were weak at all ports.

8. The average total length of the females of an age group at capture was longer than that of the males in 20 of 24 comparisons at Duluth, Bayfield, and Portage Entry, and the males held a slight advantage (7 of 10 comparisons) at Marquette.

9. With only one exception (that of the VI-group males in the 1956-59 Bayfield samples), the average length of the age groups was larger in 1956-59 than in 1950-55. The increase in average length from the early to the late period ranged from 0.4 inch for the V-group males at Bayfield to 1.1 inches for the V-group males at Portage Entry. In general, the average size of the lake herring increased from the western to the eastern part of the lake.

10. The length distributions of the age groups typically had small ranges and extensive overlap. The length range of the age groups in the 1957 Marquette sample, for example, were as small as 1.9 inches (age group II) and did not exceed 3.9 inches (VI-group fish). The length interval of 12.0-13.4 inches was represented by all five age groups.

11. The relation between the total length in inches (L) and the weight in ounces (W) of Lake Superior lake herring from all of the collections, was described by the equation, $\log W = -2.54688 + 3.17008 \log L$.

12. The weights of lake herring of corresponding lengths were heavier in 1956-61 than in 1950-55. The average percentage increase in weight, length for length, was 8.8 percent at Bayfield, 5.2 percent at Marquette, and 4.4 percent at Portage Entry. Port-to-port differences in average weight among fish of the same length in 1950-55 showed a west-to-east trend toward increased weight. In 1956-61 the Marquette lake herring were generally heaviest, but port-to-port differences in weight among fish from Duluth, Bayfield, and Portage Entry were small.

13. The growth rate of Lake Superior lake herring varied according to port and period of capture. The fish from Duluth in 1956-59 were the slowest growing, followed in rank by those from Bayfield, Portage Entry, and Marquette. With only one exception (that of first-year calculated lengths of the Portage Entry fish), the calculated lengths of lake herring taken in 1956-59 were greater than those of fish taken in 1950-55. Lake herring caught in the later period at Marquette ranged from 0.2 inch longer in the first to 1.3 inches longer in the seventh year of life. Growth in length was greatest during the first year of life in both collecting periods (from 4.3 inches at Duluth to 5.0 inches at Marquette in 1956-59). With few exceptions, the annual increments of growth in length decreased progressively until the fifth year of life, after which the increments were 1.0 inch or less.

14. Growth in weight also increased from the western to eastern ports and from the early to late collecting period. The first-year calculated increments were small (less than 0.7 ounce) in both collecting periods. The increments increased progressively to a maximum in the fourth year of life at all ports except Bayfield and Marquette in 1956-59, where the annual increments were highest in the seventh year of life. The largest increment in weight (2.9 ounces) was in the seventh year of life at Marquette in 1956-59.

15. The trends of annual fluctuations in growth in length were similar at the three ports. In general, growth was below average in 1945-53 and above average in 1954-59. The quality of growth for all years of life expressed as percentage deviation from the 1945-59 mean, ranged from a low of -23.5 at Bayfield in 1946 to a maximum of 16.3 at Bayfield in 1959.

16. The annual fluctuations of growth in weight were similar to those of growth in length. Growth in weight was below average at Bayfield in 1945-50, at Portage Entry in 1945-54, and at Marquette in 1945-52. Growth was above average at all of the ports after 1954.

17. No correlation could be established between fluctuations of growth and changes in temperature or the abundance of lake herring.

18. The number of females equalled or exceeded that of the males in each age group except I (only 1 fish) from the nonspawning-run samples. The

advantage of the females progressively increased from 52.3 percent for age group III to 81.8 percent for group VII. The percentage of females was 68.5 for all age groups combined.

19. The youngest mature lake herring in Lake Superior belonged to age group II, and all fish older than III were mature. The shortest mature male appeared in the 8.5- to 8.9-inch group, and all males were mature at lengths greater than 11.4 inches. The first mature females appeared at 9.5-9.9 inches, and all were mature at lengths greater than 11.9 inches.

20. Major spawning of Lake Superior lake herring normally takes place during the last week of November and the first week of December. Water temperature at this time usually is between 37° F. and 40° F. The fish are pelagic spawners; the eggs are broadcast and settle to the bottom at depths ranging from 20 to 80 fathoms. The spawning fish show no preference for a particular bottom type.

21. The number of eggs produced by female lake herring (range 4,314 to 10,250) tended to increase with fish length, and the number of eggs per ounce of body weight decreased with increase in length. Lake Superior lake herring typically produce fewer eggs per individual fish and fewer eggs per ounce of fish weight than do lake herring from Green Bay, Lake Michigan.

22. Crustacea were by far the most common food and were found in 83 percent of 146 stomachs examined from Lake Superior lake herring. Other food included insects and fish eggs (presumably those of lake herring).

23. The vertical distribution of the lake herring may be influenced by temperature, abundance of plankton, and spawning. During the early summer, the fish are most common near the surface where plankton is most abundant. As the surface water warms in midsummer, the lake herring move to deeper levels, despite the high concentration of plankton near the surface. After September 13, they were randomly distributed from the surface to about 20 fathoms, and during the spawning season, they were captured in good numbers at all depths down to 90 fathoms.

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LITERATURE CITED

- ALM, GUNNAR.
1959. Connection between maturity, size and age in fishes. Fishery Board of Sweden, Report of the Institute of Freshwater Research, Drottningholm, No. 40, pp. 5-145.
- BAJKOV, ALEXANDER.
1930. Fishing industry and fisheries investigations in the prairie provinces. Transactions of the American Fisheries Society, vol. 60, pp. 215-237.
- BROWN, C. J. D., AND J. W. MOFFETT.
1942. Observations on the number of eggs and feeding habits of the cisco (*Leucichthys artedii*) in Swains Lake, Jackson County, Michigan. Copeia, 1949, No. 3, pp. 149-152.
- CAHN, ALVIN ROBERT.
1927. An ecological study of southern Wisconsin fishes. Illinois Biological Monographs, vol. II, No. 1, 151 pp.
- CARLANDER, KENNETH D.
1945. Growth, length-weight relationship and population fluctuations of the tullibee, *Leucichthys artedii tullibee* (Richardson), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Transactions of the American Fisheries Society, vol. 73 (1943), pp. 125-136.
- CLEMENS, WILBERT A.
1922. A study of the ciscoes of Lake Erie. University of Toronto Studies, Biological Series, No. 20, Publications Ontario Fisheries Research Laboratory, No. 2, pp. 27-37.
- COOPER, GERALD P.
1937. Age, growth, and morphometry of the cisco, *Leucichthys artedii* (Le Sueur), in Blind Lake, Washenaw County, Michigan. Papers Michigan Academy of Science, Arts, and Letters, vol. 22 (1936), pp. 563-571.
- DEASON, HILARY J., AND RALPH HILE.
1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74 (1944), pp. 88-141.
- DRYER, WILLIAM, R.
1963. Age and growth of the whitefish in Lake Superior. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 63, No. 1, pp. 77-95.
- DYMOND, J. R.
1933. Biological and oceanographic conditions in Hudson Bay. The coregonine fishes of Hudson and James Bays. Biological Board of Canada, Contributions Canadian Biology and Fisheries, vol. 8, No. 1 (series A, general, No. 28), pp. 1-12.
- EL-ZARBA, SALAH EL-DIN.
1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay; Lake Huron. U.S. Fish and Wildlife Service, Fishery Bulletin 151, vol. 59, pp. 365-415.
- HILE, RALPH.
1936. Age and growth of the cisco, *Leucichthys artedii* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bulletin of the U.S. Bureau of Fisheries, No. 19, vol. 48, pp. 211-317.
1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters, vol. 33, pp. 189-337.
1954. Fluctuations in growth and year-class strength of the walleye in Saginaw Bay. U.S. Fish and Wildlife Service, Fishery Bulletin 91, vol. 56, pp. 7-59.
- HJORT, JOHAN.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux, Conseil Permanent International pour l'Exploration de la Mer, vol. 20, 288 pp.
- HUBBS, CARL L., AND KARL F. LAGLER.
1958. Fishes of the Great Lakes Region. The Cranbrook Institute of Science, Bloomfield Hills, Michigan, Bulletin 26, 213 pp. (revised edition).
- JOBES, FRANK W.
1952. Age, growth, and production of yellow perch in Lake Erie. U.S. Fish and Wildlife Service, Fishery Bulletin 70, vol. 52, pp. 205-266.
- KOELZ, WALTER N.
1926. Fishing industry of the Great Lakes. Department of Commerce, Report of the U.S. Commissioner of Fisheries for 1925, Appendix II, pp. 553-617.
1929. Coregonid fishes of the Great Lakes. Bulletin of the U.S. Bureau of Fisheries, vol. 43 (1927), part 2, pp. 297-643.
- MOFFETT, JAMES W.
1952. The study and interpretation of fish scales. The Science Counselor, vol. 15, No. 2, pp. 40-42.
- PRITCHARD, ANDREW L.
1930. Spawning habits and fry of the cisco (*Leucichthys artedii*) in Lake Ontario. Biological Board of Canada, Contributions Canadian Biology and Fisheries, N.S., vol. 6 (1930), No. 9, pp. 227-240.
- PYCHA, RICHARD L.
1961. Recent changes in the walleye fishery of northern Green Bay and history of the 1943 year class. Transactions of the American Fisheries Society, vol. 90, No. 4, pp. 475-488.
- SCOTT, W. B.
1951. Fluctuations in abundance of the Lake Erie cisco (*Leucichthys artedii*) population. Contributions Royal Ontario Museum of Zoology, No. 32, 41 pp.
- SMITH, STANFORD H.
1954. Method of producing impressions of fish scales without using heat. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 16, No. 2, pp. 75-78.
1956. Life history of lake herring of Green Bay, Lake Michigan. U.S. Fish and Wildlife Service, Fishery Bulletin 109, vol. 57, pp. 87-138.

STONE, UDELL B.

1938. Growth, habits, and fecundity of the ciscoes of Irondequoit Bay, New York. Transactions of the American Fisheries Society, vol. 67 (1937), pp. 234-245.

VAN OOSTEN, JOHN.

1929. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bulletin of the U.S. Bureau of Fisheries, vol. 44 (1928), pp. 265-428.

1944. Factors affecting the growth of fish. Trans-

actions of the Ninth North American Wildlife Conference, pp. 177-183.

VAN OOSTEN, JOHN, AND RALPH HILE.

1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77 (1947), pp. 176-249.

WATT, KENNETH E. F.

1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. Journal of the Fisheries Research Board of Canada, vol. 13, No. 5, pp. 613-645.

ANNOTATED BIBLIOGRAPHY ON BIOLOGY OF MENHADENS AND MENHADENLIKE FISHES OF THE WORLD

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ABSTRACT

The bibliography has 238 references on the classification, distribution, abundance, ecology, and life history of menhadens and similar clupeid fishes of the genera *Brevoortia*, *Ethmalosa*, and *Ethmidium*. Included are major references to the North American menhaden

articles published through 1957 and all references 1958-62. All available references to the South American menhadens and the West African shad are included. Brief annotations and a subject index also are provided.

This bibliography is an expansion and a continuation of that compiled by Reintjes, Christmas, and Collins (1960) on the biology of the American menhadens. Of the literature listed in that publication pertaining to the North American menhadens, only the major references published before 1958 are included in this work; the minor references, checklists, and incidental reports are not. Any references published prior to 1958 that were omitted from the preceding bibliography are included.

The bibliography concerns the menhadens, genus *Brevoortia*, and similar clupeid or menhadenlike fishes of the genera *Ethmalosa* and *Ethmidium*. At present, *Brevoortia*, on the Atlantic Coast of the United States including the Gulf of Mexico, and *Ethmalosa*, on the Atlantic Coast of West Africa, compose the largest fishery in each area. Furthermore, *Brevoortia* and *Ethmidium* offer resource potentials for the Atlantic and Pacific Coasts of South America.

Knowledge of the scientific and technical information on the identity, distribution, and biology of these fishes is essential for determining the

extent of their resources and their potential. The principal purpose of this bibliography is to encourage inquiry, research, and exploration, by furnishing references to the published accounts on menhaden and menhadenlike fishes.

In general, the geographical distribution of the species of menhadens and menhadenlike fishes of the world¹ may be summarized as shown in table 1.

In reviewing the literature, certain criteria were used to decide which references should be included. Included, in general, were references to taxonomy, distribution, occurrence, abundance, life history, morphology, ecology, and behavior. Excluded generally were references on the technological aspects of the fishery and the processing industry; daily, monthly, and annual landing reports and statistics; popular accounts in trade journals, newspapers, and magazines; and administrative and project reports. Mimeographed or similarly processed reports of an established series, or when principally concerned with these fishes, have been included.

The arrangement of the references is alphabetically by author's surname. With multiple authors the entry is made only under the senior author's name. Each author's works are listed chrono-

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¹ The genera *Macrura*, *Gudusia*, and *Hilsa* (in part) from the Indian Ocean, although similar, are not included in this bibliography.

TABLE 1.—*Menhadens and menhadenlike fishes by geographical areas*

Scientific name	Common name	Area
<i>Brevoortia tyrannus</i>	Atlantic menhaden.....	Atlantic Coast of North America from Nova Scotia to Florida.
<i>Brevoortia smithi</i>	Yellowfin menhaden.....	Atlantic Coast of the United States and Gulf of Mexico from North Carolina to Louisiana.
<i>Brevoortia patronus</i>	Gulf menhaden.....	Gulf of Mexico from Florida to Mexico.
<i>Brevoortia gunteri</i>	Finescale menhaden.....	Gulf of Mexico from Alabama to Mexico.
<i>Brevoortia pectinata</i>	Lacha or savelha.....	Atlantic Coast of South America from Brazil to Argentina.
<i>Brevoortia aurea</i>	Lacha or savelha.....	Atlantic Coast of South America from Brazil to Argentina.
<i>Ethmidium chilcae</i>	Machete, machuela, or trite.	Pacific Coast of South America from Peru and Chile.
<i>Ethmidium maculatum</i>	Machete, machuela, or trite.	Pacific Coast of Central and South America from Mexico to Peru.
<i>Ethmalosa fimbriata</i> ...	West African shad or bonga.	Atlantic Coast of West Africa from Senegal to Angola.

logically by year of publication, and those published in the same year are given alphabetical sequence by title. Pagination is given for the complete paper, not solely for the pages referring directly to the subject species. Such a restricted pagination was used by Reintjes, Christmas, and Collins (1960) to circumscribe limited references to menhaden occurring incidentally in larger works.

Brief annotations of the contents of the publications and the scientific names of the species concerned are given. This annotation is done not to make value judgments of the papers but to give clearer descriptions of the contents than can be obtained from their titles.

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BIBLIOGRAPHY

ABBOTT, JAMES FRANCIS.

1899. The marine fishes of Peru. Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 51, pt. 2, pp. 324-364.

Potamalosa notacanthoides and *P. maculata* described.

ANDERSON, ARTHUR E., EDWARD C. JONAS, and HOWARD T. ODUM.

1958. Alteration of clay minerals by digestive processes of marine organisms. Science, vol. 127, No. 3291, pp. 190-191.

Clay minerals in stomach contents of menhaden mentioned.

ANGELESCU, VICTOR, and ENRIQUE E. BOSCHI.

1959. Estudio biologico pesquero del langostino de Mar del Plata en conexión con la Operacion Nivel Medio. Republica Argentina, Secretaria de Marina, Servicio de Hidrografia Naval, H. 1017, 135 pp.

Brevoortia aurea taken by shrimp trawls in the region of Mar del Plata.

ANONYMOUS.

1948. Note on *Ethmalosa fimbriata* (Bowdich). Cybium, Fiche Ichtyologique, No. 2, pp. 5-7; No. 3, pp. 7-8.

Vernacular names in West Africa.

1959. Menhaden—research on parasites may reveal migratory routes. U.S. Department of the Interior, Fish and Wildlife Service, Commercial Fisheries Review, vol. 21, No. 6, p. 40.

A brief comment on the use of parasites as natural tags to infer menhaden migrations.

ARNOLD, EDGAR L., JR., RAY S. WHEELER, and KENNETH N. BAXTER.

1960. Observations on fishes and other biota of East Lagoon, Galveston Island. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 344, 30 pp.

Monthly occurrence of *Brevoortia patronus* larvae, 1953-58.

ARVE, JOHN.

1960. Preliminary report on attracting fish by oyster-shell plantings in Chincoteague Bay, Maryland. Chesapeake Science, vol. 1, No. 1, pp. 58-65.

Brevoortia tyrannus caught in wire fish traps.

BAILEY, REEVE M., ERNEST A. LACHNER, C. C. LINDSEY, C. RICHARD ROBINS, PHIL M. ROEDEL, W. B. SCOTT, and LOREN P. WOODS.

1960. A list of common and scientific names of fishes from the United States and Canada. American Fisheries Society, Special Publication No. 2, 102 pp.

Common and scientific names of the four North American species of *Brevoortia*.

BAINBRIDGE, V.

1957. Food of *Ethmalosa dorsalis* (Cuvier and Valenciennes). Nature, vol. 179, No. 4565, pp. 874-875.

Comparison of food contents of *Ethmalosa dorsalis* with plankton and relation to salinity of Sierra Leone River.

1960. The plankton of inshore waters off Freetown, Sierra Leone. British Colonial Office, Fishery Publication No. 13, 48 pp.

Relation of the plankton to the *Ethmalosa* or bonga fishery.

1961. The early life history of the bonga, *Ethmalosa dorsalis* (Cuvier and Valenciennes). Journal du Conseil, vol. 26, No. 3, pp. 347-353.

Description of developing eggs and newly hatched

- larvae of *Ethmalosa dorsalis* from eggs artificially fertilized, and the occurrence of eggs and larvae in Sierra Leone River.
1962. The larvae of *Pellonula vorax* (Günther) (Clupeidae) in Sierra Leone coastal waters. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 24, No. 1, p. 262-269.
Includes a comparison of *Ethmalosa dorsalis* with other clupeid larvae (*Pellonula vorax*, *Sardinella eba*, *S. cameronensis*, and *Ilisha africana*).
- BEARDEN, CHARLES M.
1961. Common marine fishes of South Carolina. Contributions from Bears Bluff Laboratories, No. 34, 47 pp.
Brevoortia tyrannus listed.
- BEATTY, STANLEY A.
1959. Report to the Government of Brazil on the organization of fish processing research. Food and Agriculture Organization of the United Nations, Expanded Technical Assistance Program, Report No. 1174, 41 pp.
Reported *Brevoortia tyrannus* "savelha" among the principal species salted in the Rio Grande area.
1961. Brazilian fishing. In Georg Borgstrom and Arthur J. Heighway, editors, Atlantic Ocean fisheries, pp. 205-212. Fishing News (Books) Ltd., London.
Brief comments on the fishery for *Brevoortia tyrannus aurea*.
- BEHNKE, ROBERT J., and RALPH M. WETZEL.
1960. A preliminary list of the fishes found in the fresh waters of Connecticut. Copeia, 1960, No. 2, pp. 141-143.
Brevoortia tyrannus listed from fresh water.
- BERG, CARLOS.
1895. Enumeración sistemática y sinónfmica de los peces de las costas Argentina y Uruguay. Anales del Museo Nacional de Historia Natural de Buenos Aires, tomo 4, serie 2, pp. 1-120.
Clupea pectinata and *Brevoortia tyrannus* listed with synonymy.
- BERG, LEO S.
1940. Sistema ryboobraznykh i ryb, nyne zhivushchikh i iskopaemykh. Akademiã Nauk SSSR, Trudy Zoologicheskogo Instituta, Moskva, tom 5, vyp. 2, 345 pp.
Classification of genera *Brevoortia* and *Ethmidium*.
1947. Classification of fishes both recent and fossil. J. W. Edwards, Ann Arbor, Mich., 517 pp. Reprint of Berg (1940) plus English translation.
Classification of genera *Brevoortia* and *Ethmidium*.
- BLANC, A.
1948. Quelques observations sur la migration des Clupéidés dans le secteur de la Petite Côte (Sénégal). Bulletin des Services de l'Élevage et de Industries Animales de l'Afrique Occidentale Française, tome 1, No. 4, pp. 45-57.
General description of distribution and occurrence of *Ethmalosa dorsalis*.
- BLOMEFIELD, LEONARD.
See Jenyns, 1842.
- BORGSTROM, GEORG.
1961. U.S. Atlantic fisheries and current trends in supply and use. In Georg Borgstrom and Arthur J. Heighway, editors, Atlantic Ocean fisheries, pp. 225-255. Fishing News (Books) Ltd., London.
Menhaden fishery mentioned.
- BOROUGH, HOWARD, WALTER A. CHIPMAN, and THEODORE R. RICE.
1957. Laboratory experiments on the uptake, accumulation, and loss of radionuclides by marine organisms. In Report of the Committee on the effects of atomic radiation on oceanography and fisheries, pp. 80-87. National Academy of Sciences—National Research Council, Publication No. 551.
Experimental uptake of ruthenium-106 by menhaden.
- BOULENGER, G. A.
1905. Poissons de la Guinée Espagnole. Memorias de la Real Sociedad Española de Historia Natural Madrid, vol. 1, No. 9, pp. 187-188.
Clupea dorsalis listed from the Rio Benito, Spanish Guinea.
- BOWDICH, THOMAS EDWARD.
1825. Excursions in Madeira and Porto Santo, during the autumn of 1823, while on his third voyage to Africa . . . to which is added, by Mrs. Bowdich . . . III. Appendix: containing zoological and botanical descriptions, and translations from the Arabic. George B. Whittaker, London, 278 pp.
Original description of *Ethmalosa fimbriata* as *Clupea fimbriata*.
1826. Excursions dans les îles de Madère et de Porto Santo, faites dans l'automne de 1823, pendant son troisième voyage en Afrique; . . . suivies . . . 3° d'un appendice contenant des observations relatives à la zoologie et à la botanique et un choix de morceaux traduits de l'arabe par Mme. Bowdich. F. G. Levrault, Paris, 447 pp.
French edition; see Bowdich, 1825.
- BREDER, C. M., JR.
1960. Design for a fry trap. Zoologica, vol. 45, pt. 4, No. 10, pp. 155-159.
Occurrence of *Brevoortia* larvae in plastic fish trap.
1962. Effects of a hurricane on the small fishes of a shallow bay. Copeia, 1962, No. 2, pp. 459-462.
Reported occurrences of *Brevoortia patronus* larvae in fish trap catches, spring and fall, 1960.
- BREUER, JOSEPH P.
1962. An ecological survey of the Lower Laguna Madre of Texas, 1953-1959. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 153-183.
Reported the common occurrence of *Brevoortia gunteri* and a few *B. patronus*. Both species utilized the Arroyo Colorado for nursery grounds.

- BRIGGS, JOHN C.
1958. A list of Florida fishes and their distribution. Bulletin of the Florida State Museum, Biological Sciences, vol. 2, No. 8, pp. 223-318.
Brevoortia tyrannus, *B. patronus*, *B. smithi*, and *B. gunteri* listed.
- BROWN, HERBERT H.
1948. Note on the organisation of fishery research in British West Africa. In Conférence de la Pêche Maritime, Dakar, 1948, pp. 279-292. Centre National d'Information Économique, Paris.
Ethmalosa fishery mentioned.
- BULLIS, HARVEY R., JR.
1961. A progress report on experimental fishing for sardine-like fishes in the Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute, 13th Annual Session, 1960, pp. 94-97.
Brevoortia patronus caught by midwater trawl.
- BUTLER, PHILIP A. (EDITOR).
1959. Annotated bibliography of unpublished estuarine research in the Gulf of Mexico, 1925-1959. Gulf States Marine Fisheries Commission, New Orleans, 51 pp. (Processed).
Includes references to the distribution of marine fishes, including menhaden, in estuaries.
1960. Annotated bibliography of unpublished estuarine research in the Gulf of Mexico, supplement 1. Gulf States Marine Fisheries Commission, New Orleans, 17 pp. (Processed).
Includes references to the distribution of marine fishes, including menhaden, in estuaries.
- BYCHOWSKY, BORIS E.
1957. Monogeneticheskie sosal'shchiki ikh sistema i filogeniâ. Akademîâ Nauk SSSR, Zoologicheskii Institut Moskva, 509 pp.
Parasites of *Brevoortia gunteri* mentioned.
1961. Monogenetic trematodes, their systematics and phylogeny. English editor, William J. Hargis, Jr. American Institute of Biological Sciences, 627 pp.
English translation of Bychowsky, 1957.
- CADENAT, J.
1947. Noms vernaculaires des principales formes d'animaux marins des Côtes de l'Afrique Occidentale Française. Institut Français d'Afrique Noire, Catalogue No. 2, pp. 1-56.
Ethmalosa fimbriata listed with local common names from Senegal, French Guinea, Ivory Coast, and Dahomey.
1948. Physionomie générale de la pêche maritime en A.O.F. In Conférence de la Pêche Maritime, Dakar, 1948. Centre National d'Information Économique, Paris. pp. 25-60.
Brief mention of *Ethmalosa* fishery.
1950. Poissons de mer du Sénégal. Institut Français d'Afrique Noire, Initiations Africaines, No. 3, 345 p.
Ethmalosa fimbriata synonym *E. dorsalis* listed with figures.
1960. Notes d'Ichtyologie ouest-africaine. XXX.— Poissons de mer ouest-africains observés du Sénégal au Cameroun et plus spécialement au large des Côtes de Sierra Leone et du Ghana. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 22, No. 4, pp. 1358-1423.
Reported occurrence of *Ethmalosa dorsalis* from Nigeria, Ghana, and Sierra Leone.
- CAMPOS AMARAL, A.
1942. Contribuição ao estudo dos clupeóides das águas brasileiras. Arquivos de Zoologia do Estado de São Paulo, vol. 3, art. 7, pp. 185-218. Also Revista do Museu Paulista, São Paulo, tomo 26.
Brief description of *Brevoortia tyrannus aurea* with synonymy and some references. Keys to genera and species of clupeid fishes of Brazil.
- CARRANZA, JORGE.
1959. Pesca y recursos pesqueros. In Enrique Beltran, editor, Los recursos naturales del Sureste y su aprovechamiento, pp. 151-238. Instituto Mexicano de Recursos Naturales Renovables, Mexico, D.F., parte 2, tomo 3, capítulo 5.
Potential menhaden resource mentioned.
- CASTILLO, LUIS, and ZACARIAS VERGARA.
1907. La pesca en la Bahía de Coquimba. Anales Agrónómicos, Santiago, 18 pp.
Clupea maculata mentioned.
- CHABANAUD, PAUL, and THÉODORE MONOD.
1926. Les poissons de Port-Étienne. Contribution à la faune ichtyologique de la région du Cap Blanc (Mauritanie française). Bulletin Comité l'Étude Histoire Scientifique de l'Afrique Occidentale Française, tome 9, No. 2, pp. 225-287.
Ethmalosa dorsalis listed.
- CHIPMAN, WALTER A.
1959. The use of radioisotopes in studies of the foods and feeding activities of marine animals. Pubblicazioni della Stazione Zoologica di Napoli, supplemento vol. 31, pp. 154-175.
Use of radioisotopes in food and feeding of larval and juvenile *Brevoortia tyrannus*.
1960. Biological aspects of disposal of radioactive wastes in marine environments. In proceedings of the Scientific Congress on the Disposal of Radioactive Wastes, Monaco, 1959, pp. 1-15. International Atomic Energy Agency, Vienna, vol. 2.
Radioactivity of *Brevoortia tyrannus* after feeding on phytoplankton cells containing ruthenium-106.
- CHRISTMAS, J. Y.
1960. Greater and lesser scaup feeding on dead gulf menhaden. Auk, vol. 77, No. 3, pp. 346-347.
Observations of ducks feeding on dead *Brevoortia patronus* discarded from the shrimp trawl fishery.
- CHRISTMAS, J. Y., and GORDON GUNTER.
1960. Distribution of menhaden, genus *Brevoortia*, in the Gulf of Mexico. Transactions of the American Fisheries Society, vol. 89, No. 4, pp. 338-343.
Review of literature on *Brevoortia* in the Gulf of Mexico with a comparison of *B. gunteri* and *B. smithi* collected together in the northern gulf.

- CHRISTMAS, J. Y., GORDON GUNTER, and EDWARD C. WHATLEY.
1960. Fishes taken in the menhaden fishery of Alabama, Mississippi, and eastern Louisiana. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 339, 10 pp.
Sampling of *Brevoortia patronus* purse seine catches for species composition.
- CUSHING, D. H., FINN DEVOLD, JOHN C. MARR, and H. KRISTJONSSON.
1952. Some modern methods of fish detection. Food and Agriculture Organization of the United Nations, Fisheries Bulletin, vol. 5, Nos. 3-4, pp. 95-119.
Aerial spotting in menhaden purse seine fishery.
- CUVIER, GEORGES, and ACHILLE VALENCIENNES.
1847. Histoire naturelle des poissons. P. Bertrand, Paris, tomo 20, 472 pp.
Descriptions of *Alausa aurea*, *A. tyrannus*, *A. menhaden*, *A. maculata*, and *A. caerulea*.
- DARNELL, REZNEAT M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publications of the Institute of Marine Science, Texas, vol. 5, pp. 353-416.
Stomachs of juvenile *Brevoortia patronus* contained phytoplankton and detritus as the principal contents.
1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology, vol. 42, No. 3, pp. 553-568.
Food of juvenile *Brevoortia patronus* and the occurrence as food of predators.
1962. Ecological history of Lake Pontchartrain, an estuarine community. American Midland Naturalist, vol. 68, No. 2, pp. 434-444.
Brevoortia patronus mentioned.
- DARWIN, CHARLES R.
1842. The zoology of the voyage of H.M.S. *Beagle*, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Smith, Elder, and Co., London.
See Jenyns, 1842.
- DE BUEN, FERNANDO.
1950. La fauna de peces del Uruguay. In El Mar de Solís y su fauna de peces, 2ª parte, Servicio Oceanográfico y de Pesca, Publicaciones Científicas, No. 2, pp. 45-144.
Brevoortia pectinata and *B. aurea* listed with synonymy and bibliography.
1953. Las familias de peces de importancia económica. Primer Centro Latinoamericano de Capacitación Pesquera, Oficina Regional de la FAO, Valparaíso, 311 pp.
Distribution of all species of *Brevoortia* reviewed briefly, after Hildebrand, 1948. *Brevoortia pectinata* used for bait in shark fishery, and salted or smoked for human consumption. *B. aurea* mentioned.
1958. Peces de la superfamilia Clupeoidae en aguas de Chile. Revista de Biología Marina, Valparaíso, vol. 8, Nos. 1-3, pp. 83-110.
Described *Ethmidium maculata* and *E. chilcae* as *Brevoortia (Ethmidium) maculata* and *B. (E.) chilcae*.
1959. Lampreas, tiburones, rayas y peces en la Estación de Biología Marina de Montemar, Chile. First Contribution. Revista de Biología Marina, Valparaíso, vol. 9, Nos. 1-3, pp. 1-200.
Brevoortia (Ethmidium) maculata and *B. (E.) chilcae* listed.
- DE CARVALHO, VICENTE ANTÃO.
1957. Nomes vulgares de peixes Brasileiros marinhos com seus correspondentes em sistemática. Conselho coordenador do Abastecimento, Rio de Janeiro, 21 pp. (Processed.)
Brevoortia tyrannus (sic), "savelha" listed.
- DEEVEY, GEORGIANA BAXTER.
1956. Zooplankton. In Oceanography of Long Island Sound, 1952-1954, pp. 113-155. Bulletin of the Bingham Oceanographic Collection, vol. 15, pt. 5.
Filter feeding of menhaden mentioned.
- DELFIN, FEDERICO T.
1900. Catálogo de los peces de Chile (continuación). Revista Chilena de Historia Natural, Año 4, núm. 1, pp. 4-6; núm. 2, pp. 21-25.
Clupea caerulea, *C. notocanthus*, *C. maculata*, and *C. advena* listed with synonymy.
1902. Concordancia de nombres vulgares y científicos de los peces de Chile. Revista Chilena de Historia Natural, Año 6, núm. 2, pp. 71-76.
Generally the same as Delfin, 1900, with common names.
- DE OLIVERA, HELENE PAES.
1942. Espécies de sardinhas que ocorrem no litoral brasileiro. Serviço de Informação Agrícola Brasil, Ministerio de Agricultura, Rio de Janeiro, pp. 1-30.
A description of *Brevoortia tyrannus aurea* with figure and key to genera of Clupeidae.
- DE SYLVA, DONALD P., FREDERICK A. KALBER, JR., and CARL N. SHUSTER, JR.
1962. Fishes and ecological conditions in the shore zone of the Delaware River Estuary, with notes on other species collected in deeper waters. University of Delaware Marine Laboratories, Information Series Publication No. 5, 164 pp.
Occurrence and size distribution of *Brevoortia tyrannus* in seine collections for bimonthly intervals, August 1958 to February 1960.
- DEUBLER, EARL E., JR.
1958. A comparative study of the postlarvae of three flounders (*Paralichthys*) in North Carolina. Copeia, 1958, No. 2, pp. 112-116.
Diurnal variation of *Brevoortia tyrannus* postlarvae in experimental trawl catches.
- DEVINCENZI, GARIBALDI J.
1920. Peces del Uruguay. Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 1, entrega 4, pp. 97-138.

- Review of the literature referring to *Brevoortia* in the region.
1924. Peces del Uruguay (Conclusion). Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 1, entrega 5, pp. 139-293.
Clupea pectinata Jenyns reported as *Brevoortia tyrannus* with counts and body proportions for nine specimens.
1925. El primer ensayo sobre ictiología del Uruguay. La clase "Peces" de la zoología de don Dámaso A. Larrañaga. Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 1, entrega 6, pp. 295-323.
Clupea laccia vel 20-radiata described as *Brevoortia tyrannus*.
- DEVINCENZI, GARIBALDI J., and LUIS P. BARATTINI.
1928. Álbum ictiológico del Uruguay. Anales del Museo de Historia Natural de Montevideo, serie 2, tomo 2, entrega 4, 24 plates.
A drawing of *Brevoortia tyrannus*.
- DOLLO, LOUIS.
1904. Poissons. Expédition Antartique Belge. Résultats du Voyage du S.Y. *Belgica*, Zoologie, pt. 4, 239 pp.
Potamalosa notacanthus reported from South America.
- DOUTRE, M. P.
1959. Composition chimique du poisson. Variations annuelles de la teneur en matières grasses de trois clupéidés du Senegal (*Ethmalosa fimbriata* Bowdich, *Sardinella eba* C.V., *Sardinella aurita* C.V.). Communications de la Section Technique des Pêches Maritimes, Dakar, No. 124, 4 pp.
Average body fat contents by month.
- DUMERIL, AUGUSTE.
1861. Reptile et poissons de l'Afrique Occidentale . . . Archives du Muséum d'Histoire Naturelle, Paris, 1858-61, vol. 10, pp. 137-160, 233-240, 261-264.
Clupea aurea from Senegal.
- EDWARDS, HENRI MILNE.
See Milne-Edwards, 1840.
- ELLISON, WILLIAM A., JR.
1951. The menhaden. In Survey of marine fisheries of North Carolina. Harden F. Taylor and associates: pp. 85-107. University of North Carolina Press, Chapel Hill, N.C.
General account of menhaden and the menhaden purse seine fishery.
- EVERMANN, BARTON WARREN, and WILLIAM CONVERSE KENDALL.
1906. Notes on a collection of fishes from Argentina, South America, with descriptions of three new species. Proceedings of the U.S. National Museum, vol. 31, No. 1482, pp. 67-108.
Brevoortia specimens not distinguished from *B. tyrannus*.
- FOWLER, HENRY W.
1911. Notes on clupeoid fishes. Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 63, pp. 204-221.
- Reported occurrence of *Brevoortia tyrannus* along the Atlantic Coast of the U.S., *B. tyrannus patronus* from the Gulf of Mexico, *B. tyrannus aurea* from Brazil, and *B. tyrannus dorsalis* from Gaboon River, West Africa.
1936. The marine fishes of West Africa based on the collection of the American Museum Congo Expedition, 1909-1915. Bulletin of the American Museum of Natural History, New York, vol. 70, pt. 1, pp. 1-605.
Brevoortia tyrannus reported from Senegal, description of specimens from United States. *Ethmalosa fimbriata* described with extensive synonymy and some references not included in this bibliography.
1940. Fishes obtained by the Wilkes Expedition, 1838-1842. Proceedings of the American Philosophical Society, vol. 82, No. 5, pp. 733-800.
Brevoortia pectinata listed with figure. *Ethmidium maculatum* listed with figure.
1942. A list of the fishes known from the coast of Brazil. Arquivos de Zoologia do Estado de São Paulo, vol. 3, art. 6, pp. 115-184. Also Revista do Museu Paulista, São Paulo, tomo 26.
Brevoortia tyrannus with synonymy for *B. aurea* and *B. pectinata* listed. A figure of *B. tyrannus aurea*.
1944. Fishes of Chile. Systematic catalog. Pt. 2. Revista Chilena de Historia Natural Pura y Aplicada. Años 46-47, pp. 15-116.
Ethmidium maculatum listed with synonymy.
1945. Los peces del Peru. Catálogo Sistemático de los peces que habitan en aguas peruanas. Museo de Historia Natural "Javier Prado" Universidad Nacional Mayor de San Marcos, Lima, 298 pp.
Ethmidium maculatum listed with synonymy.
1948. Os peixes de água doce do Brasil. Arquivos de Zoologia do Estado de São Paulo, vol. 6, pt. 1, pp. 1-204.
Original description of new subfamily Brevoortinae. *Brevoortia aurea* listed.
- 1951a. Analysis of the fishes of Chile. Revista Chilena de Historia Natural Pura y Aplicada, Años 51-53, pp. 263-326.
Ethmidium maculatum placed in subfamily Brevoortinae.
- 1951b. The Brazilian and Patagonian fishes of the Wilkes Expedition, 1838-1842. Boletim do Instituto Paulista de Oceanografia, São Paulo, tomo 2, fasc. 1, pp. 1-39.
Brevoortia pectinata listed and compared with *B. tyrannus*.
- GAY, CLAUDIO.
1848. Peces de Guichinot. In Historia física y política de Chile. . . Zoologia, tomo 2, pp. 137-370. Paris.
Alosa maculata and *A. caerulea* listed.
- GILL, THEODORE.
1861. Synopsis of the subfamily Clupeinae, with descriptions of new genera. Proceedings of the

- Academy of Natural Sciences, Philadelphia, vol. 13, pp. 33-38.
- Original description of genus *Brevoortia*.
- GOODE, G. BROWN.
1878. A revision of the American species of the genus *Brevoortia*, with a description of a new species from the Gulf of Mexico. Proceedings of the U.S. National Museum, vol. 1, pp. 30-42.
- Original descriptions of *Brevoortia patronus* and *B. tyrannus brevicaudata* including remarks about *B. pectinata* and *B. aurea*.
1879. The natural and economical history of the American menhaden. Report of the U.S. Commission of Fish and Fisheries, 1877, app. A, 529 pp.
- An extensive review of the biology, fishery, and industry for the Atlantic menhaden, *Brevoortia tyrannus*. Also included are summary remarks about *B. patronus*, *B. aurea*, and *B. pectinata*.
- GORDON, BERNARD L.
1961. A guide book to the marine fishes of Rhode Island. Book & Tackle Shop, Watch Hill, R.I., 136 pp.
- Brief description and general account of *Brevoortia tyrannus*.
- GRANT, GEORGE C.
1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Science, vol. 3, No. 1, pp. 45-47.
- Stomach content analysis of young bluefish showed juvenile menhaden to be one of the more important foods.
- GRAS, ROGER.
1961. Liste des poissons du Bas-Dahomey faisant partie de la collection du laboratoire d'hydrobiologie du service des eaux, forêts, et chasses du Dahomey. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 23, No. 2, pp. 572-586.
- Ethmalosa fimbriata* listed as abundant.
- GUICHENOT.
1848. See Gay, Claudio, 1848.
- GUNTER, GORDON.
1957. Predominance of the young among marine fishes found in fresh water. Copeia, 1957, No. 1, pp. 13-16.
- Brevoortia tyrannus* mentioned after Massmann, 1954.
1958. Population studies of the shallow water fishes of an outer beach in south Texas. Publications of the Institute of Marine Science, Texas, vol. 5, pp. 186-193.
- Brevoortia* sp. occurred on the outer beach April-August, 1949.
1961. Some relations of estuarine organisms to salinity. Limnology and Oceanography, vol. 6, No. 2, pp. 182-190.
- Relation of haul seine catches of *Brevoortia patronus* to low salinity.
- GUNTER, GORDON, and J. Y. CHRISTMAS.
1960. A review of literature on menhaden, *Brevoortia patronus* Goode. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 363, 31 pp.
- GUNTER, GORDON, and WILLIAM J. DEMORAN.
1961. Lateral lines and an undescribed sensory area on the head of the gulf menhaden, *Brevoortia patronus*. Copeia, 1961, No. 1, pp. 39-42.
- Description of the cephalic sensory canals and review of the literature of the structure in other fishes.
- GUNTER, GORDON, and WILLIAM E. SHELL, JR.
1958. A study of an estuarine area with water-level control in the Louisiana marsh. Proceedings of the Louisiana Academy of Science, vol. 21, pp. 5-34.
- Monthly catches of *Brevoortia patronus*, 1951-53, with the relation of haul seine catches to low salinity.
- GÜNTHER, ALBERT.
1868. Catalogue of the fishes in the British Museum. Taylor and Francis, London, vol. 7, 512 pp.
- Clupea menhaden*, *C. aurea*, *C. pectinata*, and *C. dorsalis* listed and briefly described.
- HALKETT, ANDREW.
1913. Check list of the fishes of the Dominion of Canada and Newfoundland. C. H. Parmelee, Ottawa, 138 pp.
- Brevoortia tyrannus* listed.
- HALL, F. G., and F. H. McCUTCHEON.
1938. The affinity of hemoglobin for oxygen in marine fishes. Journal of Cellular and Comparative Physiology, vol. 11, No. 2, pp. 205-212.
- Affinity of hemoglobin of *Brevoortia tyrannus* for oxygen in buffered solutions at different hydrogen ion concentrations.
- HARDER, WILHELM.
1958. Zur Anatomie des Darmtraktes einiger Familien der Clupeoidea: Clupeidae, Dorosomatidae, Dussumieriidae und Engraulididae (Clupeiformes, Pisces). Kurze Mitteilungen aus dem Institut für Fischereibiologie der Universität Hamburg, Nr. 8, Dezember, pp. 11-61.
- Descriptions and drawings of the digestive tracts of juvenile *Brevoortia tyrannus* and *B. patronus*.
1960. Vergleichende Untersuchungen zur Morphologie des Darmes bei Clupeoidea. Zeitschrift für wissenschaftliche Zoologie, Band 163, Heft 1½, pp. 65-167.
- Brevoortia tyrannus* mentioned.
- HARGIS, WILLIAM J., JR.
1959. Systematic notes on the monogenetic trematodes. Proceedings of the Helminthological Society of Washington, vol. 26, No. 1, pp. 14-31.
- Parasites of *Brevoortia patronus* and *B. gunteri* mentioned.
1961. See Bychowsky, 1961.
- HASKELL, WINTHROP A.
1961. Gulf of Mexico trawl fishery for industrial species. Commercial Fisheries Review, vol. 23, No. 2, pp. 1-6. Also Separate No. 612, 6 pp.
- Monthly occurrence of three species, listed as

- Brevoortia* spp., in the otter trawl landings of industrial fish during 1959.
- HEDGPETH, JOEL W.
1957. II. Biological aspects. Treatise on marine ecology and paleoecology (Joel W. Hedgpeth, editor). Geological Society of America, Memoir 67, vol. 1, ch. 23, Estuaries and lagoons, pp. 693-749.
Distribution of *Brevoortia tyrannus* and *B. gunteri* in relation to salinity.
- HÉLLIER, THOMAS R., JR.
1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 1-22.
Brevoortia patronus and *B. gunteri* listed.
- HERMAN, SIDNEY S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnology and Oceanography, vol. 8, No. 1, pp. 103-109.
Monthly occurrences of *Brevoortia tyrannus* eggs and larvae.
- HERRINGTON, WILLIAM C., and ROBERT A. NESSBIT.
1943. Fishery management. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report No. 18, 69 pp.
Mention of the exaggeration of estimated numbers of menhaden.
- HILDEBRAND, HENRY H.
1958. Estudio biológicos preliminares sobre la Laguna Madre de Tamaulipas. Ciencia, Mexico, vol. 17, Nos. 7-9, pp. 151-173.
Brevoortia gunteri reported as rare in beach seine catches.
- HILDEBRAND, SAMUEL F.
1946. A descriptive catalog of the shore fishes of Peru. Bulletin of the U.S. National Museum, No. 189, 530 pp.
Original description of *Ethmidium chilcae*.
1948. A review of the American menhaden, genus *Brevoortia*, with a description of a new species. U.S. National Museum, Smithsonian Institution, Miscellaneous Collection, vol. 107, No. 18, pp. 1-39.
Comparison and summary review of the seven species of menhaden occurring along the Atlantic coasts of North and South America: *Brevoortia tyrannus*, *B. patronus*, *B. brevicaudata*, *B. pectinata*, *B. aurea*, *B. smithi*, and *B. gunteri*.
- HOESE, HINTON D.
1958. A partially annotated checklist of the marine fishes of Texas. Publications of the Institute of Marine Science, Texas, vol. 5, pp. 312-352.
Brevoortia patronus and *B. gunteri* listed.
- HORNELL, JAMES.
1928. Report on the fishery resources of Sierra Leone. Government Printing Office, Freetown, 51 pp.
Brief account of the fishery for *Ethmalosa fimbriata*.
- HUBBS, CLARK.
1958. A check-list of Texas freshwater fishes. Texas Game and Fish Commission, Inland Fisheries Series, No. 3, 14 pp.
Reported *Brevoortia gunteri* from fresh water.
- HYRTL, JOSEPH.
1855. Über die accessorischen Kiemenorgane der Clupeaceen, nebst Bemerkungen über den Darmcanal derselben. Denkschriften Koenigliche Akademie der Wissenschaften, Vienna, Band 10, pp. 47-57.
Branchiostegals of Clupanodon aureus (B. aurea) and Alausa tyrannus (B. tyrannus).
- IHERING, H. VON
1897. Os peixes da costa do mar no Estado do Rio Grande do Sul. Revista do Museu Paulista, São Paulo, vol. 2, pp. 25-63.
Brevoortia tyrannus "savelha" mentioned briefly.
Species used principally for agricultural fertilizer.
- IRVINE, FREDERICK ROBERT.
1947. The fishes and fisheries of the Gold Coast. Crown Agents, London, 352 pp.
General description of *Ethmalosa dorsalis*.
- JENYNS, LEONARD.
1842. The fishes. In Charles R. Darwin, editor, The zoology of the voyage of H.M.S. *Beagle*, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836, pt. 4, pp. 1-169. Smith, Elder, and Co., London.
Original description of *Alosa pectinata*.
- JOHNSON, MALCOLM C.
1954. Preliminary experiment on fish culture in brackish-water ponds. Progressive Fish-Culturist, vol. 16, No. 3, pp. 131-133.
Occurrence of menhaden in brackish water pond mentioned.
- JOSEPH, EDWIN B., and RALPH W. YERGER.
1956. The fishes of Alligator Harbor, Florida, with notes on their natural history. Florida State University Studies No. 22, pp. 111-156.
Brevoortia patronus listed.
- JUNE, FRED C.
1958. Variation in meristic characters of young Atlantic menhaden, *Brevoortia tyrannus*. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-verbaux des Réunions, vol. 143, pt. 2, pp. 26-35.
Two populations of menhaden along the Atlantic coast of the United States, indicated from meristic differences of juveniles.
- 1961a. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1957; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 373, 39 pp.
A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.
- 1961b. The menhaden fishery of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Leaflet No. 521, 13 pp. [Processed.]
Brief review of the fishery and life history of *Brevoortia tyrannus*.

- JUNE, FRED C., and J. LOCKWOOD CHAMBERLIN.
1959. The role of the estuary in the life history and biology of Atlantic menhaden. Proceedings of the Gulf and Caribbean Fisheries Institute, 11th Annual Session, 1958, pp. 41-45.
Observations on the entry of larval *Brevoortia tyrannus* and their development and distribution in the estuarine nursery grounds.
- JUNE, FRED C., and WILLIAM R. NICHOLSON.
1964. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1958; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 446, 40 pp.
A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.
- JUNE, FRED C., and JOHN W. REINTJES.
1959. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1952-55; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 317, 65 pp.
A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.
1960. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1956; with a brief review of the commercial fishery. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 336, 38 pp.
A detailed review of the catch composition and the fishery with appendix tables of age, sex, weight, and length, by geographic areas with summary analyses of the data.
- JUNE, FRED C., and CHARLES M. ROITHMAYR.
1960. Determining age of Atlantic menhaden from their scales. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin No. 171, vol. 60, pp. 323-342.
Methods and results of determining age of *Brevoortia tyrannus* by viewing scales.
- KNER, RUDOLF, and FRANZ STEINDACHNER.
1866. Neue Fische aus dem Museum der Herren Joh. Ces. Godeffroy and Sohn in Hamburg. Sitzungsberichte der Mathematisch - Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Vienna, Band 54, Heft 1, pp. 356-395.
Original description of *Alausa fimbriata* of Valparaiso (sic) similar to *A. pectinata* Jenyns.
- KUNTZ, ALBERT, and LEWIS RADCLIFFE.
1917. Notes on the embryology and larval development of twelve teleostean fishes. Bulletin of the U.S. Bureau of Fisheries, vol. 35, pp. 88-134.
Description of eggs and larvae of *Brevoortia tyrannus*.
- LAGLER, KARL F., JOHN E. BARDACH, and ROBERT R. MILLER.
1962. Ichthyology. John Wiley and Sons, New York, 545 pp.
Filter feeding rate and body fat content of *Brevoortia tyrannus* mentioned. Brief mention of general migration and gill area of *Brevoortia*.
- LARRAÑAGA, DÁMASO ANTONIO.
1923. Escritos . . . Revista del Instituto Histórico y Geográfico del Uruguay, Montevideo, tomo 2, pp. 5-512.
Clupea 20-radiata synonym for *Brevoortia pectinata*.
- LEACH, W. E.
1818. Cymothoadées. Dictionnaire des Sciences Naturelles, Paris, tome 12, pp. 338-354.
Parasitic isopod in branchial chamber of menhaden.
- LEIM, A. H., and L. R. DAY.
1959. Records of uncommon and unusual fishes from eastern Canadian waters, 1950-1958. Journal of the Fisheries Research Board of Canada, Vol. 16, No. 4, pp. 503-514.
Juvenile and adult *Brevoortia tyrannus* reported from New Brunswick.
- LONGHURST, ALAN R.
1957. The food of the demersal fish of a West African estuary. Journal of Animal Ecology, vol. 26, No. 2, pp. 369-387.
Ethmalosa reported as food of guitarfish, *Rhinobatus rarus*; catfish, *Arius latiscutatus*; and shine-nose, *Galeoides decadactylus*.
- 1960a. Fish landings in Sierra Leone during 1959. Fisheries Development and Research Unit, Freetown, Occasional Paper No. 1 (unpaged).
A brief review of the fishery and landings of *Ethmalosa dorsalis*.
- 1960b. Local movements of *Ethmalosa fimbriata* off Sierra Leone from tagging data. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 22, No. 4, pp. 1337-1340.
Recovery of 24 of 2,012 tagged *Ethmalosa fimbriata* showed movement northward from Freetown.
1961. Report on the fisheries of Nigeria, 1961. Federal Fisheries Service, Ministry of Economic Development, Lagos, 42 pp. (processed).
Distribution and fishery for *Ethmalosa* reviewed briefly.
- LOZANO-REY, LUIS.
1950. Etude systématique des Clupéides et des Engraulidés de l'Espagne, du Maroc et du Sahara Espagnols. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-verbaux des Réuniones, vol. 126, pp. 7-20.
Brief description and synonymy of *Ethmalosa fimbriata*.

- LUNZ, G. ROBERT.
1956. Harvest from an experimental one-acre salt-water pond at Bears Bluff Laboratories, South Carolina. *Progressive Fish-Culturist*, vol. 18, No. 2, pp. 92-94.
Percentage occurrence of *Brevoortia* by number and weight in a salt water pond.
- MAINGUY, P., and M. DOUTRE.
1958. Variations annueites de la teneur en matières grasses de trois Clupéidés du Sénégal. *Revue des Travaux. Institut Scientifique et Technique des Pêches Maritimes*, Paris, tome 22, fasc. 3, pp. 303-321.
Annual variations in body fat content of *Ethmaloosa fimbriata*.
- MAIRS, DONALD F., and CARL J. SINDERMANN.
1962. A serological comparison of five species of Atlantic clupeoid fishes. *The Biological Bulletin*, vol. 123, No. 2, pp. 331-343.
Brevoortia tyrannus compared with *Alosa sapidissima*, *A. aestivalis*, *A. pseudoharengus*, and *Clupea harengus*.
- MANN F., GUILLERMO.
1950. Peces de Chile. Clave de determinación de las especies importantes. Instituto Investigaciones Veterinarias, Ministerio de Agricultura, Santiago, 44 pp., 89 figs.
Ethmidium maculatum and *E. chilcae* in a key to fishes of commercial importance.
1954. Vida de los peces en aguas chilenas. Instituto Investigaciones Veterinarias, Ministerio de Agricultura, Santiago, 342 pp.
A description of *Ethmidium maculatum maculatum* and *E. m. chilcae* with brief notes on biology.
- MANSUETI, ROMEO J.
1962. Distribution of small, newly metamorphosed sea lampreys, *Petromyzon marinus*, and their parasitism on menhaden, *Brevoortia tyrannus*, in mid-Chesapeake Bay during winter months. *Chesapeake Science*, vol. 3, No. 2, pp. 137-139.
Reported occurrence of sea lampreys attached to Atlantic menhaden in the Chesapeake Bay.
- MARAK, ROBERT R., and JOHN B. COLTON, JR.
1961. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1953. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 398, 61 pp.
One *Brevoortia tyrannus* egg collected at the surface with 1-meter plankton net, 10 miles S.W. of Martha's Vineyard on June 3, 1953.
- MARAK, ROBERT R., JOHN B. COLTON, JR., and DONALD B. FOSTER.
1962. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1955. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 411, 66 pp.
Twelve *Brevoortia tyrannus* eggs collected at the surface with Hardy plankton sampler, 75 miles south of Nantucket on May 16, 1955.
- MARAK, ROBERT R., JOHN B. COLTON, JR., DONALD B. FOSTER, and DAVID MILLER.
1962. Distribution of fish eggs and larvae, temperature and salinity in the Georges Bank-Gulf of Maine area, 1956. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 412, 95 pp.
Three *Brevoortia tyrannus* larvae (4.5-8.2 mm.) collected in a 1-meter plankton net on the surface off Woods Hole, Mass., on June 24, 1956.
- MARVIN, KENNETH T., and LARENCE M. LANSFORD.
1962. Phosphorus content of some fishes and shrimp in the Gulf of Mexico. *Publications of the Institute of Marine Science, Texas*, vol. 8, pp. 143-146.
Percent of phosphorus by weight for two lots of *Brevoortia patronus*.
- MASSMANN, WILLIAM H.
1954. Marine fishes in fresh and brackish waters of Virginia rivers. *Ecology*, vol. 35, No. 1, pp. 75-78.
Occurrence of *Brevoortia tyrannus* in fresh water.
1961. Fishes and fish larvae collected from Atlantic plankton cruises of R/V *Pathfinder*, December 1959-December 1960. Institute of Marine Science, Virginia Fisheries Laboratory, Special Scientific Report No. 26, 3 pp. (Processed.)
Monthly occurrence of *Brevoortia tyrannus* larvae in plankton collections with size range in millimeters.
- MASSMANN, WILLIAM H., JOHN J. NORCROSS, and EDWIN B. JOSEPH.
1962. Atlantic menhaden larvae in Virginia coastal waters. *Chesapeake Science*, vol. 3, No. 1, pp. 42-45.
Occurrence of larval *Brevoortia tyrannus* in plankton collections from the Atlantic Ocean off the mouth of Chesapeake Bay from November to April, 1959-60.
- MCALLISTER, D. E.
1960. List of the marine fishes of Canada. National Museum of Canada, Bulletin No. 168, Biological Series, No. 62, 76 pp.
Brevoortia tyrannus listed from the Atlantic Ocean.
- McHUGH, J. L.
1960. The pound-net fishery in Virginia. Pt. 2—Species composition of landings reported as menhaden. *Commercial Fisheries Review*, vol. 22, No. 2, pp. 1-16. Also Separate No. 518, 16 pp.
Semi-monthly landings of *Brevoortia tyrannus* and associated species from pound nets.
- McHUGH, J. L., R. T. OGLESBY, and A. L. PACHECO.
1959. Length, weight, and age composition of the menhaden catch in Virginia waters. *Limnology and Oceanography*, vol. 4, No. 2, pp. 145-162.
Aspects of biology and life history of *Brevoortia tyrannus* from pound net and purse seine catches in Chesapeake Bay.
- MERRIMAN, DANIEL, and RUTH C. SCLAR.
1952. The pelagic fish eggs and larvae of Block Island Sound. In *Hydrographic and biological studies of Block Island Sound*, pp. 165-219. Bul-

- letin of the Bingham Oceanographic Collection, vol. 13, art. 3.
Absence of menhaden eggs and larvae noted from monthly plankton collections, 1943-46.
- MIGDALSKI, EDWARD C.
1958. Angler's guide to the salt water game fishes. Ronald Press, New York, 506 pp.
A popular account listing Atlantic menhaden as food of swordfish, tuna, Atlantic bonito, cobia, gray weakfish, spotted weakfish, channel bass, black drum, and striped bass.
- MILNE-EDWARDS, HENRI.
1840. Histoire naturelle des Crustacés. Paris, tome 3, 605 pp.
Parasitic isopods in *Brevoortia tyrannus*.
- MONOD, THÉODORE.
1927. Contribution à l'étude de la faune du Cameroun. I. Pisces. Faune des colonies françaises, tome I, pp. 643-742.
Young *Ethmalosa dorsalis* from the stomach contents of several demersal fishes. Figure of gills and stomach ("gizzard").
1949. Sur l'appareil branchiospinal de quelques Téléostéens tropicaux. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 11, Nos. 1-2, pp. 36-76.
Ethmalosa fimbriata branchial apparatus and pharynx described and figured.
1961. *Brevoortia* Gill 1861 et *Ethmalosa* Regan 1917. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 23, No. 2, pp. 506-547.
Comparison of the genera including scales, dermal head structure, intestinal tract, branchial apparatus, and vertebral column. Conclusion: Similar but distinct genera.
- MOODY, HAROLD L.
1961. Exploited fish populations of the St. Johns River, Florida. Quarterly Journal of the Florida Academy of Sciences, vol. 24, No. 1, pp. 1-18.
Brevoortia smithi reported from the St. Johns River.
- NICOL, J. A. COLIN.
1960. The biology of marine animals. Interscience Publishers, Inc., New York, 707 pp.
Brevoortia gill area and scale composition mentioned.
- OLIVER SCHNEIDER, CARLOS.
1943. Catalogo de los peces marinos del litoral de Concepción y Arauco. Boletín de la Sociedad de Biología de Concepción, tomo 17, pp. 75-126.
Clupea maculata listed.
- OSORIO, BALTHAZAR.
1905. Indicações de algumas especies que devem ser acrescentados á fauna ichthyologica da ilha de S. Thomé. Jornal de Ciencias Mathematicas, Physicas e Naturaes, Lisbon, vol. 7, No. 27, pp. 156-158.
Clupea dorsalis listed.
- OTORUBIO, FUBARA O.
1959. Fisheries development in Nigeria with special reference to the Western Region. Fishermen's Bulletin, Haifa, No. 20, pp. 31-32.
Ethmalosa fimbriata mentioned.
- PEARCY, WILLIAM G., and SARAH W. RICHARDS.
1962. Distribution and ecology of fishes of the Mystic River Estuary, Connecticut. Ecology, vol. 43, No. 2, pp. 248-259.
Two *Brevoortia tyrannus* larvae in collections from June and July.
- PECK, JAMES I.
1894. On the food of menhaden. Bulletin of the U.S. Fish Commission, vol. 13, pp. 113-126.
A detailed account of the food organisms found in *Brevoortia tyrannus* and a description of the gill arrangement for filtering organisms, principally phytoplankton, from the water.
- PÉREZ CANTO, C.
1912. La fauna ictiológica de Chile considerada como riqueza nacional. Santiago, pp. 3-45.
Clupea maculata and *C. notocanthus* listed.
- PERLMUTTER, ALFRED.
1959. Changes in the populations of fishes and in their fisheries in the middle Atlantic and Chesapeake regions, 1930-1955. Transactions of the New York Academy of Science, series 2, vol. 21, No. 6, pp. 484-496.
Menhaden fishery briefly mentioned.
1961. Guide to marine fishes. New York University Press, New York, 431 pp.
Brief general description and key to *Brevoortia tyrannus*.
- PERUGIA, ALBERTO.
1891. Appunti sopra alcuni pesci sud-americani conservati nel Museo Civico di Storia Naturale di Genova. Annali del Museo Civico di Storia Naturale di Genova, 1890-1891, serie 2, vol. 10, No. 30, pp. 605-657.
Reports *Clupea aurea* from La Plata River.
- PORTER, CARLOS E.
1909a. Breve nota de ictiología—Enumeración de las especies más importantes comunes á Chile y de Perú. Revista Universitaria, Organó de la Universidad Mayor de San Marcos, Lima, Año 3, pp. 1-14.
Clupea notocanthus listed.
1909b. Ictiología. Enumeración de especies importantes comunes a las aguas de Chile y de Perú. Revista Chilena de Historia Natural. Año 13, núms. 4-5, pp. 280-293.
Clupea (sic) *notocanthus* listed.
- POSTEL, E.
1950. Note sur *Ethmalosa fimbriata* (Bowdich). Bulletin des Services de l'Élevage et des Industries Animales de l'Afrique Occidentale Française, tome 3, No. 1, pp. 49-59.
Distribution, occurrence, life history, and fishery for *Ethmalosa fimbriata*.
1959. Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du cap Spartel au cap Roxo, suivie d'un bref aperçu sur leur répartition bathymétrique et géographique. Bul-

- letin de la Société Scientifique de Bretagne, tome 34, fasc. 1-2, pp. 129-170.
Brevoortia tyrannus and *Ethmalosa fimbriata* listed.
- PRICE, EMMETT W.
 1961. North American monogenetic trematodes. IX. The families Mazocraeidae and Plectanocotylidae. Proceedings of the Biological Society of Washington, vol. 74, pp. 127-155.
 Parasites of *Brevoortia patronus*, *B. gunteri* and *B. tyrannus*.
- QUIJADA B., BERNARDINO.
 1913. Catálogo ilustrado i descriptivo de los peces chilenos i extranjeros conservados en el museo nacional. Boletín del Museo Nacional de Chile, tomo 5, núm. 1, Santiago, pp. 7-128.
Clupea maculatus and *C. advena* listed.
- REED, EDWYN C.
 1897. Catálogo de los peces chilenos. Anales Universidad de Chile, tomo 98, pp. 653-673. Also printed separately, pp. 3-24.
Clupea caerulea, *C. maculata*, *C. notocanthus*, and *C. pectinata* (not Jenyns) listed.
- REGAN, C. TATE.
 1915. A collection of fishes from Lagos. Annals and Magazine of Natural History, London, series 8, vol. 15, No. 85, pp. 124-130.
Clupea dorsalis mentioned.
 1917. A revision of the clupeoid fishes of the genera *Pomolobus*, *Brevoortia*, and *Dorosoma*, and their allies. Annals and Magazine of Natural History, series 8, vol. 19, No. 112, pp. 297-316.
 Brief description and synonymy of *Brevoortia tyrannus*, *B. pectinata*, and *Ethmidium maculatum*.
 A new genus, *Ethmalosa* for *Alausa dorsalis* Valenciennes (1847).
- REINTJES, JOHN W.
 1960. Continuous distribution of menhaden along the South Atlantic and gulf coasts of the United States. Proceedings of the Gulf and Caribbean Fisheries Institute, 12th Annual Session, 1959, pp. 31-35.
 A brief review of the distribution of the North American menhadens, with some evidence of greater abundance in southern Florida waters than reported previously.
 1961. Menhaden eggs and larvae from M/V *Theodore N. Gill* cruises, South Atlantic coast of the United States, 1953-54. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 393, 7 pp.
Brevoortia species eggs and larvae collected during three winter cruises but not during six cruises from April to November.
 1962. Development of eggs and yolk-sac larvae of yellowfin menhaden. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin 202, vol. 62, pp. 93-102.
- Descriptions and illustrations of artificially fertilized eggs and resulting yolk-sac larvae of *Brevoortia smithi*.
- REINTJES, JOHN W., JAMES Y. CHRISTMAS, JR., and RICHARD A. COLLINS.
 1960. Annotated bibliography on biology of American menhaden. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin 170, vol. 60, pp. 297-322.
 Bibliography of genus *Brevoortia* in publications before and during 1957. Some very brief annotations and a subject index are included.
- REINTJES, JOHN W., and FRED C. JUNE.
 1961. A challenge to the fish meal and oil industry in the Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute, 13th Annual Session, 1960, pp. 62-66.
 Some observations on the distribution and abundance of menhaden and other clupeoid fishes in the Gulf of Mexico, with suggestions for exploration.
- REINTJES, JOHN W., and CHARLES M. ROITHMAYR.
 1960. Survey of the ocean fisheries off Delaware Bay, supplement report, 1954-57. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 347, 18 pp.
 Menhaden purse seine fishery mentioned but excluded from the report.
- RENFRO, WILLIAM C.
 1960. Salinity relations of some fishes in the Aransas River, Texas. Tulane Studies in Zoology, vol. 8, No. 3, pp. 83-91.
 Occurrence of juvenile *Brevoortia patronus* in salinity of 54.3‰ and larvae from 0.5 and 47.6‰.
- RICHARDS, SARAH W.
 1959. Pelagic fish eggs and larvae of Long Island Sound. In Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic Collection, vol. 17, art. 1, pt. 6, pp. 95-124.
 Occurrence of eggs and larvae of *Brevoortia tyrannus* from May to October, 1954-55.
 1963a. The demersal fish population of Long Island Sound. I. Species composition and relative abundance in two localities, 1956-57. Bulletin of the Bingham Oceanographic Collection, vol. 18, art. 2, pp. 5-31.
 Twenty-nine *Brevoortia tyrannus* collected with experimental shrimp trawl in November, December, January, February, and June. Size ranged from 16 to 305 mm.
 1963b. The demersal fish population of Long Island Sound. II. Food of the juveniles from a sand-shell locality (Station I). Bulletin of the Bingham Oceanographic Collection, vol. 18, art. 2, pp. 32-72.
 Stomach contents of 28 juvenile and yearling *Brevoortia tyrannus* were primarily crustaceans with *Balanus* nauplii and cyprids, and *Neomysis americanus* constituting the bulk of the food. Difference noted from Peck

- (1894) who described phytoplankton the primary summer diet.
- 1963c. The demersal fish population of Long Island Sound. III. Food of the juveniles from a mud locality (Station 3A). Bulletin of the Bingham Oceanographic Collection, vol. 18, art. 2, pp. 73-101.
- One *Brevoortia tyrannus* (100 mm.) contained *Acartia* spp., *Anchoa mitchilli* larvae, and *Labidocera aestiva*.
- RICHMOND, E. AVERY.**
1962. The fauna and flora of Horn Island, Mississippi. Gulf Coast Research Laboratory, Ocean Springs, Miss., Gulf Research Reports, vol. 1, No. 1, pp. 59-106.
- Reported the occurrence of *Brevoortia patronus*.
- ROBAS, JOHN S.**
1959. Menhaden purse seining. In H. Kristjonsson, editor, Modern fishing gear of the world, pp. 394-399. Fishing News (Books) Ltd., London.
- Description of menhaden purse seine fishing with an account of modern development.
- ROCHERRUNE, ALPHONSE TRÉMEAU DE**
1883. Poissons. In Octave Doin, editor, Faune de la Sénégambie, Paris, pp. 1-166 and 6 plates in the Atlas volume.
- Clupea aurea* listed. Confirmed Dumeril, 1861.
- ROITHMAYR, CHARLES M.**
1963. Distribution of fishing by purse seine vessels for Atlantic menhaden, 1955-1959. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 434, 22 pp.
- Monthly distribution of purse seine sets along the Atlantic coast of the U.S., for a 5-year period. Information obtained from logbooks kept by vessel personnel.
- ROSEN, ALBERT.**
1959. Summary of Florida commercial marine landings, and an analysis of the catch and effort of certain species, 1958. University of Miami, Marine Laboratory, Publication No. 59-4, 55 p.
- Landings of menhaden in Florida by county.
1960. Summary of Florida commercial marine landings, 1959, and an analysis of the catch and effort of certain species. University of Miami, Marine Laboratory, Publication No. 60-2, 53 pp.
- Landings of menhaden in Florida by county.
- ROSEN, ALBERT, and RICHARD K. ROBINSON.**
1961. Summary of Florida commercial marine landings, 1960, and an analysis of the catch and effort of certain species. University of Miami, Institute of Marine Science, No. 61-2, 32 pp.
- Landings of menhaden in Florida by county.
- 1962a. Summary of Florida commercial marine landings, 1961. University of Miami, Institute of Marine Science, No. 62-5, 20 pp.
- Landings of menhaden in Florida by county.
- 1962b. Summary of Florida commercial marine landings, 1961, and an analysis of the catch and effort of certain species. University of Miami, Institute of Marine Science, No. 62-7, 32 pp.
- Landings of menhaden in Florida by county.
- SALZEN, E. A.**
1958. Observations on the biology of the West African shad, *Ethmalosa fimbriata* (Bowdich). Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 20, No. 4, pp. 1388-1426.
- A detailed account of the fishery and life history including size, weight, and sexual maturity from catches in the Sierra Leone River Estuary.
- SANTOS, EURICO.**
1952. Nossos peixes marinhos. F. Griguit e Cia., Rio de Janeiro, 265 pp.
- Brevoortia tyrannus aurea* "savelha" mentioned.
- SCHWARTZ, FRANK J.**
1961. Fishes of Chincoteague and Sinepuxent Bays. American Midland Naturalist, vol. 65, No. 2, pp. 384-408.
- Occurrence of juvenile *Brevoortia tyrannus* during June and July.
- SHUSTER, CARL N., JR.**
1959. A biological evaluation of the Delaware River Estuary. University of Delaware, Marine Laboratories, Information Series, Publication No. 3, 77 pp.
- Fishery for *Brevoortia tyrannus* reviewed briefly.
- SILVA, R. D.**
1944. Nomes vulgares de peixes encontrados no entreposto de pesca do Rio de Janeiro, com seus correspondentes em sistematica. Servico de Informacão Agricola Brasil, Ministerio de Agricultura, Rio de Janeiro, Boletim, vol. 33, No. 9, pp. 57-66.
- Brevoortia* "savelha" listed.
- SIMMONS, ERNEST G.**
1957. An ecological survey of the upper Laguna Madre of Texas. Publications of the Institute of Marine Science, Texas, vol. 4, No. 2, pp. 156-200.
- Brevoortia patronus* and *B. gunteri* occurred in the area. The latter species spawned in February 1956.
- SIMMONS, ERNEST G., and JOSEPH P. BREUER.**
1962. A study of redfish, *Sciaenops ocellata* Linnaeus, and black drum, *Pogonias cromis* Linnaeus. Publications of the Institute of Marine Science, Texas, vol. 8, pp. 184-211.
- Incidence of occurrence of *Brevoortia* was 0.23 percent in the stomach contents of 1,197 redfish from Rockport, Tex.
- SIMMONS, ERNEST G., and H. DICKSON HOESE.**
1959. Studies on the hydrography and fish migrations of Cedar Bayou, a natural tidal inlet on the central Texas coast. Publications of the Institute of Marine Science, Texas, vol. 6, pp. 56-80.
- Brevoortia* sp. ranked eighth in list of fishes taken by fish trap, 1950-51.
- SINDERMANN, CARL J.**
1961. Serological techniques in fishery research. Transactions of the 26th North American Wildlife and Natural Resources Conference, pp. 298-309.
- Relationship of *Brevoortia* to western Atlantic clupeids, *Alosa* and *Clupea*.

- SKUD, BERNARD E., and WILLIAM B. WILSON.
1960. Role of estuarine waters in gulf fisheries. Transactions of the 25th North American Wildlife and Natural Resources Conference, pp. 320-326. *Brevoortia* mentioned.
- SMITH, KEITH A.
1961. Air-bubble and electrical-field barriers as aids to fishing. Proceedings of the Gulf and Caribbean Fisheries Institute, 13th Annual Session, 1960, pp. 73-86.
Behavior of menhaden during fishing trials.
- SPARKS, ALBERT K.
1958. Some digenetic trematodes of fishes of Grand Isle, Louisiana. Proceedings of the Louisiana Academy of Science, vol. 20, pp. 71-82.
Parasites of Brevoortia patronus.
- SPRINGER, VICTOR G.
1960. Ichthyological surveys of the lower St. Lucie and Indian Rivers, Florida east coast. Florida State Board of Conservation, Marine Laboratory Report No. 60-16, 17 pp. (Processed).
Brevoortia tyrannus and *B. smithi* reported.
- SPRINGER, VICTOR G., and KENNETH D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Florida State Board of Conservation, Marine Laboratory, Professional Papers Series No. 1, 104 pp.
Brevoortia patronus, *B. smithi*, and *B. tyrannus* larvae and juveniles reported from Florida.
- SPROSTON, NORA G.
1946. A synopsis of the monogenetic trematodes. Transactions of the Zoological Society of London, vol. 25, pt. 4, pp. 185-600.
Parasites of Brevoortia tyrannus mentioned.
- STEINDACHNER, FRANZ.
1869. Ichthyologische Notizen (IX). Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse, Band 60, Abt. 1, pp. 290-318.
Clupea (Alosa) notocanthoides original description from Mazatlan, Mexico.
1882. Beiträge zur Kenntniss der Fische Afrika's und Beschreibung einer neuen *Paraphoxinus*-Art aus der Herzogwina. Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse, Band 45, pp. 1-18.
Clupea (Alosa) setosa from Liberia, Sherbero, and Gabun.
1895. Die Fische Liberia's. Notes from Leyden Museum, vol. 16, No. 1, pp. 1-96.
Clupea senegalensis described.
- STEVEN, G. A.
1947. Report on the fisheries of Sierra Leone. Crown Agents, London, 66 pp.
General account of the fishery for *Ethmalosa fimbriata*.
- SUTHERLAND, DOYLE F.
1958. Use of diagnostic X-ray for determining vertebral numbers of fish. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 244, 9 pp.
Methods and equipment for making X-ray photographs of menhaden.
1963. Variation in vertebral numbers of juvenile Atlantic menhaden. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 435, 21 pp.
Analysis of variance of mean vertebral numbers of *Brevoortia tyrannus* indicated two subpopulations along the Atlantic Coast of the United States.
- SUTTKUS, ROYAL D.
1958. Distribution of menhaden in the Gulf of Mexico. Transactions of the 23rd North American Wildlife Conference, pp. 401-410.
Proportional measurements and meristic counts of 23 specimens of *Brevoortia smithi*.
- SUTTKUS, ROYAL D., and BANGALORE I. SUNDARARAJ.
1961. Fecundity and reproduction in the largescale menhaden, *Brevoortia patronus* Goode. Tulane Studies in Zoology, vol. 8, No. 6, pp. 177-182.
Age, sexual maturity, and fecundity of *Brevoortia patronus* from examination of scales and ovaries.
- SVETOVIDOV, A. N.
1952. Sel'devye (Clupeidae). In Fauna SSSR, Ryby. Akadmiã Nauk SSSR, Zoologicheskii Institut, tom 2, vyp. 1, 331 pp.
Inclusion of *Brevoortia*, *Ehmidium*, and *Ethmalosa* in a general account of the genera of clupeid fishes.
1953. O nekotorykh faktorakh, obuslovlivavshchikh chislennost' sel'devykh. Akademiã Nauk SSSR, Ikhtologicheskaiã Komissiiã, Trudy Soveshchaniï, No. 1, pp. 99-109. (Trudy Vsesoiuznoi Konferentsii po Voprosam Rybnogo Khozãistva, 1951.)
Brevoortia tyrannus mentioned among the clupeid fisheries of the world.
1961. Some factors determining the abundance of Clupeidae (O nekotorykh faktorakh, obuslovlivavshchikh chislennost' sel'devykh), pp. 1-14. In Herring: Selected articles from Soviet periodicals. Israel Program for Scientific Translations, Jerusalem.
English translation of Svetovidov, 1953.
1963. Clupeidae. In Fauna of U.S.S.R., Fishes. Zoological Institute of the Academy of Sciences of the U.S.S.R., vol. 2, No. 1, 428 p. Israel Program for Scientific Translations, Jerusalem.
English translation of Svetovidov, 1952.
- TABB, DURBIN C., and RAYMOND B. MANNING.
1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. Bulletin of Marine Science of the Gulf and Caribbean, vol. 11, No. 4, pp. 552-649.
Adults and juveniles of *Brevoortia smithi* reported.
1962. Aspects of the biology of northern Florida Bay and adjacent estuaries. In Durbin C. Tabb, David L. Dubrow, and Raymond B. Manning. The ecology of northern Florida Bay and adjacent

- estuaries, pt. II, pp. 39-79. State of Florida Board of Conservation, Technical Series No. 39.
- Juvenile *Brevoortia smithi* reported from Coot Bay Pond and adult *Brevoortia* sp. from Florida Bay.
- TAGATZ, MARLIN E., and DONNIE L. DUDLEY.
1961. Seasonal occurrence of marine fishes in four shore habitats near Beaufort, N.C., 1957-60. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 390, 19 pp.
- Occurrence of juvenile *Brevoortia tyrannus* in haul seine collections. Reported among the more abundant fishes at each habitat location.
- THOMPSON, SETON H.
1960. The commercial fisheries of the Gulf and South Atlantic—a report of progress. Proceedings of the Gulf and Caribbean Fisheries Institute, 12th Annual Session, 1959, pp. 1-4.
- Brief mention of the research work on *Brevoortia tyrannus*.
1961. What is happening to our estuaries. Transactions of the 26th North American Wildlife and Natural Resources Conference, pp. 318-322.
- Menhaden mentioned.
- THOMPSON, WILL F.
1916. Fishes collected by the United States Bureau of Fisheries steamer "Albatross" during 1888, between Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. Proceedings of the U.S. National Museum, vol. 50, No. 2133, pp. 401-476.
- Brevoortia tyrannus* reported from Montevideo.
- Ethmidium*, new genus with *Clupea notocanthoides* Steindachner, as type. *Ethmidium caerulea* (Cuvier and Valenciennes) reported.
- TORTONESE, ENRICO.
1942. Studio di una collezione di pesci proveniente da Valparaiso (Chile). Bollettino dei Musei di Zoologia e di Anatomia Comparata R. della Università di Torino, vol. 60, serie 4, No. 129, 26 pp.
- Ethmidium caeruleum* listed.
1951. Materiali per 10 studio sistematico e zoogeografico dei pesci della coste occidentali del Sud America. Revista Chilena de Historia Natural, Pura y Aplicada, Años 51-53, pp. 83-118.
- Ethmidium maculatum* listed and *E. chilcae* mentioned.
- VALENCIENNES, ACHILLE.
- See Cuvier, Georges, and Achille Valenciennes, 1847.
- VON IHERING, H.
- See Ihering, H. von, 1897.
- WALFORD, LIONEL A.
1958. Living resources of the sea. Roland Press Co., New York, 321 pp.
- Brief mention of oil yield, parasites, and electro-fishing of menhaden.
- WATTS, J. C. D.
1962. Evidence of over-fishing in the Sierra Leone trawl fishery. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 24, No. 3, pp. 909-912.
- Brief mention of Longhurst, 1960b.
1963. A note on *Ethmalosa fimbriata* (Bowd.) from Sierra Leone. Bulletin de l'Institut Français d'Afrique Noire, série A, Sciences Naturelles, tome 25, No. 1, pp. 235-237.
- A brief summary of fishery and biology of *Ethmalosa fimbriata* with the common names for immature, mature, and extra large fish in Sierra Leone.
- YAÑEZ ANDRADE, PARMENIO.
1955. Peces utiles de la costa chilena. Revista de Biología Marina, Valparaiso, vol. 6, Nos. 1-3, pp. 29-81.
- Brief description of *Ethmidium maculatum*.

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- De Sylva, Kalber, and Shuster, 1962.
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Bibliography:

- Butler, 1959, 1960.
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Mansueti, 1962.
Marak and Colton, 1961.
Marak, Colton, and Foster, 1962.
Marak, Colton, Foster, and Miller, 1962.
Massmann, 1954.
Massmann, Norcross, and Joseph, 1961, 1962.
McAllister, 1960.
McHugh, 1960.
McHugh, Oglesby, and Pacheco, 1959.
Milne-Edwards, 1840.
Percy and Richards, 1962.
Peck, 1894.
Perlmutter, 1959, 1961.
Postel, 1959.
Price, 1961.
Reintjes, 1961.
Richards, 1959, 1963a, 1963b, 1963c.
Roithmayr, 1962.
Schwartz, 1961.
Springer, 1960.
Springer and Woodburn, 1960.
Sproston, 1946.
Sutherland, 1958, 1963.
Svetovidov, 1952, 1953, 1961, 1963.
Tagatz and Dudley, 1961.

Classification:

Berg, 1940, 1947.
Cuvier and Valenciennes, 1847.
De Buen, 1958.
Fowler, 1942, 1948.
Hildebrand, 1948.
Monod, 1961.
Regan, 1917.
Svetovidov, 1952, 1963.

Clupanodon aureus: See *Brevoortia aurea*.

Clupea advena: See *Ethmidium*.

Clupea aurea: See *Brevoortia aurea*.

Clupea caerulea: See *Ethmidium*.

Clupea dorsalis: See *Ethmalosa fimbriata*.

Clupea fimbriata: See *Ethmalosa fimbriata*.

Clupea laccia vel 20-radiata: See *Brevoortia pectinata*.

Clupea pectinata: See *Brevoortia pectinata*.

Clupea maculata: See *Ethmidium maculatum*.

Clupea menhaden: See *Brevoortia tyrannus*.

Clupea notocanthus: See *Ethmidium chilcae*.

Clupea notocanthoides: See *Ethmidium chilcae*.

Clupea 20-radiata: See *Brevoortia pectinata*.

Clupea senegalensis: See *Ethmalosa fimbriata*.

Clupea setosa: See *Ethmalosa fimbriata*.

Common names:

Anonymous, 1948.
Bailey, et al., 1960.
Cadenat, 1947.
De Carvalho, 1957.
Delfin, 1902.
Hildebrand, 1948.
Silva, 1944.
Watts, 1963.

Distribution:

Briggs, 1958.
Christmas and Gunter, 1960.
Hildebrand, 1948.
Reintjes, 1960.
Reintjes and June, 1961.
Roithmayr, 1962.
Svetovidov, 1952.

Eggs:

Bainbridge, 1961.
Herman, 1963.
Kuntz and Radcliffe, 1917.
Marak and Colton, 1961.
Marak, Colton, and Foster, 1962.
Merriman and Sclar, 1952.
Reintjes, 1961, 1962.
Richards, 1959.

Ethmalosa dorsalis: See *Ethmalosa fimbriata*.

Ethmalosa fimbriata:

Anonymous, 1948.
Bainbridge, 1957, 1960, 1961, 1962.
Blanc, 1948.
Boulenger, 1905.
Bowdich, 1825, 1826.
Cadenat, 1947, 1950, 1960.
Chabanaud and Monod, 1926.
Cuvier and Valenciennes, 1847.
Dumeril, 1861.
Fowler, 1911, 1936.
Gras, 1961.
Günther, 1868.
Hornell, 1928.
Irvine, 1947.
Longhurst, 1957, 1960a, 1960b, 1961.
Lozano Rey, 1950.
Mainguy and Doutre, 1958.
Monod, 1927, 1949, 1961.
Osorio, 1905.
Otorubio, 1959.
Postel, 1950, 1959.
Regan, 1915, 1917.
Steindachner, 1882, 1895.
Steven, 1947.
Svetovidov, 1952.
Watts, 1963.

Ethmalosa fishery:

Bainbridge, 1960.
Brown, 1948.
Cadenat, 1948.
Hornell, 1928.
Irvine, 1947.
Longhurst, 1960a, 1961.
Postel, 1950.
Steven, 1947.
Watts, 1963.

Ethmidium:

Berg, 1940, 1947.
De Buen, 1958, 1959.
Delfin, 1900, 1902.
Cuvier and Valenciennes, 1847.
Gay, 1848.
Quijada B., 1913.
Reed, 1897, 1901.
Svetovidov, 1952.
Thompson, 1916.

Ethmidium chilcae:

Abbott, 1899.
De Buen, 1958, 1959.
Delfin, 1900, 1902.
Dollo, 1904.
Cuvier and Valenciennes, 1847.
Gay, 1848.
Hildebrand, 1946.
Mann F., 1950, 1954.
Perez Canto, 1912.
Porter, 1909a, 1909b.
Quijada B., 1913.
Reed, 1897.
Steindachner, 1869.
Svetovidov, 1952.
Thompson, 1916.
Tortonese, 1942, 1951.

Ethmidium maculatum:

Abbott, 1899.
Castillo and Vergara, 1907.
De Buen, 1958, 1959.
Delfin, 1900, 1902.
Fowler, 1940, 1944, 1945, 1951a.
Cuvier and Valenciennes, 1847.
Gay, 1848.
Mann F., 1950, 1954.
Oliver Schneider, 1943.
Perez Canto, 1912.
Quijada B., 1913.
Reed, 1897.
Regan, 1917.
Svetovidov, 1952.
Thompson, 1916.
Tortonese, 1942, 1951.
Yanez Andrade, 1955.

Finescale menhaden: See *Brevoortia gunteri*.

Food and feeding:

Anderson, Jonas, and Odum, 1958.
Bainbridge, 1957, 1960.
Chipman, 1959, 1960.

Darnell, 1958, 1961.
Deevey, 1956.
Harder, 1958, 1960.
Lagler, Bardach, and Miller, 1962.
Peck, 1894.
Richards, 1963b, 1963c.

Gulf menhaden: See *Brevoortia patronus*.

Lacha: See *Brevoortia pectinata* and *B. aurea*.

Larvae and juveniles:

Arnold, Wheeler, and Baxter, 1960.
Bainbridge, 1961, 1962.
Breder, 1960, 1962.
Breuer, 1962.
Butler, 1959, 1960.
Chipman, 1959, 1960.
De Sylva, Kalber and Shuster, 1962.
Deubler, 1958.
Herman, 1963.
June, 1958.
June and Chamberlin, 1959.
Kuntz and Radcliffe, 1917.
Leim and Day, 1959.
Marak, Colton, Foster, and Miller, 1962.
Massmann, Norcross, and Joseph, 1961, 1962.
Merriman and Sclar, 1952.
Pearcy and Richards, 1962.
Reintjes, 1961, 1962.
Renfro, 1960.
Richards, 1959, 1963a, 1963b, 1963c.
Schwartz, 1961.
Simmons, 1957.
Springer and Woodburn, 1960.
Tabb and Manning, 1961, 1962.

Machete: See *Ethmidium maculatum* or *E. chilcae*.

Machuela: See *Ethmidium maculatum* or *E. chilcae*.

Menhaden fishery:

Borgstrom, 1961.
Christmas, Gunter, and Whatley, 1960.
Cushing, et al., 1952.
Ellison, 1951.
Goode, 1879.
June, 1961a, 1961b.
June and Nicholson, 1963.
June and Reintjes, 1959, 1960.
McHugh, 1960.
Reintjes, 1960.
Reintjes and June, 1961.
Robas, 1959.
Roithmayr, 1963.
Rosen, 1959, 1960.
Rosen and Robinson, 1961, 1962a, 1962b.
Shuster, 1959.
Smith, 1961.

Methods of capture:

See *Ethmalosa* fishery.
See Menhaden fishery.
Angelescu and Boschi, 1959.
Arve, 1960.

Methods of capture—Continued

Beatty, 1959, 1961.
Breder, 1960, 1962.
Bullis, 1961.
Haskell, 1961.
Hildebrand, 1958.
McHugh, 1960.
Reintjes, 1960.
Reintjes and June, 1961.
Richards, 1963a.
Simmons and Hoese, 1959.
Smith, 1961.
Tagatz and Dudley, 1961.
Walford, 1958.

Morphology:

Doutre, 1959.
Gunter and Demoran, 1961.
Harder, 1958, 1960.
Hyrtl, 1855.
June, 1958.
June and Roithmayr, 1960.
Lagler, Bardach, and Miller, 1962.
Mainguy and Doutre, 1958.
Mairs and Sindermann, 1962.
Monod, 1927, 1949, 1961.
Nicol, 1960.
Peck, 1894.
Sindermann, 1961.
Sutherland, 1958, 1963.
Suttkus, 1958.
Suttkus and Sundararaj, 1961.

Occurrence in fresh water:

Behnke and Wetzel, 1960.
Butler, 1959, 1960.
Gunter, 1957, 1961.
Gunter and Shell, 1958.
Hedgpeth, 1957.
Hubbs, 1958.
Johnson, 1954.
June and Chamberlin, 1959.
Massmann, 1954.
Renfro, 1960.

Parasites:

Anonymous, 1959.
Bychowsky, 1957, 1961.
Hargis, 1959, 1961.
Leach, 1818.
Mansueti, 1962.
Milne-Edwards, 1840.
Price, 1961.

Sparks, 1958.
Sproston, 1946.
Walford, 1958.

Physiology:

Burroughs, Chipman, and Rice, 1957.
Chipman, 1959, 1960.
Doutre, 1959.
Hall and McCutcheon, 1938.
Lagler, Bardach, and Miller, 1962.
Mainguy and Doutre, 1958.
Mairs and Sindermann, 1962.
Marvin and Lansford, 1962.
Sindermann, 1961.

Potamalosa maculata: See *Ethmidium maculatum*.

Potamalosa notocanthoides: See *Ethmidium chilcae*.

Potamalosa notocanthus: See *Ethmidium chilcae*.

Predators:

Darnell, 1961.
Grant, 1962.
Longhurst, 1957.
Migdalski, 1958.
Monod, 1927.
Simmons and Breuer, 1962.

Savelha: See *Brevoortia aurea* or *B. pectinata*.

Serology:

Mairs and Sindermann, 1962.
Sindermann, 1961.

Sexual maturity:

See Eggs.
June, 1961a.
June and Nicholson, 1963.
June and Reintjes, 1969, 1960.
Reintjes, 1962.
Salzen, 1958.
Simmons, 1957.
Suttkus and Sundararaj, 1961.

Taxonomy:

Berg, 1940, 1947.
Gill, 1861.
Goode, 1878.
Günther, 1868.
Hildebrand, 1948.
Monod, 1961.
Regan, 1917.
Svetovidov, 1952, 1963.
Thompson, 1916.

Trite: See *Ethmidium maculatum* or *E. chilcae*.

West African shad: See *Ethmalosa fimbriata*.

Yellowfin menhaden: See *Brevoortia smithi*.

OCEAN MORTALITY AND MATURITY SCHEDULES OF KARLUK RIVER SOCKEYE SALMON AND SOME COMPARISONS OF MARINE GROWTH AND MORTALITY RATES

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ABSTRACT

Four population models representing different temporal distributions of natural mortality during the ocean life of Karluk sockeye salmon (*Onchorhynchus nerka*) are developed and discussed. The first model simulates a constant monthly instantaneous mortality rate throughout ocean life of sockeye. In the second model, the monthly instantaneous mortality rate is greatest during the first month of ocean residence and decreases arithmetically in each succeeding month. In the third model, the monthly instantaneous mortality rate decreases geometrically during the first 6 months of ocean life and remains constant thereafter. The fourth model simulates a "catastrophic", age-specific first-month instantaneous mortality rate and a constant, age-independent mortality rate in the second and succeeding months of ocean life.

Data collected on the releases and returns of marked Karluk sockeye in the late 1920's and early 1930's are used to estimate ocean mortality rates of the different fresh-water age groups of fish. The rates vary with the population model used, year of ocean life and fresh-water age. Mortality of the smaller, 3-fresh-water smolts is greater than for the larger, 4-fresh-water fish during at least a part of ocean residence.

Maturity schedules are estimated for 3- and 4-fresh-water smolts in each population model. Depending on the distribution of ocean mortality, from 53 to 62 percent of the 3-fresh-water fish and 74 to 80 percent of

the 4-fresh-water sockeye achieve maturity by the end of their second year at sea.

The estimated instantaneous ocean mortality rates are compared with available estimates of Karluk sockeye ocean growth rates (weighted by the proportions of fish that mature as 1-, 2-, 3- and 4-ocean sockeye) on a monthly and annual basis to determine the net increase or decrease in weight during ocean residence. Except during the last year of ocean life of the relatively small fraction of Karluk sockeye that spend 4 years at sea, and then only for the first of 4 mortality distributions considered, ocean growth exceeds natural mortality.

The ranges of the estimated increases in bulk of Karluk sockeye during the first, second, and third years of ocean life, respectively, are 609 to 1,035 percent, 54 to 144 percent, and 26 to 84 percent. During the fourth year of ocean life, the bulk of Karluk sockeye is estimated to decrease by 8 to 10 percent under the first population model, and increase by 11 to 38 percent under the other 3 models.

The estimated percentage changes in bulk show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential yield, provided there exists an inshore fishery capable of catching the fish not needed for reproduction of the stock.

Information on the distribution and magnitude of ocean mortality of salmon and their maturity schedules is useful for comparing marine growth and mortality rates to determine the changes in bulk (net increase or decrease in weight) of a year

class during ocean residence. Knowledge of changes in bulk, in turn, is useful for comparing salmon yields obtained by a pelagic fishery with the potential yields available to an inshore fishery.

Among the data available for studying the natural mortality of salmon during their ocean

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life are those reported by Barnaby (1944), who gives the details of a number of experiments involving the marking of sockeye smolts at Karluk River during the late 1920's and early 1930's and the enumeration of returns of marked fish to that river system after 1-4 years of ocean residence. These experiments provide an impressive array of population data that are particularly useful for estimating ocean mortality of salmon, because they were obtained before the development of a large-scale pelagic salmon fishery west of longitude 175° W. in the North Pacific Ocean and likely are free of the confounding effects of high seas fishing.

Ricker (1962) utilized certain data from the Karluk marking experiments in his excellent analysis of the ocean growth and mortality of sockeye salmon during their last 2 years at sea. Parker (1962) also used the Karluk data in his unique study of the ocean mortality of Pacific salmon. Much of Barnaby's experimental population data are used here in an ocean mortality analysis that differs from the analyses and results presented by Ricker and Parker, respectively, in that (a) a somewhat different mathematical model is used to estimate ocean mortality for the case where the mortality rate is assumed to be constant throughout ocean residence, and (b) estimates of ocean mortality are made for three situations where the rate is considered to vary during ocean residence.

The portion of Barnaby's experimental population data used in this paper consists of the releases and returns of smolts that were marked by the removal of the adipose and one or both of the ventral fins. This analysis will be primarily concerned with the two fresh-water age groups of Karluk sockeye that, according to Rounsefell (1958, table 17), account for over 95 percent of the annual run to that system. These are the 3- and 4-fresh-water smolts, or fish that migrate to sea in their third and fourth years of life respectively.¹

For each of the four temporal distributions of ocean mortality considered in this study, I will estimate the percentages of 3- and 4-fresh-water smolts that mature after 1, 2, 3, and 4 years of ocean residence.

The estimates of ocean mortality presented here

¹ Ricker (1962) refers to these two groups as 2- and 3-fresh-water sockeye respectively; Parker (1962) refers to them as 2- and 3-annual smolts; Rounsefell (1958) refers to them as 3- and 4-year-old seaward migrants.

are compared with available growth rate data to determine changes in bulk of Karluk sockeye during ocean life. A number of such determinations are given in the last section of the paper. On the basis of these determinations, some inferences are drawn regarding the effects of high-seas fishing on the potential yield in weight of Karluk sockeye.

DURATION OF OCEAN RESIDENCE OF KARLUK SOCKEYE

Barnaby (1944) states that the major part of the seaward migration of Karluk sockeye takes place during the last week of May and the first 2 weeks of June each year. He also notes that the older smolts, that is, 4- and 5-fresh-water fish, migrate to sea earlier within the 3-week period of seaward migration than the younger smolts, that is, the 2- and 3-fresh-water fish. On the basis of these observations, I will assume for purposes of this study that 5-fresh-water smolts begin ocean life on June 1, 4-fresh-water smolts on June 5, 3-fresh-water smolts on June 10, and 2-fresh-water smolts on June 15.

From Rounsefell (1958, appendix table A-4) we can estimate the nearest dates ending in 5 or 0 on which 50 percent of the sockeye of different fresh-water and ocean ages return to the Karluk River. These estimates are given in table 1.

Using the dates of return given in table 1 as end points of ocean residence, the estimated duration of ocean life for each of 15 age groups of Karluk River sockeye is as shown in table 2.

For purposes of this study, it is assumed that the maximum ocean residence of 2- and 3-fresh-water smolts is 47.83 months, the maximum ocean residence of 4-fresh-water smolts is 48.17 months, and the maximum ocean residence of 5-fresh-water smolts is 36.50 months.

TABLE 1.—Estimated dates on which 50 percent of the sockeye of different fresh-water and ocean ages return to Karluk River

Fresh-water age group	Ocean age group ¹			
	1	2	3	4
2.....	July 15	June 30	June 15	June 10
3.....	Aug. 15	July 20	June 10	June 5
4.....	Sept. 5	Aug. 25	June 10	June 10
5.....	Sept. 10	Aug. 30	June 15	-----

¹ Ocean age is designated here as the nearest number of full years the fish spend in the ocean. A fish that spends, say, 26 months in the ocean is referred to as a 2-ocean fish.

TABLE 2.—Estimated duration of ocean residence, in months, of 15 age groups of Karluk River sockeye

Fresh-water age group	Ocean age group			
	1	2	3	4
2-----	13.00	24.50	36.00	47.83
3-----	14.17	25.33	36.00	47.83
4-----	15.00	26.67	36.17	48.17
5-----	15.33	27.00	36.50	-----

EFFECT OF MARKING ON OCEAN SURVIVAL

The extent to which the removal of adipose-ventral fins affected the percentage returns of marked Karluk smolts cannot be determined from the Karluk sockeye data, since the entire smolt run was not counted in any year of marking and comparative survival rates of marked and unmarked smolts are not available. That the removal of adipose and ventral fins probably caused a differential mortality among marked Karluk smolts is indicated by results of experiments in other systems in which sockeye smolts were marked by the removal of adipose-ventral fin combinations. Ricker (1962), using data from Cultus Lake sockeye marking studies (Foerster, 1934, 1936, 1937), estimated that on a day-to-day basis, marked sockeye were about 27 percent more vulnerable to the causes of death in operation than unmarked fish. This means that the instantaneous ocean mortality rate of marked sockeye was about 1.27 times the instantaneous natural mortality rate encountered by unmarked sockeye during their ocean life.

RELEASES AND RETURNS OF MARKED KARLUK SOCKEYE SMOLTS

Barnaby (1944, tables 33-35, 37, 39, 41, and 43) reports the numbers of smolts of each fresh-water age group that were marked by the removal of the adipose and one or both of the ventral fins in seven different marking experiments between 1929 and 1933 at the Karluk River. He also shows the estimated returns of marked fish by ocean age for each experiment. Except for the correction of a few minor errors in the estimated returns and an added estimate of a return of 17 4-ocean fish from the 3-fresh-water smolts marked in the second experiment in 1930, Barnaby's data on releases and returns are shown in table 3.

For purposes of this study, I will use the factor 1.27 in estimating the instantaneous ocean mortal-

TABLE 3.—Estimated releases and returns of Karluk River sockeye smolts marked by the removal of the adipose and one or both ventral fins.

[Barnaby, 1944, tables 33-35, 37, 39, 41, and 43]

Year of release	Experiment number	Fresh-water age group	Group number	Estimated release (N ₀)	Estimated returns					Estimated total percentage returns (ΣR)/(N ₀)
					1-ocean (R ₁)	2-ocean (R ₂)	3-ocean (R ₃)	4-ocean (R ₄)	Total (ΣR)	
					Number	Number	Number	Number	Number	
1929	1	3	1	21,858	656	2,882	450	-----	3,988	18.24
			2	28,041	1,002	5,362	783	7,147	25.49	
			3	162	22	-----	-----	22	13.58	
			4	252	-----	-----	12	12	4.76	
			5	14,676	28	1,730	725	2,483	16.92	
1930	1	3	4	9,773	146	2,237	235	2,618	26.79	
			5	299	5	-----	-----	67	22.41	
			2	237	-----	-----	-----	-----	-----	
			3	14,923	42	1,587	808	17	2,454	16.44
			4	9,554	208	2,396	160	2,764	28.93	
1931	1	3	5	286	-----	123	-----	123	43.01	
			2	84	23	23	-----	46	54.76	
			3	41,403	39	3,845	4,587	46	8,787	21.22
			4	8,145	119	2,949	399	3,897	34.46	
			5	323	150	150	-----	150	40.76	
1932	1	3	3	6,275	13	833	339	11	1,196	19.06
			4	8,568	109	1,212	412	23	1,756	20.44
			5	132	-----	-----	4	4	3.03	
			3	9,381	-----	1,256	926	45	2,227	23.74
			4	5,580	50	594	306	12	982	17.24
1933	1	3	5	89	-----	-----	-----	-----	-----	-----
			2	250	-----	15	32	-----	47	18.80
			3	25,394	7	3,208	1,441	-----	4,656	18.24
			4	13,692	45	2,423	941	-----	3,409	24.90
			5	664	-----	77	29	-----	106	15.96
Totals	-----	2	-----	823	-----	36	67	-----	105	12.76
			3	133,910	785	15,341	9,546	110	25,791	19.26
			4	83,378	1,679	16,573	3,178	35	21,463	25.74
			5	1,950	5	434	33	-----	472	24.20
			-----	-----	-----	-----	-----	-----	-----	-----

ity rates of unmarked Karluk sockeye from the release and return data given in table 3.

POPULATION MODEL 1

In this population model, the assumption is carried that the instantaneous ocean mortality rate of Karluk sockeye is constant throughout their ocean life. Notation is as follows:

- N_0 = The number of marked smolts of a given fresh-water age.
- M = The monthly instantaneous mortality rate of unmarked sockeye during their ocean life.
- 1.27—A factor to adjust for the effects of marking on ocean survival.
- $t_1 + k_1$ = The number of full months (t_1) plus the additional fraction of a month (k_1) elapsing between the time of seaward migration and the return of mature 1-ocean fish to the Karluk River.
- N_1 = The number of 1-ocean sockeye surviving at the end of $t_1 + k_1$ months of ocean residence.
- p_1 = The proportion of the surviving 1-ocean sockeye that mature and return to the Karluk River at the end of $t_1 + k_1$ months.
- R_1 = The number of 1-ocean sockeye that return to the Karluk River at the end of $t_1 + k_1$ months of ocean residence.
- $1 - p_1$ = The proportion of the surviving 1-ocean sockeye that do not mature at the end of $t_1 + k_1$ months of ocean residence.
- N'_1 = The number of the surviving, immature 1-ocean sockeye at the end of $t_1 + k_1$ months at sea.
- $t_2 + k_2$ = The number of full months (t_2) plus the additional fraction of a month (k_2) elapsing between the time of seaward migration and the return of mature 2-ocean fish to the Karluk River.
- N_2 = The number of 2-ocean sockeye surviving at the end of $t_2 + k_2$ months of ocean residence.
- p_2 = The proportion of the surviving 2-ocean sockeye that mature and return to the Karluk River at the end of $t_2 + k_2$ months.
- R_2 = The number of 2-ocean sockeye that return to the Karluk River at the end of $t_2 + k_2$ months of ocean residence.
- $1 - p_2$ = The proportion of the surviving 2-ocean sockeye that do not mature at the end of $t_2 + k_2$ months of ocean residence.
- N'_2 = The number of surviving, immature 2-ocean sockeye at the end of $t_2 + k_2$ months at sea.
- $t_3 + k_3$ = The number of full months (t_3) plus an additional fraction of a month (k_3) elapsing between the time of seaward migration and the return of mature 3-ocean sockeye to the Karluk River.
- N_3 = The number of 3-ocean sockeye surviving at the end of $t_3 + k_3$ months of ocean residence.
- p_3 = The proportion of the surviving 3-ocean sockeye that mature and return to the Karluk River at the end of $t_3 + k_3$ months. (In the case of the 5-fresh-water smolts, $t_3 + k_3$ is equal to 36.50 months, and p_3 is assumed to be equal to one.)

R_3 = The number of 3-ocean sockeye that mature and return to the Karluk River at the end of $t_3 + k_3$ months of ocean residence.

$1 - p_3$ = The proportion of the surviving 3-ocean sockeye that do not mature at the end of $t_3 + k_3$ months of ocean residence.

N'_3 = The number of surviving, immature 3-ocean sockeye at the end of $t_3 + k_3$ months of ocean residence.

$t_4 + k_4$ = The number of full months (t_4) plus the additional fraction of a month (k_4) elapsing between the time of seaward migration and the return of mature 4-ocean sockeye to the Karluk River.

N_4 = The number of 4-ocean sockeye surviving at the end of $t_4 + k_4$ months of ocean residence.

p_4 = The proportion of the surviving 4-ocean sockeye that mature and return to the Karluk River at the end of $t_4 + k_4$ months of ocean residence. (In this study, it is assumed that the maximum ocean residence of 2-, 3- and 4-fresh-water smolts is $t_4 + k_4$ months. Hence p_4 is assumed to be equal to one for these fresh-water age groups.)

R_4 = The number of 4-ocean sockeye that mature and return to the Karluk River at the end of $t_4 + k_4$ months of ocean residence.

Identities among the foregoing quantities are as follows:

$$N_1 = N_0 e^{-1.27M(t_1+k_1)} \quad (1)$$

$$R_1 = p_1 N_1 = p_1 N_0 e^{-1.27M(t_1+k_1)} \quad (2)$$

$$N'_1 = (1 - p_1) N_1 = N_1 - p_1 N_1 = N_1 - R_1 \quad (3)$$

$$\begin{aligned} N_2 &= N'_1 e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \\ &= N_1 e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \\ &\quad - R_1 e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \end{aligned}$$

$$= N_0 e^{-1.27M(t_2+k_2)} - R_1 e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \quad (4)$$

$$\begin{aligned} R_2 &= p_2 N_2 \\ &= p_2 N_0 e^{-1.27M(t_2+k_2)} \\ &\quad - p_2 R_1 e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \end{aligned} \quad (5)$$

$$N'_2 = (1 - p_2) N_2 = N_2 - p_2 N_2 = N_2 - R_2 \quad (6)$$

$$\begin{aligned} N_3 &= N'_2 e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \\ &= N_2 e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} - R_2 e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \\ &= N_0 e^{-1.27M(t_3+k_3)} - R_1 e^{-1.27M[(t_3+k_3)-(t_1+k_1)]} \\ &\quad - R_2 e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \quad (7)$$

$$\begin{aligned} R_3 &= p_3 N_3 = p_3 N_0 e^{-1.27M(t_3+k_3)} \\ &\quad - p_3 R_1 e^{-1.27M[(t_3+k_3)-(t_1+k_1)]} \\ &\quad - p_3 R_2 e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \quad (8)$$

$$N_3' = (1 - p_3)N_3 = N_3 - p_3N_3 = N_3 - R_3 \quad (9)$$

$$\begin{aligned} N_4 &= R_4 = N_3' e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \\ &= N_3 e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} - R_3 e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \\ &= N_0 e^{-1.27M(t_4+k_4)} - R_1 e^{-1.27M[(t_4+k_4)-(t_1+k_1)]} \\ &\quad - R_2 e^{-1.27M[(t_4+k_4)-(t_2+k_2)]} \\ &\quad - R_3 e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \quad (10) \end{aligned}$$

Equation (10), which is analogous to equation (11) of Parker (1962), can be used to estimate the monthly instantaneous ocean mortality rates for 2-, 3-, and 4-fresh-water smolts by entering observed or assumed quantities for N_0 , R_1 , R_2 , R_3 , R_4 , t_1+k_1 , t_2+k_2 , t_3+k_3 , and t_4+k_4 in the equation, and inserting trial values for M until one which results in a balanced expression is obtained. In a similar manner, equation (8) can be used to estimate M for 5-fresh-water smolts, since p_3 is assumed to be equal to one for this fresh-water age group.

Estimates of Monthly Instantaneous Mortality Rates

Of the 25 groups of marked sockeye smolts (table 3), there were 11 in which the numbers of fish released were small. These were the four groups of 2-fresh-water smolts and seven groups of 5-fresh-water smolts. The returns from each of these groups were also small in number, and they occurred in only 1 or 2 years following seaward migration. Because of the small numbers of fish involved, the instantaneous mortality rates are not estimated for the individual groups of 2- and 5-fresh-water smolts. Instead, the data for the four groups of marked 2-fresh-water smolts are combined, as are the data for the seven groups of marked 5-fresh-water smolts, for estimating the instantaneous ocean mortality rates for these two fresh-water age groups.

An estimate of the monthly instantaneous mortality rate can be obtained for each of the remaining 14 groups of marked sockeye, consisting of seven groups of 3-fresh-water smolts and seven groups of 4-fresh-water smolts.

Substitution of the appropriate t - and k -values in equations (10) and (8) yields the following expressions for estimating the monthly instantaneous ocean mortality rates for the four fresh-water age groups:

2-fresh-water smolts:

$$R_4 = N_0 e^{-60.74M} - R_1 e^{-44.28M} - R_2 e^{-29.63M} - R_3 e^{-15.02M}$$

3-fresh-water smolts:

$$R_4 = N_0 e^{-60.74M} - R_1 e^{-42.75M} - R_2 e^{-28.58M} - R_3 e^{-15.02M}$$

4-fresh-water smolts:

$$R_4 = N_0 e^{-61.18M} - R_1 e^{-42.13M} - R_2 e^{-27.30M} - R_3 e^{-15.24M}$$

5-fresh-water smolts:

$$R_3 = N_0 e^{-46.36M} - R_1 e^{-26.80M} - R_2 e^{-12.06M}$$

The estimates of monthly instantaneous ocean mortality rates, as derived from the appropriate equations and release and return data, are given in table 4. The marked group numbers associated with the estimates are shown in parentheses.

TABLE 4.—Estimated instantaneous ocean mortality rates of Karluk River sockeye, population model 1

[Effects of marking adjusted by factor of 1.27]

Fresh-water age group	Monthly instantaneous ocean mortality rate (M)	Mean M for 3- and 4-fresh-water smolts	Standard deviation of mean M
2-----	0.0496 (Groups 4, 8, 12, and 22 combined).		
3-----	0.0520 (1); 0.0480 (5); 0.0477 (9); 0.0381 (13); 0.0445 (16); 0.0365 (19); 0.0455 (23).	0.0446	0.0021
4-----	0.0402 (2); 0.0380 (6); 0.0366 (10); 0.0303 (14); 0.0426 (17); 0.0456 (20); 0.0369 (24).	.0386	.0018
5-----	0.0402 (Groups 3, 7, 11, 15, 18, 21, and 25 combined).		

Relation Between Monthly Instantaneous Mortality Rate and Age and Size of Smolts

The estimates of monthly instantaneous ocean mortality rates shown in table 4 indicate a general decrease with an increase in the fresh-water age of smolts: 0.0496 for 2-fresh-water smolts; an average of 0.0446 for 3-fresh-water smolts; an average of 0.0386 for 4-fresh-water smolts; and 0.0402 for 5-fresh-water smolts. Since the estimates for the 2- and 5-fresh-water smolts are based on relatively small numbers of fish, they should, in a comparison of ocean mortality rate with age at time of outmigration, be considered as rough approximations. Each of the estimated average mortality rates for the 3- and 4-fresh-water smolts on the other hand are based on seven groups of marked sockeye. Each group contained large numbers of marked fish. Six of seven paired groups, that is, two groups of smolts marked in the same way in the same year, showed a higher ocean mortality rate for 3-fresh-water smolts than for 4-fresh-water smolts. The standard deviations of the means show that the difference between the mean mortality rates for 3- and 4-fresh-water smolts is significant at about the 85 percent confidence level.

From Barnaby (1944, table 27), we can estimate the average body length of fish in each of the four fresh-water age groups of smolts in the seaward migration through the week ending June 14 for the years 1929 to 1933 combined. The average lengths for the 2-, 3-, 4-, and 5-fresh-water smolts were 108, 131, 143, and 146 millimeters, respectively. Plotting the estimated monthly instantaneous mortality rates for the four fresh-water age groups against average lengths of smolts at time of seaward migration, as in figure 1, we see a general decrease in ocean mortality as size of smolts increases.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

The mortality rates for the different ocean age groups and ocean years of life of 3- and 4-fresh-water smolts, the two fresh-water age groups which account for practically the entire run of Karluk sockeye, can be estimated from the average monthly instantaneous ocean mortality rates (table 4) and estimates of the duration of ocean residence of different ocean age groups (table 2).

For sockeye of a given fresh-water age that

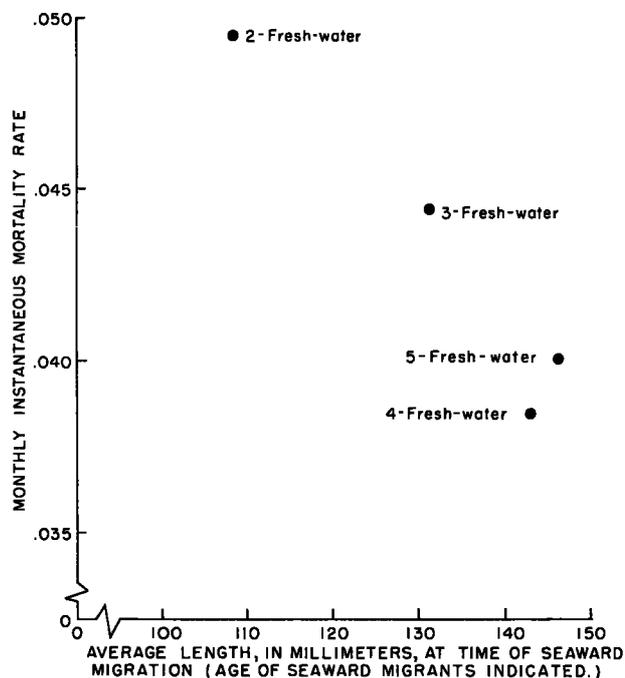


FIGURE 1.—Estimates of monthly instantaneous ocean mortality rates for Karluk sockeye of different lengths at time of seaward migration. (Data from table 4, and Barnaby, 1944, table 27).

mature at ocean age x , the total ocean mortality rate is estimated from the expression:

$$a_x = 1 - e^{-M(t_x + k_x)}$$

where t_x is the number of full months of ocean residence and k_x is the fraction of an additional month (if any) of ocean residence.

The annual ocean mortality rates during the first, second, third, and fourth years of ocean residence of sockeye of a given fresh-water age are obtained from the following expression:

$$a'_x = 1 - e^{-M[(t_x + k_x) - (t_{x-1} + k_{x-1})]}$$

where the quantity $[(t_x + k_x) - (t_{x-1} + k_{x-1})]$ represents the number of months elapsing between the time that one ocean age group returns to the Karluk River and the time that the next ocean age group returns to the Karluk River. This quantity generally is not equal to 12 months, hence the annual ocean mortality rates usually apply to periods of time other than 12 months. For example, table 2 shows for 3-fresh-water smolts that 1-ocean mature sockeye spend an average of 14.17 months at sea, 2-ocean mature sockeye spend an additional 11.16 months at sea, and so forth. Only in the case of 4-ocean mature sockeye of the 4-fresh-water smolts do the fish spend 12 months more in the ocean than sockeye that mature in the preceding year.

Table 5 shows the total ocean mortality rates for each ocean age group and the annual mortality rates for each ocean year of life for 3- and 4-fresh-water smolts.

TABLE 5.—Estimated mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 1

Fresh-water age group	Average monthly instantaneous ocean mortality rate, M	Ocean age		Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous ocean mortality rate during year	Annual ocean mortality rate (a'_x)
		Years	Months					
3-----	0.0446	1	14.17	0.6320	46.8	14.17	0.6320	46.8
		2	25.33	1.1297	67.7	11.16	.4977	39.2
		3	36.00	1.6056	79.9	10.67	.4759	37.9
		4	47.83	2.1332	88.2	11.83	.5276	41.0
4-----	.0386	1	15.00	.5790	44.0	15.00	.5790	44.0
		2	26.67	1.0295	64.3	11.67	.4505	36.3
		3	36.17	1.3962	75.2	9.50	.3667	30.7
		4	48.17	1.8594	84.4	12.00	.4632	37.1

The estimated total ocean mortality rates for 3-fresh-water smolts range from 46.8 percent for those sockeye that mature as 1-ocean fish to 88.2 percent for those that mature as 4-ocean fish. Corresponding estimates for 4-fresh-water smolts are 44.0 and 84.4 percent, respectively.

The annual mortality rates generally decreased with the progression of ocean years. This is due, of course, to a general decrease in the number of months elapsing between the times that one ocean age group matured and the next older ocean age group matured. If the durations of ocean residence were 12, 24, 36, and 48 months for the four ocean age groups, the annual ocean mortality rates would be approximately 41.4 percent for 3-fresh-water smolts and 37.1 percent for 4-fresh-water smolts.

Maturity Schedules of 3- and 4-Fresh-Water Smolts

The maturity schedules of the 3- and 4-fresh-water smolts, that is, the proportions of a given population of seaward migrants that mature after 1, 2, 3, and 4 years of ocean residence, can be roughly estimated from the ratios, $R_1/\Sigma R$, $R_2/\Sigma R$, $R_3/\Sigma R$, and $R_4/\Sigma R$, which can be obtained from table 3. Such ratios, however, do not account for the mortality that occurs among immature sockeye from one year to the next during their ocean life. As a result, the ratios, $R_1/\Sigma R$, and $R_2/\Sigma R$, are generally overestimates of the proportions of a given smolt migration that mature as 1- and 2-ocean fish. Conversely, $R_3/\Sigma R$ and $R_4/\Sigma R$ are generally underestimates of the proportions of a given smolt migration that mature as 3- and 4-ocean fish.

The factors, p_1 , p_2 , p_3 , and p_4 , in equations (2), (5), (8), and (10) represent the proportions of surviving 1-, 2-, 3-, and 4-ocean sockeye that mature at the end of the first, second, third, and fourth years of ocean residence. The equivalents of p_1 , p_2 , and p_3 are as follows:

$$p_1 = R_1/N_0 e^{-1.27M(t_1+k_1)} \quad (11)$$

$$p_2 = R_2/\{N_0 e^{-1.27M(t_2+k_2)} - R_1 e^{-1.27M[(t_2+k_2)-(t_1+k_1)]}\} \quad (12)$$

$$p_3 = R_3/\{N_0 e^{-1.27M(t_3+k_3)} - R_1 e^{-1.27M[(t_3+k_3)-(t_1+k_1)]} - R_2 e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}\} \quad (13)$$

The factor, p_4 , is assumed to be equal to one. Except for p_1 , these factors do not reflect the maturity schedules of a given smolt migration, because they do not account for the proportions of fish that matured in the preceding year or years.

Denoting the proportions of a given smolt migration that mature as 1-, 2-, 3-, and 4-ocean sockeye by p'_1 , p'_2 , p'_3 , and p'_4 , where $p'_1 + p'_2 +$

$p'_3 + p'_4 = 1$, we see that $p_1 = p'_1$; $p_2 = p'_2/(1-p'_1)$; $p_3 = p'_3/(1-p'_1-p'_2)$; and $p_4 = p'_4/(1-p'_1-p'_2-p'_3)$. Transposing we obtain the following expressions for p'_1 , p'_2 , p'_3 , and p'_4 :

$$p'_1 = p_1 \quad (14)$$

$$p'_2 = p_2(1-p'_1) \quad (15)$$

$$p'_3 = p_3(1-p'_1-p'_2) \quad (16)$$

$$p'_4 = 1-p'_1-p'_2-p'_3 \quad (17)$$

Substitution of the appropriate values for (t_1+k_1) , (t_2+k_2) , and (t_3+k_3) in equations (11), (12), and (13) provides the following expressions for p_1 , p_2 , and p_3 :

3-fresh-water smolts:

$$\begin{aligned} p_1 &= R_1/\{N_0 e^{-19.00M}\} \\ p_2 &= R_2/\{N_0 e^{-32.17M} - R_1 e^{-14.17M}\} \\ p_3 &= R_3/\{N_0 e^{-45.72M} - R_1 e^{-27.72M} - R_2 e^{-18.55M}\} \end{aligned}$$

4-fresh-water smolts:

$$\begin{aligned} p_1 &= R_1/\{N_0 e^{-19.05M}\} \\ p_2 &= R_2/\{N_0 e^{-33.87M} - R_1 e^{-14.82M}\} \\ p_3 &= R_3/\{N_0 e^{-46.94M} - R_1 e^{-28.89M} - R_2 e^{-12.06M}\} \end{aligned}$$

Using data from tables 3 and 4 to estimate p_1 , p_2 , and p_3 for each group of marked 3- and 4-fresh-water smolts, and inserting these estimates in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean fish. These are shown in table 6.

TABLE 6.—Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 1

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	1.35	51.41	45.77	1.47
4	3.34	71.04	24.61	1.01

Approximately one-half of the 3-fresh-water smolts mature by the end of 2 years in the ocean, with most of the remainder maturing after 3 years in the ocean. Nearly 75 percent of the 4-fresh-water smolts mature by the end of the second year of ocean residence.

Total Ocean Mortality Rate For a Given Outmigration

The total ocean mortality rate for a given outmigration of sockeye smolts depends upon the

magnitude of the mortality rates for the different ocean age groups and the proportions of seaward migrants that mature after 1, 2, 3, and 4 years of ocean residence. The rate is represented by the expression:

$$a = 1 - p'_1(1 - a_1) - p'_2(1 - a_2) - p'_3(1 - a_3) - p'_4(1 - a_4) \quad (18)$$

where a_1 , a_2 , a_3 , and a_4 are as shown in column 6 of table 5, and p'_1 , p'_2 , p'_3 , and p'_4 are as shown in table 6. For 3-fresh-water smolts, the average total ocean mortality rate is 73.3 percent, and for 4-fresh-water smolts, the average total ocean mortality rate is 66.5 percent.

POPULATION MODEL 2

Data presented by Ricker (1962), as well as the data shown in figure 1 of this paper, strongly suggest that the ocean mortality of sockeye salmon is greater while the fish are small than it is when they become larger. Accordingly, it seems that a population model that accounts for a decreasing monthly instantaneous natural mortality rate with increasing size of fish, or cumulative time spent in the ocean, probably represents the actual survival conditions of sockeye salmon during their ocean life far better than a population model in which a constant natural mortality rate is assumed. In this section, we will consider a population model in which the monthly instantaneous natural mortality rate is a function of the number of months spent in the ocean by 3- and 4-fresh-water smolts.

The quantities N_0 , R_1 , R_2 , R_3 , R_4 , p_1 , p_2 , p_3 , p_4 , $t_1 + k_1$, $t_2 + k_2$, $t_3 + k_3$, and $t_4 + k_4$ are as defined in Population Model 1. The factor 1.27 is used to adjust for the effects of marking. During the first month of a maximum of $t_4 + k_4$ months of ocean residence, the instantaneous ocean mortality rate

is represented by M_1 . The instantaneous mortality rate during the second month of ocean residence is represented by M_2 and is assumed to be equal to $(1-d)M_1$, where d is equal to $1/(t_4 + k_4)$. The instantaneous mortality rate during the third month of ocean residence is represented by M_3 and is assumed to be equal to $(1-2d)M_1$. In each succeeding month of ocean life, the instantaneous mortality rate is assumed to decrease by the quantity dM_1 . The sequence of monthly instantaneous mortality rates is an arithmetic progression.

During month t_x of ocean life, the instantaneous mortality rate, M_{t_x} , is equal to $[M_1 - (t_x - 1)dM_1]$ or $M_1[1 - (t_x - 1)d]$. The instantaneous mortality rate for the fraction k_x of month $(t_x + 1)$ is $k_x M_1[1 - (t_x)d]$. The rate for the remaining fraction $(1 - k_x)$ of the month is $(1 - k_x)M_1[1 - (t_x)d]$. The sum of the monthly instantaneous mortality rates from the first month of ocean life through month t_x is $(t_x/2)(M_1 + M_{t_x})$. Upon substitution for M_{t_x} and factoring, this sum is equivalent to $M_1(t_x/2)[2 - (t_x - 1)d]$. The sum of the monthly instantaneous ocean mortality rates from, say, month $(t_1 + 2)$ through month t_2 is given by $[(t_2 - t_1 - 1)/2][M_{t_1+2} + M_{t_2}]$. Upon substitution for M_{t_1+2} and M_{t_2} and factoring, this sum is equal to $M_1[(t_2 - t_1 - 1)/2][2 - (t_1 + t_2)d]$. Thus, the returns of sockeye of different ocean ages are as shown by the following equations:

$$R_1 = p_1 N_0 e^{-1.27 M_1 \left\{ \frac{t_1}{2} [2 - (t_1 - 1)d] + k_1 [1 - (t_1)d] \right\}} \quad (19)$$

$$R_2 = p_2 N_0 e^{-1.27 M_1 \left\{ \frac{t_2}{2} [2 - (t_2 - 1)d] + k_2 [1 - (t_2)d] \right\}} - p_2 R_1 e^{-1.27 M_1 \left\{ (1 - k_1) [1 - (t_1)d] + \frac{t_2 - t_1 - 1}{2} [2 - (t_1 + t_2)d] + k_2 [1 - (t_2)d] \right\}} \quad (20)$$

$$R_3 = p_3 N_0 e^{-1.27 M_1 \left\{ \frac{t_3}{2} [2 - (t_3 - 1)d] + k_3 [1 - (t_3)d] \right\}} - p_3 R_1 e^{-1.27 M_1 \left\{ (1 - k_1) [1 - (t_1)d] + \frac{t_3 - t_1 - 1}{2} [2 - (t_1 + t_3)d] + k_3 [1 - (t_3)d] \right\}} - p_3 R_2 e^{-1.27 M_1 \left\{ (1 - k_2) [1 - (t_2)d] + \frac{t_3 - t_2 - 1}{2} [2 - (t_2 + t_3)d] + k_3 [1 - (t_3)d] \right\}} \quad (21)$$

$$R_4 = N_0 e^{-1.27 M_1 \left\{ \frac{t_4}{2} [2 - (t_4 - 1)d] + k_4 [1 - (t_4)d] \right\}} - R_1 e^{-1.27 M_1 \left\{ (1 - k_1) [1 - (t_1)d] + \frac{t_4 - t_1 - 1}{2} [2 - (t_1 + t_4)d] + k_4 [1 - (t_4)d] \right\}} - R_2 e^{-1.27 M_1 \left\{ (1 - k_2) [1 - (t_2)d] + \frac{t_4 - t_2 - 1}{2} [2 - (t_2 + t_4)d] + k_4 [1 - (t_4)d] \right\}} - R_3 e^{-1.27 M_1 \left\{ (1 - k_3) [1 - (t_3)d] + \frac{t_4 - t_3 - 1}{2} [2 - (t_3 + t_4)d] + k_4 [1 - (t_4)d] \right\}} \quad (22)$$

Equation (22) can be used to solve for M_1 for the 3- and 4-fresh-water smolts by the trial method used in Population Model 1. Values for $t_1, k_1, t_2, k_2, t_3, k_3, t_4,$ and k_4 can be obtained from table 2, and the values for $N_0, R_1, R_2, R_3,$ and R_4 from table 3. For 3-fresh-water smolts, d is equal to 1/47.83 or 0.020907; for 4-fresh-water smolts, d is equal to 1/48.17 or 0.020760. Substitution of the appropriate $t-, k-,$ and $d-$ values in equation (22) yields the following expressions for estimating M_1 :

3-fresh-water smolts:

$$R_4 = N_0 e^{-31.00M_1} - R_1 e^{-18.49M_1} - R_2 e^{-7.02M_1} - R_3 e^{-2.01M_1}$$

4-fresh-water smolts:

$$R_4 = N_0 e^{-31.22M_1} - R_1 e^{-14.99M_1} - R_2 e^{-6.38M_1} - R_3 e^{-2.06M_1}$$

Estimates of Monthly Instantaneous Mortality Rates

Each of the seven groups of marked 3-fresh-water smolts provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their third year of life. Seven groups of marked 4-fresh-water smolts provide estimates of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their fourth year of life. These estimates, their averages, and the standard deviations of the means are shown in table 7. The marked group numbers associated with the estimates are shown in parentheses.

Using the averages in table 7 as the instantaneous mortality rates of 3- and 4-fresh-water smolts during their first month of ocean residence, we can estimate the mortality rates in any ocean month, m , as follows:

$$M_m = M_1 [1 - (m-1)d] \quad (23)$$

TABLE 8.—Estimated monthly instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2

Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group	
	3	4		3	4		3	4		3	4
1	0.0649	0.0549	13	0.0486	0.0412	25	0.0323	0.0275	37	0.0160	0.0139
2	0.0635	0.0538	14	0.0473	0.0401	26	0.0310	0.0264	38	0.0147	0.0127
3	0.0622	0.0526	15	0.0459	0.0389	27	0.0296	0.0253	39	0.0133	0.0116
4	0.0608	0.0515	16	0.0445	0.0378	28	0.0283	0.0241	40	0.0120	0.0104
5	0.0595	0.0503	17	0.0432	0.0367	29	0.0269	0.0230	41	0.0106	0.0093
6	0.0581	0.0492	18	0.0418	0.0355	30	0.0256	0.0218	42	0.0093	0.0082
7	0.0568	0.0481	19	0.0405	0.0344	31	0.0242	0.0207	43	0.0079	0.0070
8	0.0554	0.0469	20	0.0391	0.0332	32	0.0228	0.0196	44	0.0066	0.0059
9	0.0540	0.0458	21	0.0378	0.0321	33	0.0215	0.0184	45	0.0052	0.0048
10	0.0527	0.0446	22	0.0364	0.0310	34	0.0201	0.0173	46	0.0038	0.0036
11	0.0513	0.0435	23	0.0350	0.0298	35	0.0188	0.0161	47	0.0025	0.0025
12	0.0500	0.0424	24	0.0337	0.0287	36	0.0174	0.0150	48	0.0011	0.0013
									49		0.0002

TABLE 7.—Estimates of first-month instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2

[Effects of marking adjusted by factor of 1.27]

Fresh-water age group	First-month instantaneous ocean mortality rate, M_1	Average	Standard deviation of mean
3	0.0720 (1); 0.0695 (5); 0.0700 (9); 0.0575 (13); 0.0648 (16); 0.0545 (19); 0.0660 (23)	0.0649	0.0025
4	0.560 (2); 0.0529 (6); 0.0504 (10); 0.0424 (14); 0.0619 (17); 0.0673 (20); 0.0534 (24)	0.0549	0.0030

Table 8 gives the instantaneous mortality rates for each month of ocean residence for the two fresh-water age groups.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the estimated monthly instantaneous ocean mortality rates given in table 8, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 9.

The estimated total ocean mortality rates for 3-fresh-water smolts range from 54.7 percent for those fish that mature as 1-ocean sockeye to 79.5 percent for those fish that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts are 50.5 and 74.1 percent respectively.

Under this population model, the annual ocean mortality rates for 3-fresh-water smolts decrease from 54.7 percent during the first year (14.17 months) of ocean residence to 9.8 percent during the fourth year (11.83 months) of ocean residence. For 4-fresh-water smolts, the annual mortality rate decreases from 50.5 percent during the first year of ocean residence to 8.5 percent during

TABLE 9.—Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_2)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_2)
3-----	1	14.17	0.7929	54.7	14.17	0.7929	54.7
	2	25.33	1.2255	70.6	11.16	.4328	35.1
	3	36.00	1.4815	77.3	10.67	.2680	22.6
	4	47.83	1.5843	79.5	11.83	.1028	9.8
4-----	1	15.00	.7038	50.5	15.00	.7038	50.5
	2	26.67	1.0739	65.8	11.67	.3701	30.9
	3	36.17	1.2606	71.6	9.50	.1867	17.0
	4	48.17	1.3494	74.1	12.00	.0888	8.5

the fourth year of ocean residence. Most of the ocean mortality takes place during the first 14 or 15 months of ocean residence according to the estimates given in table 9.

MATURITY SCHEDULES

The maturity schedules for 3- and 4-fresh-water smolts under Population Model 2 are estimated by the procedure described under Population Model 1. Factorization and transposition of terms in equations (19) to (21) and substitution of appropriate values for the terms and sums of the arithmetic progressions in the exponents of these equations provide the following expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life:

3-fresh-water smolts:

$$p_1 = R_1 / [N_0 e^{-15.52M_1}]$$

$$p_2 = R_2 / [N_0 e^{-23.98M_1} - R_1 e^{-8.47M_1}]$$

$$p_3 = R_3 / [N_0 e^{-28.99M_1} - R_1 e^{-13.48M_1} - R_2 e^{-5.01M_1}]$$

4-fresh-water smolts:

$$p_1 = R_1 / [N_0 e^{-16.32M_1}]$$

$$p_2 = R_2 / [N_0 e^{-24.84M_1} - R_1 e^{-9.56M_1}]$$

$$p_3 = R_3 / [N_0 e^{-29.16M_1} - R_1 e^{-12.83M_1} - R_2 e^{-4.32M_1}]$$

Using data from tables 3 and 7 in the above expressions to obtain estimates of p_1 , p_2 , and p_3 for each group of marked 3- and 4-fresh-water smolts and inserting the resulting p-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 2. The average percentages are shown in table 10.

Under Population Model 2, slightly higher proportions (approximately 4 to 7 percent) of the

TABLE 10.—Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 2

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3-----	1.63	57.74	39.83	0.80
4-----	3.89	74.48	21.14	.49

3- and 4-fresh-water smolts mature by the end of 2 years of ocean life than under Population Model 1. The differences between the maturity schedules under Population Models 1 and 2 result from differences in the distribution of ocean mortality.

Total Ocean Mortality Rate for a Given Outmigration

The ocean mortality rate for a given outmigration of sockeye is the same under Population Model 2 as it was under Population Model 1. This rate is fixed, in our estimates, by the ratios of marked fish returning to those released. Redistribution of the monthly instantaneous ocean mortality rates does not affect it.

POPULATION MODEL 3

Population Models 1 and 2 deal with what might be considered as two extreme situations with regard to the temporal distribution of ocean mortality of Karluk sockeye. In one case we considered ocean mortality to be constant throughout the period of ocean residence. In the other case we considered ocean mortality to decrease continually throughout the period of ocean residence, becoming zero at the end of 4 years. In view of the evidence which suggests that the ocean mortality rate of sockeye is greater while they are small than it is when they become larger and in view of the lack of evidence that the ocean mortality rate continually decreases and becomes zero after an extended period of time, it seems worthwhile to examine what is intended to be an intermediate situation, one that we will consider under Population Model 3.

In this model it is assumed that the monthly instantaneous mortality rate decreases geometrically during the first 6 months of ocean residence such that M_2 , the second-month mortality rate,

is equal to $0.5M_1$, where M_1 is the first-month mortality rate; M_3 , the third-month mortality rate, is equal to $0.5M_2$ or $0.25M_1$; M_4 , the fourth-month mortality rate, is equal to $0.5M_3$ or $0.125M_1$; M_5 , the fifth-month mortality rate, is equal to $0.5M_4$ or $0.0625M_1$; and M_6 , the sixth-month mortality rate, is equal to $0.5M_5$ or $0.03125M_1$. It is further assumed that the instantaneous mortality rate during the seventh and each succeeding month of ocean residence is equal to M_6 or $0.03125M_1$.

The sum of the monthly instantaneous mortality rates during the first 6 months of ocean residence is $M_1 + 0.5M_1 + 0.25M_1 + \dots + 0.03125M_1$, or $1.96875M_1$. The sum of the monthly instantaneous mortality rates during any number of months after the sixth month of ocean residence is the product of the number of months involved and $0.03125M_1$.

The quantities N_0 , R_1 , R_2 , R_3 , R_4 , p_1 , p_2 , p_3 , p_4 , t_1+k_1 , t_2+k_2 , t_3+k_3 , and t_4+k_4 are as defined in the previous models. The factor 1.27 is used to adjust for the effects of marking. Thus, the returns of sockeye of different ocean ages are as shown by the following equations:

$$R_1 = p_1 N_0 e^{-1.27M_1[(1.96875 + (t_1+k_1-6) (0.03125))]} \quad (24)$$

$$R_2 = p_2 N_0 e^{-1.27M_1[(1.96875 + (t_2+k_2-6) (0.03125))]} - p_2 R_1 e^{-1.27M_1[(t_2+k_2) - (t_1+k_1)] (0.03125)} \quad (25)$$

$$R_3 = p_3 N_0 e^{-1.27M_1[(1.96875 + (t_3+k_3-6) (0.03125))]} - p_3 R_1 e^{-1.27M_1[(t_3+k_3) - (t_1+k_1)] (0.03125)} - p_3 R_2 e^{-1.27M_1[(t_3+k_3) - (t_2+k_2)] (0.03125)} \quad (26)$$

$$R_4 = N_0 e^{-1.27M_1[(1.96875 + (t_4+k_4-6) (0.03125))]} - R_1 e^{-1.27M_1[(t_4+k_4) - (t_1+k_1)] (0.03125)} - R_2 e^{-1.27M_1[(t_4+k_4) - (t_2+k_2)] (0.03125)} - R_3 e^{-1.27M_1[(t_4+k_4) - (t_3+k_3)] (0.03125)} \quad (27)$$

Equation (27) is used to solve for M_1 for the 3- and 4-fresh-water smolts by the trial method mentioned previously. Substitution of the appropriate t - and k -values in equation (27) yields the following expressions for estimating M_1 :

3-fresh-water smolts:

$$R_4 = N_0 e^{-4.16M_1} - R_1 e^{-1.34M_1} - R_2 e^{-0.80M_1} - R_3 e^{-0.47M_1}$$

4-fresh-water smolts:

$$R_4 = N_0 e^{-4.17M_1} - R_1 e^{-1.32M_1} - R_2 e^{-0.85M_1} - R_3 e^{-0.48M_1}$$

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TABLE 11.—Estimates of first-month instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3

[Effects of marking adjusted by factor of 1.27]

Fresh-water age	First-month instantaneous ocean mortality rate, M^1	Average	Standard deviation of mean
3-----	{ 0.5224 (1); 0.5230 (5); 0.5279 (9); 0.4410 (13); 0.4970 (16); 0.4140 (19); 0.4976 (23).	0.4876	0.0187
4-----	{ 0.4138 (2); 0.3953 (6); 0.3746 (10); 0.3181 (14); 0.4669 (17); 0.5114 (20); 0.4083 (24).	.4123	.0236

Estimates of Monthly Instantaneous Ocean Mortality Rates

Each of the seven groups of marked 3-fresh-water smolts and the seven groups of marked 4-fresh-water smolts (table 3) provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their third and fourth years of life. These estimates, their averages, and the standard deviations of the means, are shown in table 11. The marked group numbers associated with the estimates are shown in parentheses.

Using the averages in table 11 as the instantaneous mortality rates of 3- and 4-fresh-water smolts during their first month of ocean residence, we can obtain estimates of the mortality rates during the second through sixth months of ocean residence under Population Model 3 by multiplying M_1 by 0.5, 0.25, 0.125, 0.0625, and 0.03125, respectively. Table 12 gives the instantaneous mortality rates for each month of ocean residence for the two fresh-water age groups.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the estimated monthly instantaneous ocean mortality rates given in table 12, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 13.

TABLE 12.—Estimated monthly instantaneous ocean mortality rates 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3

Month at sea	Instantaneous mortality rate	
	3-fresh-water fish	4-fresh-water fish
1st-----	0.4876	0.4123
2d-----	.2438	.2062
3d-----	.1219	.1031
4th-----	.0610	.0515
5th-----	.0305	.0258
6th and each succeeding month-----	.0152	.0129

TABLE 13.—Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3.

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence in months	Total instantaneous mortality rate	Total ocean mortality rate (a_1)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a_2)
	Years	Months		Percent	Months		Percent
3-----	1	14. 17	1. 0842	66. 2	14. 17	1. 0842	66. 2
	2	25. 33	1. 2538	71. 4	11. 16	. 1696	15. 8
	3	36. 00	1. 4160	75. 7	10. 67	. 1622	18. 0
	4	47. 83	1. 5958	79. 7	11. 83	. 1798	18. 4
4-----	1	15. 00	. 9279	60. 5	15. 00	. 9279	60. 5
	2	26. 67	1. 0784	66. 0	11. 67	. 1505	14. 0
	3	36. 17	1. 2010	69. 9	9. 50	. 1226	11. 5
	4	48. 17	1. 3558	74. 2	12. 00	. 1548	14. 3

The estimated total ocean mortality rates for 3-fresh-water smolts range from 66.2 percent for those fish that mature as 1-ocean sockeye to 79.7 percent for those fish that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts, under this model, are 60.5 and 74.2 percent, respectively.

The annual ocean mortality rates for 3-fresh-water smolts decrease from 66.2 percent during the first year of ocean residence to 16.4 percent during the fourth year of ocean life. For 4-fresh-water smolts, the annual ocean mortality rate decreases from 60.5 percent during the first year of ocean life to 11.5 percent during the third year of ocean life and then increases to 14.3 percent during the longer fourth year of ocean residence.

Under this model, most of the ocean mortality takes place during the first 6 months of ocean residence.

Maturity Schedules

Factorization and transposition of terms in equations (24) to (26) and substitution of appropriate t - and k - values in the exponents of these equations provide the following expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life:

3-fresh-water smolts:

$$p_1 = R_1/[N_0e^{-2.82M_1}]$$

$$p_2 = R_2/[N_0e^{-3.37M_1} - R_1e^{-0.44M_1}]$$

$$p_3 = R_3/[N_0e^{-3.69M_1} - R_1e^{-0.87M_1} - R_2e^{-0.42M_1}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_0e^{-2.86M_1}]$$

$$p_2 = R_2/[N_0e^{-3.32M_1} - R_1e^{-0.46M_1}]$$

$$p_3 = R_3/[N_0e^{-3.70M_1} - R_1e^{-0.84M_1} - R_2e^{-0.38M_1}]$$

Using data from tables 3 and 11 in the foregoing expressions to obtain estimates of p_1 , p_2 , and p_3 for each group of marked 3- and 4-fresh-water smolts and inserting the resulting p -values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 3. The average percentages are shown in table 14.

TABLE 14.—Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 3

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p_1)	(p_2)	(p_3)	(p_4)
3-----	2. 35	59. 78	37. 05	0. 82
4-----	5. 15	74. 75	19. 62	. 48

Under this population model, approximately 2 or 3 percent more of the 3- and 4-fresh-water smolts mature by the end of the second year of ocean life than under Population Model 2.

POPULATION MODEL 4

It might be hypothesized that the difference between the ocean mortality rates of 3- and 4-fresh-water sockeye smolts is caused by some survival condition which operates differentially on small (3-fresh-water) and large (4-fresh-water) smolts early in the ocean lives of these fish, say, during the first month of ocean residence and that the mortality rate during succeeding months of ocean life is the same for the two fresh-water age groups. If this is the case, it would seem to follow that the first-month ocean mortality rates for both fresh-water age groups would be great in comparison with the mortality rates during the second and succeeding months of ocean life. In this section, we will consider a population model that simulates these survival conditions.

It is assumed that the first-month instantaneous ocean mortality rate of 4-fresh-water smolts, M_{1_4} , is 20 times M_{2_4} , their instantaneous mortality rate during the second and each succeeding month of ocean residence. The first-month instantaneous ocean mortality rate of 3-fresh-water smolts is represented by M_{1_3} or cM_{1_4} , where c measures

the differential mortality caused by some survival condition. The mortality rate of 3-fresh-water smolts during the second and each succeeding month of ocean residence is assumed to be the same as for 4-fresh-water smolts, that is M_{2_4} , or $0.05 M_{1_4}$.

The quantities N_0 , R_1 , R_2 , R_3 , R_4 , p_1 , p_2 , p_3 , p_4 , t_1+k_1 , t_2+k_2 , t_3+k_3 , and t_4+k_4 are as previously defined. The factor 1.27 is used to adjust for the effects of marking. Hence, the returns from the 4-fresh-water smolt migrations are as shown by the following expressions:

$$R_1 = p_1 N_0 e^{-1.27 M_{1_4} [1 + (t_1 + k_1 - 1) (0.05)]} \quad (28)$$

$$R_2 = p_2 N_0 e^{-1.27 M_{1_4} [1 + (t_2 + k_2 - 1) (0.05)]} - p_2 R_1 e^{-1.27 M_{1_4} (0.05) [(t_2 + k_2) - (t_1 + k_1)]} \quad (29)$$

$$R_3 = p_3 N_0 e^{-1.27 M_{1_4} [1 + (t_3 + k_3 - 1) (0.05)]} - p_3 R_1 e^{-1.27 M_{1_4} (0.05) [(t_3 + k_3) - (t_1 + k_1)]} - p_3 R_2 e^{-1.27 M_{1_4} (0.05) [(t_3 + k_3) - (t_2 + k_2)]} \quad (30)$$

$$R_4 = N_0 e^{-1.27 M_{1_4} [1 + (t_4 + k_4 - 1) (0.05)]} - R_1 e^{-1.27 M_{1_4} (0.05) [(t_4 + k_4) - (t_1 + k_1)]} - R_2 e^{-1.27 M_{1_4} (0.05) [(t_4 + k_4) - (t_2 + k_2)]} - R_3 e^{-1.27 M_{1_4} (0.05) [(t_4 + k_4) - (t_3 + k_3)]} \quad (31)$$

The returns of 1-, 2-, 3-, and 4-ocean fish from the 3-fresh-water smolt migrations are represented by equations identical to (28) through (31) respectively except that c , rather than 1, appears as the first term inside the bracketed portion of the first exponent of each equation. Thus, the returns of 4-ocean fish from the 3-fresh-water smolts migrations are represented as follows:

$$R_4 = N_0 e^{-1.27 M_{1_4} [c + (t_4 + k_4 - 1) (0.05)]} - R_1 e^{-1.27 M_{1_4} (0.05) [(t_4 + k_4) - (t_1 + k_1)]} - R_2 e^{-1.27 M_{1_4} (0.05) [(t_4 + k_4) - (t_2 + k_2)]} - R_3 e^{-1.27 M_{1_4} (0.05) [(t_4 + k_4) - (t_3 + k_3)]} \quad (32)$$

Equation (31) is used to solve for the first-month instantaneous ocean mortality rate for the 4-fresh-water smolts by the trial method used in previous population models. Substitution of appropriate t - and k -values from table 2 reduces equation (31) to the following expression:

$$R_4 = N_0 e^{-4.26 M_{1_4}} - R_1 e^{-2.11 M_{1_4}} - R_2 e^{-1.36 M_{1_4}} - R_3 e^{-0.76 M_{1_4}}$$

Estimates of Monthly Instantaneous Ocean Mortality Rates

Each of seven groups of marked 4-fresh-water smolts (table 3) provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their fourth year of life. These estimates, their average, and the standard deviation of the mean are shown in table 15. The marked group numbers associated with the estimates are given in parentheses.

TABLE 15.—Estimates of first-month instantaneous ocean mortality rates for 4-fresh-water Karluk River sockeye smolts, population model 4

[Effects of marking adjusted by factor of 1.27]

First-month instantaneous ocean mortality rate, M_{1_4}	Average, \bar{M}_{1_4}	Standard deviation of mean
0.4734 (2); 0.4501 (6); 0.4290 (10); 0.3608 (14); 0.5212 (17); 0.5656 (20); 0.4522 (24).	0.4646	0.0248

Based on the average first-month instantaneous ocean mortality rate of 0.4646, the estimated mortality rate of 4-fresh-water (and 3-fresh-water) smolts during the second and each succeeding month of ocean residence is 0.05 times 0.4646 or 0.0232.

Inserting the estimate of \bar{M}_{1_4} and appropriate t - and k -values in equation (32), we obtain the following expression for the returns of 4-ocean fish from the seaward migrations of 3-fresh-water smolts:

$$R_4 = N_0 e^{-0.59c} e^{-1.38} - R_1 e^{-0.99} - R_2 e^{-0.66} - R_3 e^{-0.35}$$

Transposing terms and taking logarithms, we obtain the following expression for c :

$$c = \ln \{ [R_4 + R_1 e^{-0.99} + R_2 e^{-0.66} + R_3 e^{-0.35}] / N_0 e^{-1.38} \} / -0.59$$

Each of seven groups of marked 3-fresh-water smolts (table 3) provides an estimate of c . Each estimate of c , in turn, can be multiplied by M_{1_4} to furnish an estimate of M_{1_3} , the first-month instantaneous ocean mortality rate for 3-fresh-water sockeye smolts. Table 16 shows the estimates of c and M_{1_3} for each marked group, the average first-month instantaneous ocean mortality rate, and the standard deviation of the mean mortality rate.

TABLE 16.—Estimates of first-month instantaneous ocean mortality rates of 3-fresh-water Karluk River sockeye smolts, population model 4

[Effects of marking adjusted by factor of 1.27]

Marked group No.	Coefficient of differential mortality, c	First-month instantaneous ocean mortality rate, M_{13}
1.....	1.67	0.7759
5.....	1.62	.7528
9.....	1.65	.7666
13.....	1.09	.5064
16.....	1.41	.6551
19.....	.95	.4414
23.....	1.47	.6830
Averages.....	1.41	0.6544
Standard deviation of mean mortality rate.....		.0500

Based on the averages given in table 16, the first month instantaneous ocean mortality rate of 3-fresh-water smolts is approximately 40 percent greater than the corresponding rate for 4-fresh-water smolts and about 28 times (1.41×20 or $0.6544/0.0232$) greater than the instantaneous mortality rate during the second and each succeeding month of ocean residence for 3- and 4-fresh-water smolts.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the average first-month instantaneous ocean mortality rates given in tables 15 and 16, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 17.

TABLE 17.—Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 4

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_s)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_s)
			Percent	Percent		Percent	Percent
3.....	Years	Months			Months		
	1	14.17	0.9599	61.7	14.17	0.9599	61.7
	2	25.33	1.2189	70.4	11.16	.2589	22.8
	3	36.00	1.4664	76.9	10.67	.2475	21.9
4.....	4	47.83	1.7408	82.5	11.83	.2745	24.0
	1	15.00	.7894	54.6	15.00	.7894	54.6
	2	26.67	1.0601	65.4	11.67	.2707	23.7
	3	36.17	1.2805	72.2	9.50	.2204	19.8
	4	48.17	1.5589	79.0	12.00	.2784	24.3

The estimated total ocean mortality rates range from 61.7 percent for those 3-fresh-water smolts that mature as 1-ocean fish to 82.5 percent for those that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts are 54.6 and 79.0 percent, respectively.

The annual ocean mortality rates for 3-fresh-water smolts decrease from 61.7 percent during the first year of ocean life to about 22 to 24 percent during each of the last 3 years of ocean residence. For 4-fresh-water smolts, the annual ocean mortality rate decreases from 54.6 percent during the first year of ocean life to about 20 to 24 percent during each of the succeeding years.

Under this model, of course, most of the ocean mortality takes place during the first month of ocean residence.

Maturity Schedules

Expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life can be obtained from equations (28) to (30) for 4-fresh-water smolts and from analogous equations (not shown in the text) for 3-fresh-water smolts. These expressions, after substitution of appropriate t - and k -values, are as follows:

3-fresh-water smolts:

$$p_1 = R_1/[N_0e^{-1.27M_{14}(c+0.6585)}]$$

$$p_2 = R_2/[N_0e^{-1.27M_{14}(c+1.2165)} - R_1e^{-0.7087M_{14}}]$$

$$p_3 = R_3/[N_0e^{-1.27M_{14}(c+1.7600)} - R_1e^{-1.3862M_{14}} - R_2e^{-0.6775M_{14}}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_0e^{-2.1590M_{14}}]$$

$$p_2 = R_2/[N_0e^{-2.9000M_{14}} - R_1e^{-0.7410M_{14}}]$$

$$p_3 = R_3/[N_0e^{-3.5033M_{14}} - R_1e^{-1.3443M_{14}} - R_2e^{-0.6032M_{14}}]$$

Using data from tables 3, 15, and 16 in the above expressions to obtain estimates of p_1 , p_2 , and p_3 for each group of marked 3- and 4-fresh-water smolts, and inserting the resulting p -values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 4. The average percentages are shown in table 18.

TABLE 18.—Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 4

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3.....	2.11	57.30	39.59	1.00
4.....	4.34	73.36	21.61	.69

The maturity schedules of 3- and 4-fresh-water smolts under this population model are very similar to those under Population Model 2.

COMPARISON OF OCEAN MORTALITY RATES

The estimated average monthly instantaneous mortality rates during the different years of ocean life of 3- and 4-fresh-water Karluk sockeye smolts under the four population models are compared in figures 2 and 3. Similar comparisons of the annual ocean mortality rates are given in figures 4 and 5.

The mortality rates obtained under Population Model 1 are lower during the first year of ocean life than those obtained under the other three models. The situation is reversed in the second year. In the third and fourth years of ocean residence, the mortality rates under Population Models 2, 3, and 4 are considerably lower than those obtained under Population Model 1. The

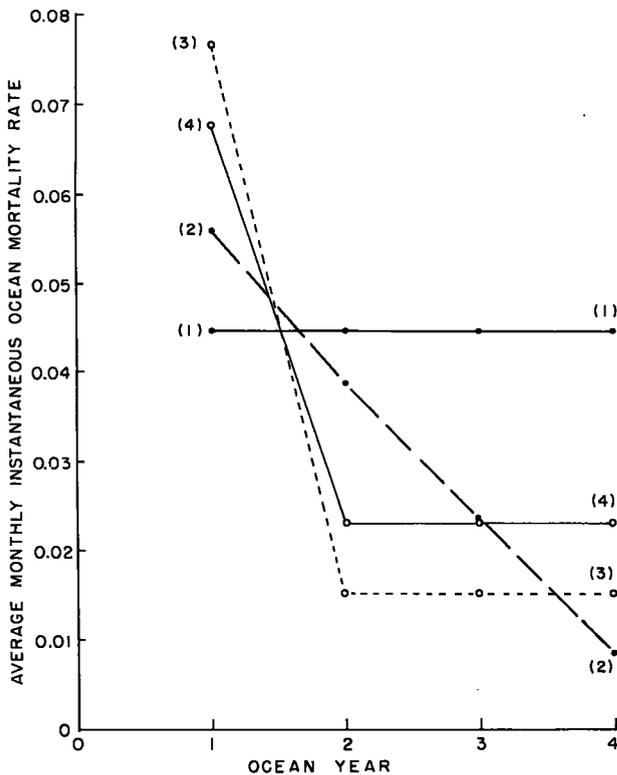


FIGURE 2.—Estimated average monthly instantaneous ocean mortality rates of 3-fresh-water Karluk River sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

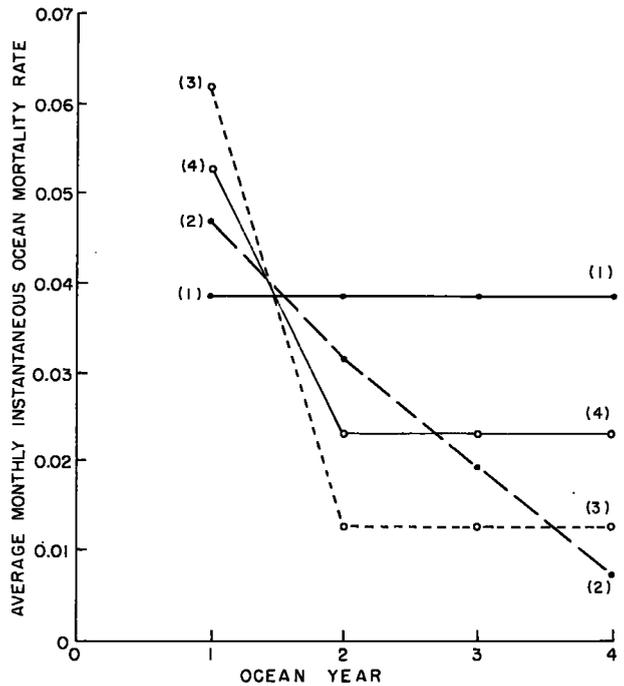


FIGURE 3.—Estimated average monthly instantaneous ocean mortality rates of 4-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

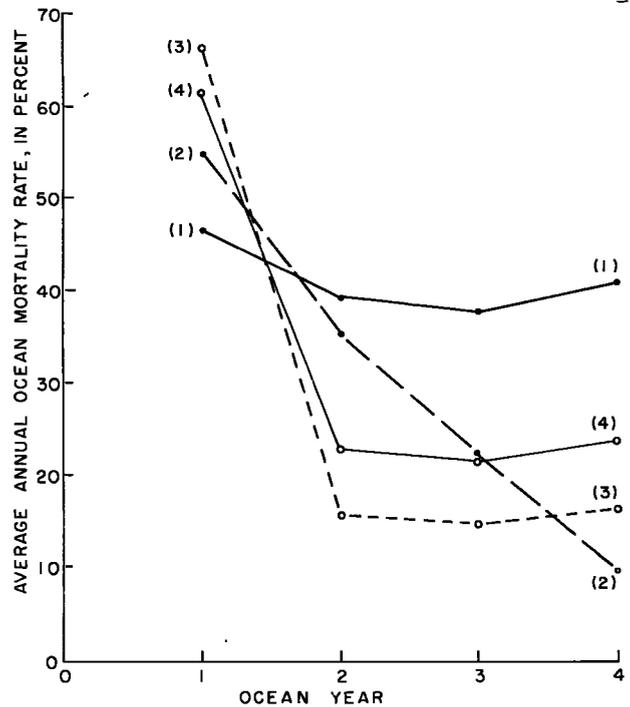


FIGURE 4.—Estimated average annual ocean mortality rates of 3-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

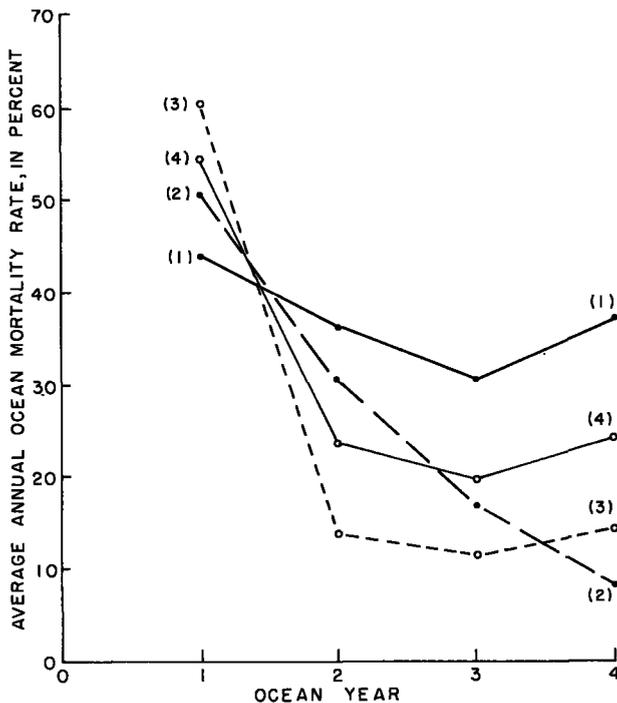


FIGURE 5.—Estimated average annual ocean mortality rates of 4-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

mortality rates during the first 3 years of ocean life are of principal interest, since only a minor fraction of the sockeye spend 4 years in the ocean.

DISCUSSION OF OCEAN MORTALITY RATES

The accuracy of the ocean mortality rate estimates presented here depends on the accuracy of the basic data used in the four population models and the validity of certain assumptions carried in the different models.

The numbers of sockeye in each marked group released were determined by counting the individual fish from which fins were removed. Since each marked fish was handled in the process of fin excision, the counting errors can be considered negligible.

The age composition of the marked smolts was estimated for each day of marking. Judging from Barnaby's report (1944, p. 272 and table 26), from 65 to 200 fish were sampled each day for this purpose. Seasonal total sample sizes ranged from about 1,000 to 2,000 fish. From this it would appear that the percentage error in the estimated

numbers of marked smolts of a given fresh-water age in any experiment was quite small, probably less than 2 or 3 percent.

In an attempt to minimize any bias caused, for example, by early-running smolts of a given fresh-water age returning as late-running adults in subsequent seasons (or, as another example, late-running smolts of a given fresh-water age returning as early-running adults in subsequent seasons), smolts were marked throughout the period of seaward migration, and sampling for returning marked adults was carried out rigorously. It was found that the percentage occurrence of returning marked fish of each age group was fairly constant throughout the season (Barnaby, 1944, p. 282). This indicates that proportionate numbers of early-, middle-, and late-running adults of a given fresh-water age had been marked as smolts.

Enumeration of returns of marked fish involved sampling as large a portion as possible of each day's catch taken near the mouth of the Karluk River by beach seine, a type of gear generally considered to be relatively nonselective with respect to age or size of fish. The numbers of sockeye of pertinent ocean ages that were examined for marks from 1930 to 1937, together with the sampling ratios, can be calculated from Barnaby's tables 33, 34, 37, 39, and 43 and are as follows:

Year of sampling for marked fish	Ocean age groups of marked fish occurring in indicated year of sampling (Year of smolt migration shown in parentheses)	Estimated fish of indicated ocean ages in total run in year of sampling	Estimated fish of indicated ocean ages examined for marks	Mark sampling ratio
1930	1 (1929)	Number 182,053	Number 801	Percent 0.5
1931	1 (1930); 2 (1929)	1,501,886	210,920	14.0
1932	1 (1931); 2 (1930); 3 (1929)	1,412,179	159,279	11.3
1933	1 (1932); 2 (1931); 3 (1930); 4 (1929)	1,812,577	178,080	9.8
1934	1 (1933); 2 (1932); 3 (1931); 4 (1930)	2,064,190	311,730	15.1
1935	2 (1933); 3 (1932); 4 (1931)	1,407,551	151,321	10.8
1936	3 (1933); 4 (1932)	330,985	41,257	12.5
1937	4 (1933)	0	0	-----

Except for 1930, approximately 10 to 15 percent of each year's total run of sockeye of the pertinent ocean age groups was examined for marks. The low sampling ratio in 1930 might account for the relatively large numbers of marked 1-ocean sockeye that were estimated to have returned from the 1929 releases of 3- and 4-fresh-water smolts.

The number of marked fish returning to the Karluk River were estimated on a weekly basis from catch statistics, weir counts, age composition

of sockeye in the catch and escapement, and the proportions of marked fish occurring in the catch samples examined.

Judging from the large numbers of fish examined for marks (except in 1930), it is likely that the statistical errors involved in applying the sample ratios of marked-to-unmarked fish to the total run are very small. A procedural error, however, might have been introduced by misallocation of sockeye catches made in waters along the northwest coast of Kodiak Island. Misallocation of Karluk sockeye to other river systems would result in underestimates of the numbers of marked fish returning to the Karluk River and overestimates of ocean mortality. Misallocation of sockeye of other systems to the Karluk runs, on the other hand, would result in overestimates of the numbers of marked fish returning to the Karluk River and underestimates of ocean mortality.

On the basis of a tagging experiment on the western shore of Uganik Bay on Kodiak Island in 1927 (Rich and Morton, 1929), Barnaby (1944) considered all sockeye caught along the Kodiak Island coast between Cape Karluk (about 3 miles west of the mouth of the Karluk River) and West Point (about 6 miles inside the western shore of Uganik Bay and about 75 miles northeasterly from the mouth of the Karluk River) to have been fish originating in the Karluk River. Rich and Morton's study shows that some of the sockeye tagged in Uganik Bay were destined to areas other than the Karluk River. This indicates that some sockeye were misallocated to the Karluk runs by Barnaby's procedure. The extent to which this probable misallocation is compensated for by the allocation of Karluk sockeye caught outside the Cape Karluk-West Point area to other river systems cannot be accurately assessed. There is, however, some information available on this matter from unpublished catch statistics, tagging studies conducted in the late 1940's (Bevan, 1962), and escapement counts.

Donald E. Power and I have made a compilation of sockeye catch statistics for the Cape Karluk-West Point area for the years from 1930 to 1936. This compilation showed that approximately 70 percent of the total sockeye catch assigned to the Karluk River from 1930 to 1936 was taken between Cape Karluk and Cape Uyak, about 8 miles northeast of the mouth of the Karluk River. Thus, the bulk of the sockeye catch assigned to the Karluk

River was taken within a relatively short distance from the mouth of the river.

Bevan (1962) shows that only a relatively small proportion of sockeye tagged in the area between Cape Karluk and Cape Uyak in 1948 was recovered in areas other than the Karluk River or near its mouth. This indicates that the great majority of sockeye caught in the Cape Karluk-Cape Uyak area were Karluk fish.

During the years 1930-36, when marked sockeye were returning to the Karluk River, approximately 60 percent of the estimated total Karluk sockeye runs consisted of fish that passed through the counting weir in the Karluk River. Thus, if all of the sockeye caught between Cape Karluk and Cape Uyak are considered to have originated in the Karluk River, those catches plus the escapements would account for about 88 percent (60 percent plus 0.7 times 40 percent) of the estimated total Karluk sockeye runs between 1930 and 1936. Of the remaining portion of the estimated total runs, that is, the sockeye caught between Cape Uyak and West Point, Rich and Morton (1929) show that a large proportion of the fish taken inside the mouth of Uganik Bay are Karluk sockeye. Bevan (1962) also shows that large proportions of the sockeye taken in the Cape Uyak-West Point area originate in the Karluk River.

That Barnaby's procedure for allocating catches to the Karluk sockeye runs likely resulted in a misallocation of Karluk fish to other river systems is indicated by the results of tagging experiments reported by Bevan (1962). Those experiments showed that large proportions of sockeye tagged outside the Cape Karluk-West Point area, namely, off Afognak Island in 1948 and off Uganik, Raspberry, and Afognak Islands in 1949, were fish that originated in the Karluk River. Bevan reports that from sockeye tagging at a wide variety of locations along the northwest coast of Kodiak Island, the Karluk system accounted for about 90 percent of the stream recoveries made on that coast.

On the basis of the foregoing information, it is reasonable to conclude that relatively small proportions of the estimated total Karluk sockeye runs from 1930 to 1936 consisted of fish originating in other river systems and that these small proportions were offset or more than offset by misallocation of Karluk sockeye to other systems.

A source of mechanical error in the estimates of

marked sockeye returning to the Karluk River is the failure to detect all of the marked fish in the catch samples that were examined. No measure of such error is available for the Karluk experiments. It is an error, however, that is generally recognized to occur in marking studies. Such an error results in underestimates of numbers of marked fish returning and overestimates of ocean mortality rates.

The estimated durations of ocean residence probably contain some error. The errors, however, cannot be great since the smolts migrate to sea within a matter of a few weeks, and the estimated dates on which 50 percent of the fish in the different age groups return to the Karluk River are based on data for 27 years. In any event, an error of 1 or 2 months in estimating the durations of ocean residence would not affect the estimates of mortality very much.

The factor used to adjust for the effects of marking on survival perhaps should be some quantity other than 1.27. Just what, if any, alternative factor should be used is difficult to say, although it is highly unlikely that it should be less than 1.0. If no adjustment is made for the effects of marking, the instantaneous ocean mortality rates would be 1.27 times those rates obtained in the four population models. If the adjustment for marking mortality is increased, the instantaneous ocean mortality rates obtained in the four population models would be reduced. As Ricker (1962) points out, there is no theoretical upper limit that the adjustment can have.

If it is assumed that mortality due to marking takes place within a very short period of time after the marked fish are released, an adjustment for such mortality can be obtained from the ratio of percentage returns of marked and unmarked smolts. Although a considerable amount of evidence indicates that marked sockeye smolts suffer practically no mortality while being held for observation (Barnaby, 1944, and Foerster, 1937), I have estimated, for comparative purposes, the average monthly instantaneous ocean mortality rates of 3- and 4-fresh-water Karluk sockeye smolts, assuming an initial marking mortality of 60 percent and a constant ocean mortality rate. The estimate of initial loss is taken from data presented by Foerster (1934, 1936, and 1937) and as shown by Ricker (1962, table E, Appendix II). The average monthly instantaneous ocean mortal-

ity rates for the two fresh-water age groups of Karluk sockeye are approximately 0.026 and 0.017 which are considerably lower than corresponding estimates obtained in Population Model 1.

With regard to Population Model 1, available evidence strongly suggests that ocean mortality of sockeye is greater when the fish are small than it is when they become larger. Accordingly, it seems likely that the assumption of a constant ocean mortality rate results in an underestimate of ocean mortality during the early period of ocean residence and an overestimate during the later period of ocean life.

Concerning Population Model 2, it is rather unlikely that the ocean mortality rate decreases uniformly from month to month. It is also doubtful that the mortality of sockeye becomes negligible during the last several months of the fourth year of ocean residence. As for the first point, an arithmetic progression not only is a convenient method of representing a decreasing mortality rate but it also provides reasonably satisfactory estimates of the average monthly instantaneous mortality rates during the different ocean years of life even though the mortality rate does not decrease uniformly. As for the second point, relatively few Karluk sockeye would benefit from the low ocean mortality rates in the fourth year following seaward migration, because practically all of them mature after 2 or 3 years in the ocean.

Ocean mortality could be represented as a function of fish length or weight rather than time spent in the ocean in Population Model 2.

As indicated previously, Population Model 3 is intended to represent an intermediate situation with respect to the distributions of ocean mortality assumed in Population Models 1 and 2. From the standpoint of annual mortality rates (figs. 2 to 5), it does not depict the best intermediate situation. A lower rate of decrease in mortality during the first 6 months of ocean residence, combined with a constant ocean mortality rate thereafter, would provide annual mortality rates that lie between the estimates obtained in Population Models 1 and 2.

I am not aware of any information at this time upon which to judge the validity of the assumptions concerning ocean mortality in Population Model 4. For a situation such as that depicted in this model to occur would require a short-term,

selective, intensive removal of smolts by predators near the mouth of the river, or a similar effect due to such factors as water temperature or salinity changes.

Some mention should be made of the fact that none of the population models presented here deals with situations such as where the mortality rate is considered to increase throughout the ocean life of sockeye or to be greater during the last month or two of ocean life of maturing sockeye than in preceding months or years.

The possibility that the mortality rate increases throughout the ocean life of sockeye salmon can be ruled out, I believe, on the basis of evidence from the Karluk marking experiments and for other sockeye populations (Ricker, 1962) that ocean mortality is greater during the early part of ocean residence than it is in later months and years.

It is of course possible that ocean mortality is greater during the last month or two of ocean life of maturing sockeye than in preceding months or years. Just what factor or factors might cause this to happen is difficult to say. As far as temporal effects of predation are concerned, smolts are subjected to considerable predation as they leave the river and enter the ocean. The size of the smolts probably renders them vulnerable to a variety of predators which cause little harm to adult sockeye. And, as Ricker (1962) mentions, although maturing sockeye are subject to predation by harbor seals and sea lions as they return to fresh water, they are leaving waters where the much more numerous fur seals occur.

Density-associated causes of mortality would seem to be less severe among maturing sockeye than smolt populations which are concentrated in small areas as they migrate to sea, and no more severe than for immature sockeye at sea.

Sockeye smolts appear to undergo at least as severe physical and chemical changes in their environment during their seaward migration as maturing sockeye undergo in their return to fresh water from the ocean.

Perhaps some physiological change associated with maturation causes an increased mortality among sockeye returning to fresh water. If so, it is not reflected in the general appearance of the fish. Sockeye taken in coastal waters are similar to maturing sockeye caught on the high seas insofar as body brightness and firmness of flesh

are concerned (personal communication with R. R. French). Nor does it result in a loss of body weight, according to data on growth rates given by Ricker (1962).

The foregoing considerations, of course, do not rule out the possibility that ocean mortality of maturing sockeye is greater during the last month or two of ocean life than in preceding months or years. In this connection, further investigation of the distribution and extent of ocean mortality of salmon is under way. For the time being, however, it should be noted, as Ricker (1962) notes with respect to his estimates of ocean mortality, that if the mortality during the last few months of ocean life of maturing salmon is greater than the estimates presented here, then the mortality rates during preceding months must be less than those estimated here, since the total mortality is fixed.

COMPARISON OF OCEAN GROWTH AND MORTALITY

Ricker (1962, Appendix tables A, B, and C), using data from Barnaby (1932), gives estimates of the instantaneous growth rates for nine Karluk sockeye fresh-water-ocean age groups during different years of ocean growth. These estimates, together with extrapolated estimates for some age groups not included in his tables, are shown in table 19.

The average instantaneous growth rates of 3- and 4-fresh-water sockeye during each of the 4 years of ocean growth can be estimated by weighting the individual estimates of g shown in table 19 by the proportions of sockeye that mature as 1-, 2-, 3-, and 4-ocean fish. Each of the four population models provides estimates of the weighted average annual growth rates of the two fresh-water age groups.

Using the maturity schedule obtained in Population Model 1 (table 6), the weighted average instantaneous growth rates of 3-fresh-water smolts during the first, second, third, and fourth years of ocean growth are estimated as follows:

$$\begin{aligned} \bar{g}_1 &= [3.159(.0135) + 2.811(.5141) + 2.894(1.4577) \\ &\quad + 2.650(.0147)]/1 = 2.8513 \\ \bar{g}_2 &= [1.262(.5141) + 1.053(.4577) + 0.964(.0147)]/0.9865 \\ &\quad = 1.1606 \\ \bar{g}_3 &= [0.867(.4577) + 0.794(.0147)]/0.4724 \\ &\quad = 0.8647 \\ \bar{g}_4 &= [0.434(.0147)]/0.0147 \\ &\quad = 0.4340 \end{aligned}$$

TABLE 19.—Estimated instantaneous growth rates of Karluk River sockeye during four ocean growth years

[Data from Ricker (1962); see footnotes for details on estimates shown in parentheses]

Fresh-water age group	Ocean age	Growth rate (\bar{g}) during ocean growth year:			
		1	2	3	4
3-----	Years				
	1	3.159			
	2	2.811	1.262		
	3	2.894	1.053	0.867	
4-----	1	(2.650)	(0.964)	(0.794)	(0.434)
	2	2.922			
	3	2.655	.974		
	4	(2.548)	(0.927)	(0.763)	
		(2.333)	(0.849)	(0.699)	(0.382)

$$^1 (2.650) = \frac{1}{4} \left[\frac{2.811 + 2.894 + 1.053}{3.159 + 2.811 + 1.262} + \frac{2.655}{2.922} \right] (2.894)$$

$$^2 (0.964) = \frac{1}{4} \left[\frac{2.811 + 2.894 + 1.053}{3.159 + 2.811 + 1.262} + \frac{2.655}{2.922} \right] (1.053)$$

$$^3 (0.794) = \frac{1}{4} \left[\frac{2.811 + 2.894 + 1.053}{3.159 + 2.811 + 1.262} + \frac{2.655}{2.922} \right] (0.867)$$

$$^4 (0.434) = \frac{1}{3} \left[\frac{1.262 + 0.867 + 0.974}{2.811 + 1.053 + 2.655} \right] [(0.794)]$$

$$^5 (2.548) = \frac{1}{3} \left[\frac{2.922 + 2.655 + 0.974}{3.159 + 2.811 + 1.262} \right] (2.894)$$

$$^6 (0.927) = \frac{1}{3} \left[\frac{2.922 + 2.655 + 0.974}{3.159 + 2.811 + 1.262} \right] (1.053)$$

$$^7 (0.763) = \frac{1}{3} \left[\frac{2.922 + 2.655 + 0.974}{3.159 + 2.811 + 1.262} \right] (0.867)$$

$$^8 (2.333) = \frac{1}{4} \left[\frac{2.811 + 2.894 + 1.053}{3.159 + 2.811 + 1.262} + \frac{2.655}{2.922} \right] [(2.548)]$$

$$^9 (0.849) = \frac{1}{4} \left[\frac{2.811 + 2.894 + 1.053}{3.159 + 2.811 + 1.262} + \frac{2.655}{2.922} \right] [(0.927)]$$

$$^{10} (0.699) = \frac{1}{4} \left[\frac{2.811 + 2.894 + 1.053}{3.159 + 2.811 + 1.262} + \frac{2.655}{2.922} \right] [(0.763)]$$

$$^{11} (0.382) = \frac{1}{3} \left[\frac{1.262 + 0.867 + 0.974}{2.811 + 1.053 + 2.655} \right] [(0.699)]$$

Using this procedure to estimate the weighted average growth rates of 4-fresh-water smolts during each year of ocean growth under Population Model 1 and to obtain corresponding estimates for the two fresh-water age groups under Population Models 2, 3, and 4, we obtain the set of weighted average instantaneous growth rates shown in table 20.

TABLE 20.—Estimated weighted average instantaneous growth rates (\bar{g}) of 3- and 4-fresh-water Karluk River sockeye smolts during 4 years of ocean growth, under population models 1, 2, 3, and 4

Fresh-water age group	Year of ocean growth	Population model			
		1	2	3	4
3-----	1	2.8513	2.8484	2.8486	2.8496
	2	1.1606	1.1749	1.1802	1.1744
	3	.8647	.8656	.8654	.8652
	4	.4340	.4340	.4340	.4340
4-----	1	2.6343	2.6412	2.6462	2.6412
	2	.9607	.9630	.9636	.9625
	3	.7605	.7615	.7615	.7610
	4	.3820	.3820	.3820	.3820

In estimating the growth rates shown in table 20, the greatest weight is given to the growth rates for sockeye that mature after 2 or 3 years in the ocean. This means that in most cases the extrapolated estimates given in table 19 do not greatly affect the weighted averages. Also, with regard to the estimating procedure, the weighted growth rates are generally minimal values, since they represent the growth between the time that sockeye leave fresh water and the time that the first ocean annulus is formed, or the time between the formation of successive ocean annuli. The relatively rapid rates of growth that take place between the time the last ocean annulus is formed and the time that mature sockeye return to the Karluk River are not included in the estimates.

It is presumed here that the growth rates in each of the years of ocean growth pertain to periods of 12 months. Thus the duration of an ocean-growth-year differs somewhat from the durations of the ocean-mortality-years used in estimating mortality rates. To obtain a set of growth rate estimates that pertain to the time periods for which mortality estimates have been made, it is necessary to estimate the average monthly instantaneous growth rates in each ocean-growth-year and combine the resulting averages for parts of two ocean-growth-years. For example, the duration of the first year of ocean residence of 3-fresh-water fish has been estimated to be 14.17 months. The total instantaneous growth rate of 3-fresh-water smolts, under Population Model 1, during the first 14.17 months of ocean residence is estimated to be [(12) (2.8513)/12] + [(2.17)(1.1606)/12], or 3.0612. The average monthly instantaneous growth rate during this period is, in turn, estimated to be 3.0612/14.17, or 0.2160. Also, for example, the duration of the second year of ocean residence of 3-fresh-water fish is considered to be 11.16 months. The total instantaneous growth rate of these fish during this period under Population Model 1 is estimated to be [(9.83) (1.1606)/12] plus [(1.33) (0.8647)/12], or 1.0465. The average monthly instantaneous growth rate is estimated to be 1.0465/11.16, or 0.0938.

Table 21 shows the total and monthly instantaneous rates of growth and mortality for 3- and 4-fresh-water Karluk sockeye during each ocean year of life for each population model. Estimates

TABLE 21.—Estimated instantaneous rates of growth and mortality and changes in bulk of 3- and 4-fresh-water Karluk River sockeye during each year of ocean life, population models 1, 2, 3, and 4

[Mortality rate data from tables 5, 9, 13, and 17; growth rate data from table 20, adjusted for duration of ocean year (see text)]

Population model	Fresh-water age group	Ocean year	Duration of ocean year	Instantaneous rates of growth and mortality						Changes in bulk ¹	
				Yearly basis			Monthly basis			Per ocean year	Per month
				Growth	Mortality	Difference	Growth	Mortality	Difference		
1	3	1	Months							Percent	Percent
			14. 17	3. 0612	0. 6320	2. 4292	0. 2160	0. 0446	0. 1714	1, 035. 0	18. 7
			11. 16	1. 0465	. 4977	. 5488	. 0988	. 0446	. 0492	73. 1	5. 0
			10. 67	. 7699	. 4759	. 2930	. 0721	. 0446	. 0275	34. 0	2. 8
	4	1	15. 00	2. 8745	. 5790	2. 2955	. 1916	. 0396	. 1530	869. 0	16. 5
			11. 67	. 8907	. 4505	. 4392	. 0762	. 0396	. 0376	53. 6	3. 8
			9. 50	. 5972	. 3667	. 2305	. 0629	. 0396	. 0243	25. 9	2. 5
			12. 00	. 3820	. 4632	-. 0812	. 0318	. 0396	-. 0068	-7. 8	-0. 7
2	3	1	14. 17	3. 0809	. 7929	2. 2880	. 2160	. 0560	. 1600	866. 0	17. 4
			11. 16	1. 0894	. 4326	. 6568	. 0948	. 0388	. 0560	87. 0	5. 8
			10. 67	. 7697	. 2560	. 5137	. 0721	. 0240	. 0481	67. 1	4. 9
			11. 88	. 4278	. 1028	. 3250	. 0362	. 0087	. 0275	38. 4	2. 8
	4	1	15. 00	2. 8820	. 7088	2. 1732	. 1921	. 0469	. 1452	783. 0	15. 6
			11. 67	. 8917	. 3701	. 5216	. 0764	. 0317	. 0447	68. 5	4. 6
			9. 50	. 5980	. 1867	. 4113	. 0629	. 0196	. 0433	50. 9	4. 4
			12. 00	. 3820	. 0888	. 2932	. 0318	. 0074	. 0244	34. 1	2. 5
3	3	1	14. 17	3. 0620	1. 0842	1. 9778	. 2161	. 0765	. 1396	622. 7	15. 0
			11. 16	1. 0627	. 1696	. 8931	. 0652	. 0152	. 0800	144. 3	8. 3
			10. 67	. 7695	. 1622	. 6073	. 0721	. 0152	. 0569	83. 5	5. 8
			11. 88	. 4278	. 1798	. 2480	. 0362	. 0152	. 0210	28. 1	2. 1
	4	1	15. 00	2. 8971	. 9279	1. 9692	. 1925	. 0619	. 1306	609. 4	13. 9
			11. 67	. 8921	. 1505	. 7416	. 0764	. 0129	. 0635	109. 9	6. 6
			9. 50	. 5980	. 1226	. 4754	. 0629	. 0129	. 0500	60. 9	5. 1
			12. 00	. 3820	. 1648	. 2272	. 0318	. 0129	. 0189	25. 5	1. 9
4	3	1	14. 17	3. 0620	. 9599	2. 1021	. 2161	. 0677	. 1484	718. 3	16. 0
			11. 16	1. 0579	. 2589	. 7990	. 0948	. 0232	. 0716	122. 3	7. 4
			10. 67	. 7693	. 2475	. 5218	. 0721	. 0232	. 0489	68. 5	5. 0
			11. 88	. 4278	. 2745	. 1533	. 0362	. 0232	. 0130	16. 6	1. 3
	4	1	15. 00	2. 8818	. 7894	2. 0924	. 1921	. 0526	. 1395	710. 4	15. 0
			11. 67	. 8912	. 3707	. 6205	. 0764	. 0232	. 0532	86. 0	5. 5
			9. 50	. 5976	. 2204	. 3772	. 0629	. 0232	. 0397	45. 8	4. 0
			12. 00	. 3820	. 2784	. 1066	. 0318	. 0232	. 0066	10. 9	. 9

¹ Exponential of difference between growth and mortality, less 1.

of the changes in bulk of sockeye during ocean life are also given.

Under Population Model 1, the estimated natural mortality rates for 3- and 4-fresh-water sockeye are less than the estimated growth rates during each of the first 3 years of ocean life. The bulk (poundage) of 3-fresh-water fish is estimated to increase by 1,035, 73 and 34 percent, respectively, during the first, second, and third ocean years. The bulk of 4-fresh-water fish is estimated to increase by 893, 54 and 26 percent, respectively, during their first, second, and third years of ocean residence.

The estimated natural mortality rates during the fourth year of ocean life for the very small proportions of Karluk sockeye that mature as 4-ocean fish exceed the estimated growth rates. Hence, under the first population model, the bulk of Karluk sockeye in their fourth year at sea is estimated to decrease by about 10 percent (3-

fresh-water fish) or 8 percent (4-fresh-water fish).

In the second model, the estimated ocean mortality rates for both fresh-water age groups are exceeded by the estimated growth rates throughout ocean life. During the first, second, third, and fourth ocean years, the bulk of 3-fresh-water sockeye is estimated to increase by 866, 87, 67, and 38 percent, respectively. Corresponding estimated increases for 4-fresh-water sockeye are 783, 69, 51, and 34 percent, respectively.

Under Population Model 3, the bulk of 3- and 4-fresh-water Karluk sockeye is estimated to increase in each year of ocean life. Estimated percentage increases in bulk during the first, second, third, and fourth years of ocean life are 623, 144, 84, and 28, respectively, for 3-fresh-water fish, and 609, 110, 61, and 26, respectively, for 4-fresh-water fish.

In the fourth population model also, the estimated natural mortality rates of 3- and 4-fresh-

water fish are exceeded by the estimated growth rates in each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 718, 122, 69, and 17 percent, respectively, during the first, second, third, and fourth years of ocean life. Increases in bulk of 4-fresh-water fish are estimated to be 710, 86, 46, and 11 percent, respectively, for the first through the fourth ocean years.

The percentage changes in bulk in table 21 show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential poundage yield, provided there exists an inshore fishery capable of catching the fish not needed for reproduction of the stock. The extent of the loss depends upon the distribution of ocean mortality and the year of ocean life in which the salmon would be captured by a high seas fishery. Computations of losses are not given here. It can be pointed out, however, that any mortality caused by net injury or inadvertent capture of Karluk sockeye during their first year of ocean life would result in an especially great loss of potential catch.

Attention is called to two matters relating to the estimated changes in bulk of Karluk sockeye during their ocean life. One, the estimates of net increase in bulk in table 21 are generally minimal due to the fact that the weighted average growth rates do not include the rapid growth that takes place during the last few months of ocean life of maturing sockeye. Secondly, if the distribution of ocean mortality is altered to reflect an increase in the mortality of maturing sockeye during their last month or two of ocean life, the bulk of the nonmaturing sockeye, as well as the loss in yield resulting from the capture of such fish, must also increase, because the total ocean mortality is fixed.

SUMMARY

Four population models simulating different temporal distributions of natural mortality during the ocean life of Karluk River sockeye salmon are developed. Assumptions employed in each of the models are discussed. Data collected in the late 1920's and early 1930's on the releases and returns of marked fish are used to estimate ocean mortality rates and maturity schedules of different fresh-water age groups of Karluk sockeye. The esti-

mates primarily concern 3- and 4-fresh-water fish, the two fresh-water age groups that generally account for 95 percent or more of the annual runs to the Karluk system. The ocean mortality rate estimates are compared with available growth rate data to determine the changes in bulk (net increase or decrease in weight) of Karluk sockeye during ocean life.

In the first population model, natural mortality is assumed to be constant throughout ocean life. The estimates of monthly instantaneous ocean mortality rates obtained in this model generally decrease as the age and size of smolts increase: 0.0496 for 2-fresh-water smolts averaging 108 millimeters in length; 0.0446 for 3-fresh-water smolts averaging 131 millimeters in length; 0.0386 for 4-fresh-water smolts averaging 143 millimeters in length; and 0.0402 for 5-fresh-water smolts averaging 146 millimeters in length. These monthly instantaneous rates generate annual (12-month) ocean mortality rates of 44.8, 41.4, 37.1, and 38.3 percent, respectively.

Approximately 1.3, 51.4, 45.8, and 1.5 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye respectively. Corresponding percentages for 4-fresh-water smolts are about 3.3, 71.0, 24.6, and 1.0 percent.

The estimated natural mortality rates during the first 3 years of ocean life are less than the estimated ocean growth rates for both the 3-, and 4-fresh-water age groups of Karluk sockeye. During successive periods (called ocean years) of about 14, 11, and 11 months of ocean life, the bulk (poundage) of 3-fresh-water sockeye is estimated to increase by 1,035, 73, and 34 percent, respectively. During their first, second, and third ocean years (corresponding to periods of about 15, 12, and 10 months), 4-fresh-water sockeye are estimated to increase in bulk by 893, 54, and 26 percent, respectively.

The estimated natural mortality rates during the fourth year of ocean life for the very small proportions of 3- and 4-fresh-water fish that mature as 4-ocean fish exceed the estimated growth rates. Hence, under the first population model, the bulk of Karluk sockeye in their fourth year at sea is estimated to decrease by about 10 percent for 3-fresh-water fish and about 8 percent for 4-fresh-water fish.

In the second population model, the instantaneous natural mortality rate is assumed to be

greatest in the first month of ocean life and then decreases arithmetically in each of the following 47 or 48 months until it becomes zero. The first-month instantaneous mortality rates are estimated to be 0.0649 for 3-fresh-water sockeye and 0.0549 for 4-fresh-water sockeye. The instantaneous rates are estimated to decrease each month by about 0.0014 for 3-fresh-water fish and 0.0011 for 4-fresh-water fish.

The natural mortality rates during the first, second, third, and fourth ocean years for 3-fresh-water fish are 54.7, 35.1, 22.6, and 9.8 percent, respectively. Corresponding estimates for 4-fresh-water fish are 50.5, 30.9, 17.0, and 8.5 percent.

Under the second population model, about 1.6, 57.7, 39.8 and 0.8 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye, respectively. Corresponding percentages for the 4-fresh-water smolts are about 3.9, 74.5, 21.1, and 0.5.

For both the 3- and 4- fresh-water age groups, the estimated ocean mortality rates are exceeded by the estimated growth rates throughout ocean life. During the first, second, third, and fourth ocean years, the bulk of 3-fresh-water sockeye is estimated to increase by 866, 87, 67, and 38 percent, respectively, while the bulk of 4-fresh-water sockeye is estimated to increase by 783, 68, 51, and 34 percent, respectively.

In the third population model, the monthly instantaneous natural mortality rate is assumed to be greatest during the first month of ocean life, decreases geometrically by a factor of 0.5 in each of the next 5 months, and remains constant during the sixth and each succeeding month. First-month instantaneous mortality rates are estimated to be 0.4876 for 3-fresh-water sockeye and 0.4123 for 4-fresh-water sockeye. The instantaneous mortality rates in the sixth and each succeeding month are estimated to be 0.0152 for 3-fresh-water fish and 0.0129 for 4-fresh-water fish.

The natural mortality rates for 3-fresh-water fish during their first ocean year (approximately 14 months) is estimated to be 66.2 percent. The rate for succeeding 12-month periods is estimated to be 16.7 percent. The natural mortality rate for 4-fresh-water fish during their first ocean year (15 months) is estimated to be 60.5 percent. The rate for succeeding 12-month periods is estimated to be 14.3 percent.

About 2.4, 59.8, 37.0, and 0.8 percent of the

3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye, respectively, under the third population model. Corresponding estimates for the 4-fresh-water smolts are 5.2, 74.8, 19.6, and 0.5 percent.

The estimated natural mortality rates of 3- and 4-fresh-water fish are less than the estimated growth rates during each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 623, 144, 84, and 28 percent during the first, second, third, and fourth ocean years, respectively. Corresponding estimates of percentage increases in bulk of 4-fresh-water fish are 609, 110, 61, and 26.

In the fourth population model, the instantaneous natural mortality rate is assumed to be greater for 3-fresh-water sockeye than for 4-fresh-water fish during the first month of ocean life, greater for both fresh-water age groups during the first month than during the second and succeeding months, and constant and the same for the two fresh-water age groups during each month of ocean residence following the first month.

Starting with the assumption that the first-month instantaneous ocean mortality rate of 4-fresh-water sockeye is 20 times the mortality rate of this fresh-water age group in each of the following months, the instantaneous mortality rates of sockeye of that fresh-water age group are estimated to be 0.4646 during the first month of ocean life and 0.0232 during each succeeding month. Under this model, 0.0232 is also the estimated monthly instantaneous natural mortality rate of 3-fresh-water sockeye after their first month in the ocean. The first-month instantaneous mortality rate of 3-fresh-water fish is estimated to be 0.6544, about 40 percent greater than the corresponding estimate for 4-fresh-water fish and about 28 times the mortality rate of 3-fresh-water fish during the second and succeeding months of ocean life.

The total ocean mortality rate for 3-fresh-water fish during their first ocean year is estimated to be 61.7 percent. The corresponding estimate for 4-fresh-water sockeye is 54.6 percent. For both fresh-water age groups the rate for succeeding 12-month periods is estimated to be 24.3 percent.

The maturity schedules of 3- and 4-fresh-water smolts are estimated to be about the same in the fourth population model as in the second model.

The estimated natural mortality rates of 3- and

4-fresh-water sockeye are exceeded by the estimated growth rates in each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 718, 122, 68, and 17 percent, respectively, during the first, second, third and fourth years of ocean life. Corresponding estimates of increases in bulk of 4-fresh-water fish are 710, 86, 46, and 11 percent.

The estimated percentage changes in bulk show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential yield, provided there exists a coastal fishery capable of catching the fish not needed for reproduction of the stock.

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LITERATURE CITED

- BARNABY, JOSEPH T.
1932. The growth of the red salmon (*Oncorhynchus nerka* Walbaum) of the Karluk River and the growth of its scales. M.A. Thesis, Stanford University, 50 p.
1944. Fluctuations in abundance of red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 39, vol. 50, pp. 237-295.
- BEVAN, DONALD EDWARD
1962. Estimation by tagging of the size of migrating salmon populations in coastal waters. In Studies of Alaska red salmon, edited by Ted S. Y. Kov, University of Washington (Seattle), Publications in Fisheries, new series, vol. 1, pp. 373-449. 34 figs.
- FOERSTER, R. E.
1934. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 4. The life history cycle of the 1925 year class with natural propagation. Contributions to Canadian Biology and Fisheries, N.S., vol. 8, No. 27, pp. 345-355.
1936. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 5. The life history cycle of the 1926 year class with artificial propagation involving the liberation of free-swimming fry. Journal of the Biological Board of Canada, vol. 2, No. 3, pp. 311-333.
1937. The return from the sea of sockeye salmon (*Oncorhynchus nerka*) with special reference to percentage survival, sex proportions and progress of migration. Journal of the Biological Board of Canada, vol. 3, No. 1, pp. 26-42.
- PARKER, ROBERT R.
1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). Journal of the Fisheries Research Board of Canada, vol. 19, No. 4, pp. 561-589.
- RICH, WILLIS H., and FREDERICK G. MORTON
1929. Salmon tagging experiments in Alaska, 1927 and 1928. Bulletin of the U.S. Bureau of Fisheries, 1929 (1930), vol. 45 (Doc. 1057; issued October 12, 1929), pp. 1-23.
- RICKER, W. E.
1962. Comparisons of ocean growth and mortality of sockeye salmon during their last two years. Journal of the Fisheries Research Board of Canada, vol. 19, No. 4, pp. 531-560.
- ROUNSEFELL, GEORGE A.
1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 130, vol. 58, pp. 83-169.

A METHOD OF MEASURING MORTALITY OF PINK SALMON EGGS AND LARVAE

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ABSTRACT

A method of estimating total mortality of salmon eggs and larvae from time of spawning to time of sampling is described. The method provides a measure of mortality, regardless of cause, and is unaffected by the disappearance of dead eggs or larvae.

Total mortality rate is calculated from estimates of abundance and fecundity of parent female spawners (potential egg deposition) and abundance of live eggs and larvae in spawning beds at the time of sampling. A hydraulic sampler, developed to collect samples of eggs and larvae, is described.

Two sources of bias are considered in mortality rates calculated from percentages of dead eggs and larvae in samples: (1) eggs not initially buried by spawners, and (2) eggs and larvae disappearing from the spawning bed. Neither source of bias exists where mortality is calculated

from estimated potential egg deposition and abundance of live eggs and larvae at time of sampling.

The efficiency of estimating abundance of eggs and larvae is affected by their tendency to be clustered. Clustering causes the sample variance to increase with the sample mean, and confidence limits of estimates of abundance may be widely separated. The use of a logarithmic transformation improved the efficiency of estimates in certain instances.

A chi-square test based on the premise that a change in the total mortality level would be associated with a change in frequency of occurrence of dead or live eggs and larvae in samples is described. This test was useful in identifying periods when significant mortality occurred, especially where confidence limits of total mortality percentages were widely separated.

Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant of the Pacific salmon and in most years provide a larger commercial catch than all other salmon species. In the eastern Pacific, pink salmon are commercially important from Bristol Bay, Alaska, to Puget Sound, Washington. They support a major fishery in southeastern Alaska where there are about 1,100 spawning streams (Martin, 1959).

Spawning female pink salmon bury their eggs in gravel beds of coastal streams and die soon after spawning. Their eggs are deposited in summer or autumn and hatch within 60 to 90

days. The larvae usually remain in the streambed over winter and the fry emerge and migrate immediately to salt water the following spring. In most instances fry do not feed in fresh water.

There is evidence that fry production is ultimately limited by the area available for spawning. Ricker (1954) and Neave (1958) note that escapements of large numbers of spawners do not necessarily result in large yields of fry. Their findings indicate that the yield of fry approaches an asymptote (and may even decline at high spawning densities) with increased density of spawners. Ricker points out that optimum escapement would most likely occur at a level intermediate between low and high density of spawners.

Determining optimum escapement will depend

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ultimately on a thorough understanding of factors limiting fry production. Total fresh-water mortality of pink salmon has been measured in McClinton, Hook Nose, and Morrison Creeks, British Columbia (Pritchard, 1948; Neave, 1953; Hunter, 1959) and in Sashin Creek, southeastern Alaska (Davidson and Hutchinson, 1942; Hutchinson and Shuman, 1942; Merrell, 1962). Mortalities in those streams ranged from 76 to over 99 percent.

Periods in the fresh-water life of pink salmon during which major mortalities occur have not yet been sufficiently elucidated. Variable mortalities occur among adults before spawning, among eggs and larvae, and among fry. The period beginning with egg deposition and terminating with emergence of fry typically encompasses 80 to 90 percent of the total fresh-water life of pink salmon, and during most of this period the developing embryos and larvae are immobilized and concealed by the surrounding solids of the streambed. While buried in the streambed, eggs and larvae are subjected to numerous stresses imposed by the environment that may cause death.

The measurement of mortality in spawning beds is complicated in many instances by the disappearance of eggs and larvae from decomposition, scavenging, predation, and bed movement. Where disappearance of eggs and larvae has taken place, the percentages of dead eggs and larvae collected in samples will underestimate the true total mortality percentage. There is a need, then, to devise methods of estimating changes in density of eggs and larvae in spawning beds so that estimates of total mortality can be calculated. This paper describes procedures that can be employed to measure total mortality percentage of pink salmon eggs and larvae from egg deposition to any selected time during the period of streambed residence.

Studies on environmental factors causing mortality of pink salmon eggs and larvae were initiated by the Fisheries Research Institute, University of Washington, in 1948. These early studies were undertaken in streams near Ketchikan, Alaska, with financial support from the Alaska salmon industry. Industry-supported studies were discontinued after 1955, and in 1956 Saltonstall-Kennedy Act funds were provided by the Bureau

of Commercial Fisheries to study the effects of logging on pink salmon. Mortality studies were continued as part of this program. The study streams were Harris River and Indian and Twelve-mile Creeks, located on Prince of Wales Island about 40 miles west of Ketchikan.

Three important problems were considered in the development of methods used to measure periodically egg and larval mortality. First, equipment and methods for obtaining samples of eggs and larvae representative of the populations sampled were developed and tested. Second, equations for calculating total mortality percentage from the time of spawning to the time of sampling were formulated. Third, statistical methods to test for significant changes in total mortality percentage were tried.

COLLECTING EGGS AND LARVAE

Several workers have examined samples of eggs and larvae collected from spawning beds and have calculated the mortality percentage from the proportion of dead eggs and larvae in samples (Hobbs, 1937 and 1940; Cameron, 1940; Briggs, 1953; Hatch, 1957; Hunter, 1959; Mathisen, 1962). This method introduces bias into calculated total mortality percentages if parent females have failed to deposit eggs or eggs and larvae have disappeared from the spawning bed. To overcome these sources of bias, periodic estimates of abundance of eggs and larvae must be obtained. A method for calculating total mortality percentage from estimated density of live eggs and larvae was used.

Density of eggs and larvae in the spawning bed was estimated by collecting specimens from small discrete quadrats or circular plots (sampling units) ranging from 2 to 4 square feet in area. An estimate of the average number of eggs and larvae per square foot of spawning bed was obtained by sampling a number of units located randomly within a spawning bed. The accuracy of this estimate was influenced largely by the thoroughness with which eggs and larvae were collected from within a sampling unit without losing any, yet excluding eggs and larvae adjacent to the sampling unit. To meet the requirements of the sampling scheme special equipment for collecting eggs and larvae was developed. The apparatus, called a hydraulic sampler, was first tried in 1956.

DESCRIPTION OF THE HYDRAULIC SAMPLER

The hydraulic sampler utilizes suction created by passing water at high velocity through an annular aperture to mix air with water. The air and water mixture is injected into the streambed to free eggs and larvae from bottom materials. The device is patterned after equipment used by Mathisen (1962). The major difference is that Mathisen excavated both gravel and eggs with the suction created.

Basic components of the hydraulic sampler are a 7,200-gallon per hour centrifugal water pump and a cone assembly that creates a mixture of air and water. Water is delivered by the pump to the cone through flexible rubber hose of 1½-inch diameter. The mixture of air and water from the cone assembly is injected into the streambed through a nozzle (fig. 1).

A jacket between the terminal openings of the cone assembly receives water from the pump which is forced under pressure from the jacket at high speed through an annular aperture on the inside of the tube. Water flowing through the aperture creates a suction at the opening opposite the direction of flow, and water and air mix beyond the aperture as they flow toward the nozzle. The size of the aperture can be adjusted to regulate the quantity of air in the mixture. A disassembled cone is shown in figure 2. Drawings of the cone assembly are shown in figure 3.

OPERATION OF THE HYDRAULIC SAMPLER

Eggs and larvae were flushed from the streambed by rising air bubbles and water currents and were collected in a net attached to the downstream side of a metal frame outlining the sampling unit (fig. 4). Square frames enclosing 4 square feet and circular frames enclosing 2 square feet were tried. The circular frame is recommended because it has the smallest perimeter for a given area, which minimizes the number of eggs and larvae removed from outside the boundary of the sampling unit and not collected.

Penetration of the nozzle into the streambed was greatly facilitated by the flow of water and air from the nozzle. The depth of penetration depended largely upon size composition of bottom materials, being least where large cobbles were present. In mixtures of fine gravel and sand it was possible to penetrate readily more than 24 inches.

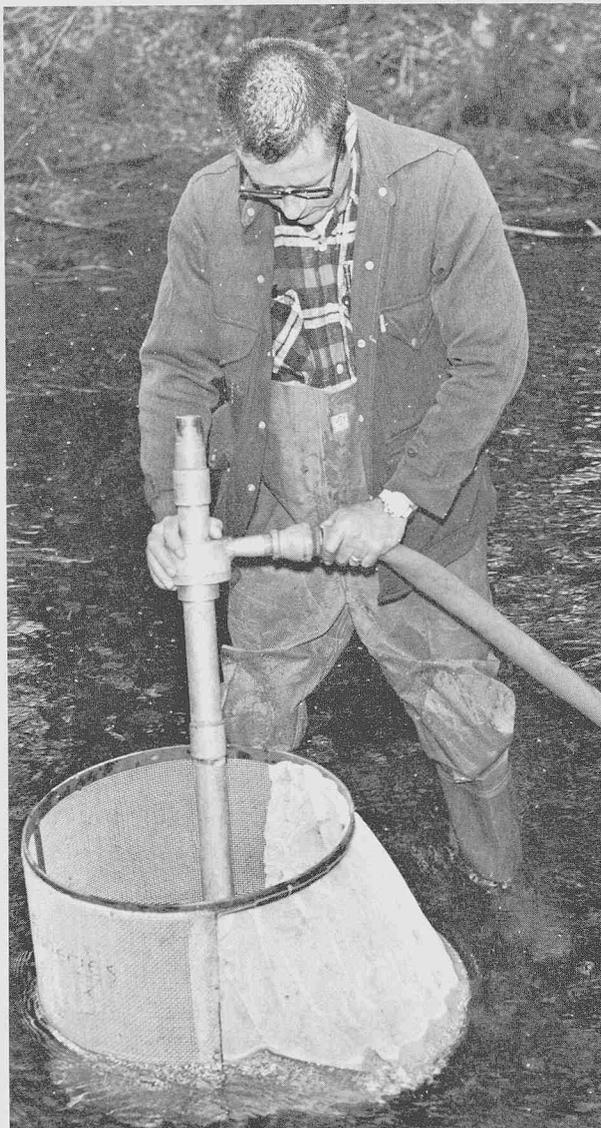


FIGURE 1.—Collecting pink salmon eggs or larvae with hydraulic sampler.

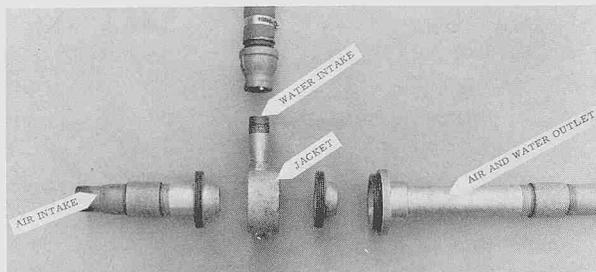


FIGURE 2.—Disassembled cone assembly of hydraulic sampler.

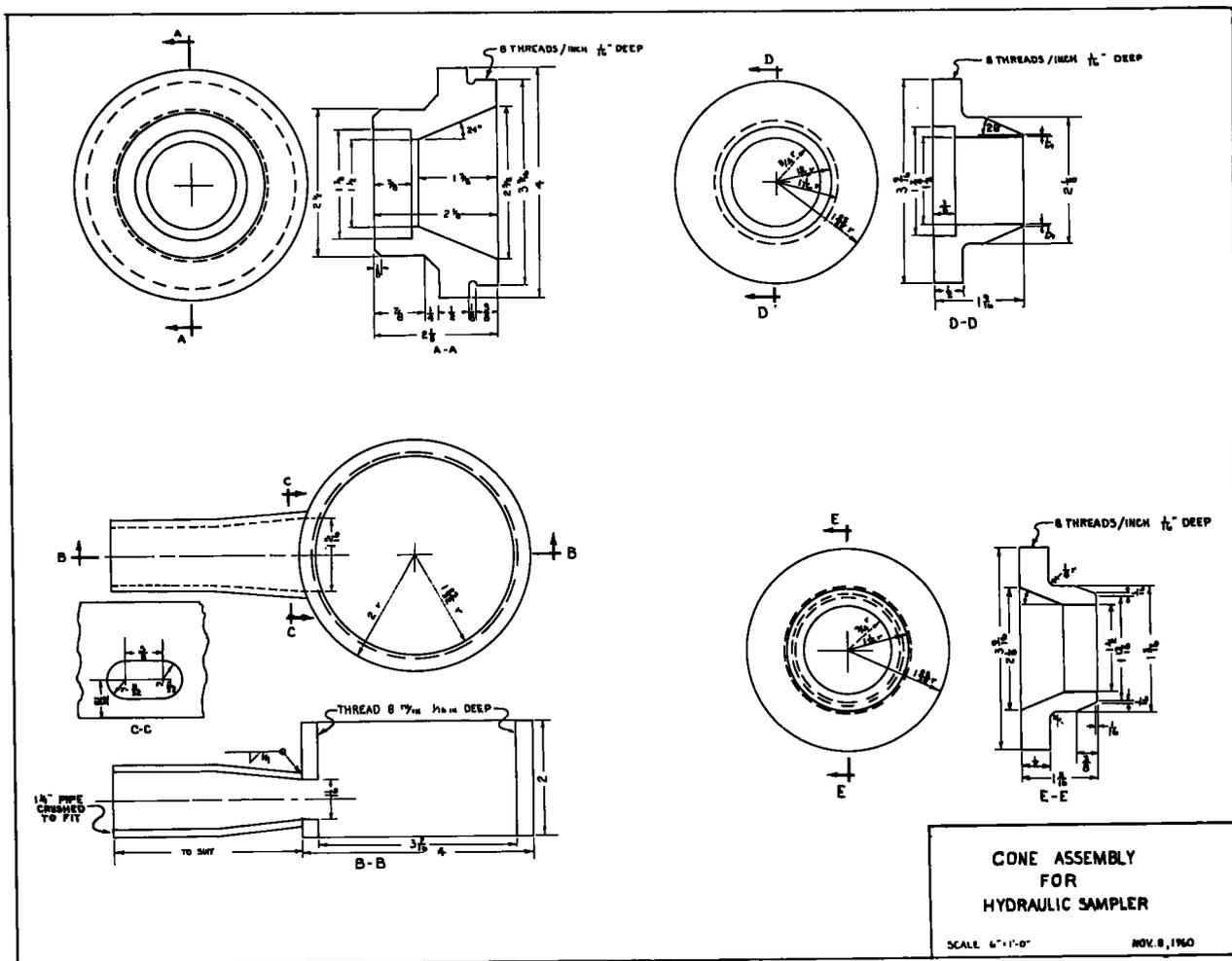


FIGURE 3.—Machine drawing of cone assembly of hydraulic sampler.

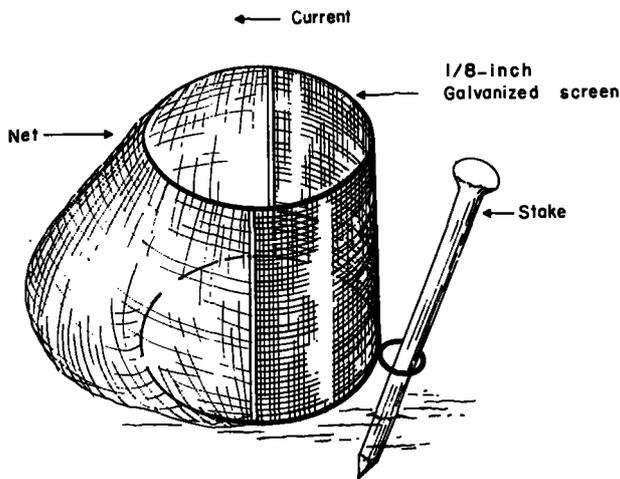
In this study, each sampling unit was sampled by two persons. As soon as the first person felt he had removed all eggs and larvae from within a sampling unit, the second person attempted to remove any that might have been missed.

PERFORMANCE OF THE HYDRAULIC SAMPLER

When a streambed is excavated with a shovel, it is difficult to collect eggs and larvae from one sampling unit without collecting specimens from adjacent units. Difficulties occur because stream bottom materials containing eggs and larvae shift horizontally when a hole is dug. With the hydraulic sampler, heavier materials were not transported away, and very little horizontal shift of the streambed occurred. Furthermore, the action of air and water currents was restricted to an area adjacent to the nozzle orifice, and the

disturbance of the streambed beyond the boundaries of the sampling unit was minimized.

The percentage of eggs and larvae recovered from a sampling unit with the hydraulic sampler was estimated from results of two tests. First, after completion of the initial sampling by two persons, sampling units were resampled by a third person in an attempt to remove additional specimens. In the opinion of those doing the work, sufficient effort was expended in resampling to remove virtually all specimens within the boundaries of sampling units. In tests of this type, the two persons doing the initial sampling were not advised that the resampling was to be done. Second, known numbers of preserved eggs were buried. The persons doing the sampling were not advised either of the number or of the exact location of preserved eggs buried within a



Suggested dimensions:

Inside diameter - 19.2 inches

Height - 20.0 inches

FIGURE 4.—Circular frame and collection net used with hydraulic sampler.

sampling unit. In tests of this type, no resampling was done to recover eggs not recovered by two persons sampling.

The mean percentage of eggs recovered after two persons had sampled was about the same for both types of tests—93 percent. Results of tests where the initial effort by two persons was followed by resampling by a third person are given in table 1. Table 2 gives results of tests where known numbers of preserved eggs were buried and recovered by two persons sampling.

TABLE 1.—Number and percentage of naturally spawned eggs collected by two persons sampling followed by resampling

Collected by two persons sampling	Collected by a third person resampling	Collected by two persons sampling
Number	Number	Percent
30.....	5	85.7
327.....		100.0
108.....	7	93.9
85.....	1	98.8
249.....	5	98.0
235.....	126	65.1
634.....	12	98.1
521.....	35	93.7
45.....		100.0
203.....	6	97.1
Mean.....		93.0
Standard deviation.....		10.7

To estimate the density of salmon eggs and larvae in a spawning bed, a recovery percentage

of 90 percent was assumed. Furthermore, because a high percentage of eggs present in the test sampling units was collected, it was concluded that the possibility of introducing significant bias to estimates of abundance through an error in the assumed recovery percentage was minimized.

BROKEN SHELLS

Hobbs (1937), Cameron (1940), and Mathisen (1962) noted the presence of clean broken shells among eggs recovered from the gravel. The shells apparently originated from eggs damaged during excavation. Each author eliminated clean broken shells from his analysis because it was not possible to determine if these eggs were dead or alive when damaged.

TABLE 2.—Number and percentage of buried preserved eggs collected by two persons sampling

Buried	Recovered by two persons sampling	Recovered by two persons sampling
Number	Number	Percent
200.....	175	87.5
200.....	195	97.5
200.....	174	87.0
200.....	183	91.5
582.....	552	94.8
10.....	10	100.0
50.....	50	100.0
150.....	129	86.0
200.....	171	85.5
200.....	191	95.5
173.....	159	91.9
80.....	77	96.2
140.....	136	97.1
19.....	17	89.5
380.....	364	95.8
40.....	39	97.5
200.....	194	97.0
60.....	57	95.0
120.....	116	96.7
100.....	83	83.0
Mean.....		93.1
Standard deviation.....		5.1

We found that fewer eggs were broken by the hydraulic sampler than by a shovel. Comparisons were made between eggs collected by the two methods on Indian Creek in November 1956 (table 3). Observations were given equal weight for this comparison. Since clean broken shells averaged only 0.24 percent of the total eggs per sample, they are not included in our mortality estimates.

MEASURING MORTALITY

The percentage of eggs and larvae dying from the time of spawning to the time of sampling can be calculated from estimates of potential egg deposition and abundance of live eggs and larvae in the spawning bed at the time of sampling. It

will be shown how total mortality percentage calculated in this manner is unbiased either by failure of females to deposit or bury their eggs or by disappearance of eggs and larvae from the spawning bed. Eggs that are not deposited may be retained in the coelom of the female and, may be consumed by predators, or may drift free of the spawning bed. Factors causing eggs and larvae to disappear include consumption by predators or scavengers, decomposition, superimposition of redds, and erosion of spawning beds by floods, ice, or debris.

TABLE 3.—Number and percentage of broken shells in samples collected with a shovel compared with those collected with the hydraulic sampler, Indian Creek, November 1956

Shovel			Hydraulic sampler		
Collected	Broken	Broken	Collected	Broken	Broken
Number	Number	Percent	Number	Number	Percent
276	6	2.17	115	1	0.87
260	15	5.77	608		
585	8	1.37	368		
493	16	3.25	128		
24			779	3	.39
602	5	.83	447		
329	2	.61	149		
223	1	.45	13		
157	3	1.91	221	1	.45
240	4	1.67	445	4	.90
372	4	1.08	2,105	4	.19
723	27	3.73	893	1	.11
438	16	3.65	872		
879	7	1.03	1,125	11	.98
773	3	.39	341	2	.59
621	12	2.30	103		
			234		
			295		
			1,080	1	.09
Mean		1.89			.24

The notations listed below will be used in the discussions that follow:

- D = Actual number of dead eggs and larvae in a spawning bed at time of sampling.
- A = Actual number of live eggs and larvae in a spawning bed at time of sampling.
- $P = D + A$.
- E = Potential number of eggs available for deposition in a spawning bed.
- x = Fraction of E surviving to time of sampling.
- y = Fraction of E not deposited in the spawning bed or lost from the spawning bed prior to sampling.
- $1 \geq x + y$.
- M_r = Mortality percentage calculated from the proportions of dead eggs and larvae collected in samples.
- M_t = Calculated total mortality percentage from time of spawning to time of sampling.

BIAS IN CALCULATED MORTALITY LEVELS

An estimate of mortality level commonly reported in the literature is the ratio of number of

dead to total number of eggs and larvae collected in k samples from a spawning bed, i.e.

$$M_r = \frac{1}{k} \left(\sum_{i=1}^k \left(\frac{\text{live}}{\text{live} + \text{dead}} \right) i \right) \quad (1)$$

If it is assumed that live and dead eggs and larvae are collected in the same ratio as they occur in the total population, then the expected value of M_r is

$$\frac{D}{P} = 1 - \frac{A}{P} \quad (2)$$

Substituting

$$P = E - yE \text{ and} \\ A = xE$$

gives

$$M_r = 1 - \frac{x}{1-y} \quad (3)$$

where y is the bias introduced by disappearance of eggs and larvae and by failure of eggs to be deposited.

An estimate of total mortality level (M_t) which is not biased by y may be obtained from estimates of the actual population of live eggs and larvae in the spawning bed (A) and the potential egg deposition (E) in the following manner:

$$M_t = 1 - \frac{A}{E} = 1 - x \quad (4)$$

If all eggs are deposited in the spawning bed, and if there are no subsequent losses of eggs or larvae from the spawning bed, the value of y in equation (3) is zero; and equations (3) and (4) are identical. In this case, the observer can calculate the total mortality percentage by the two methods and select the one that is most efficient.

The calculation of total mortality level (M_t) based on E and A , equation (4), requires estimates of potential egg deposition and the number of live specimens in the spawning area at the time of sampling. Consideration will be given to certain important problems in obtaining estimates of E and A , but considerable additional research will be required before the methods of estimating mortality described in this paper become fully developed.

ESTIMATION OF POTENTIAL EGG DEPOSITION

An estimate of potential egg deposition can best be obtained from weir counts, but in some instances it may be desirable or necessary to estimate num-

bers of females spawning within defined stream sections or in streams where the construction of a weir is not feasible. The present study was conducted in intertidal spawning beds, making it impractical to construct weirs. The number of female salmon spawning in a study area was determined from observation. The method is illustrated for Harris River in 1959 as follows:

Daily counts of the number of female pink salmon spawning in the sampling area were obtained (fig. 5). Daily observations were made of 43 tagged pink salmon females to obtain an estimate of the average time each spawning female occupied the spawning ground. In 1959, tagged female pink salmon occupied the spawning bed an average of 10.35 days (range: 4 to 20 days), and it was assumed that untagged females occupied the spawning bed an equal time. To estimate the total number of females spawning within the sampling area, the area under the curve (fig. 5) was divided by the average number of days each female occupied the spawning bed. The estimate was

$$\frac{15,850 \text{ female-days}}{10.35 \text{ days}} = 1,531 \text{ female pink salmon.}$$

The average fecundity of pink salmon that spawned in McClinton Creek, northern British Columbia (Foerster and Pritchard, 1941), was used as an estimate of fecundity, since adequate data on fecundity of Harris River pink salmon were not available. For the years 1930-40, McClinton Creek pink salmon averaged 1,733 eggs per female. An average of 1,700 eggs per Harris River female was assumed. The potential

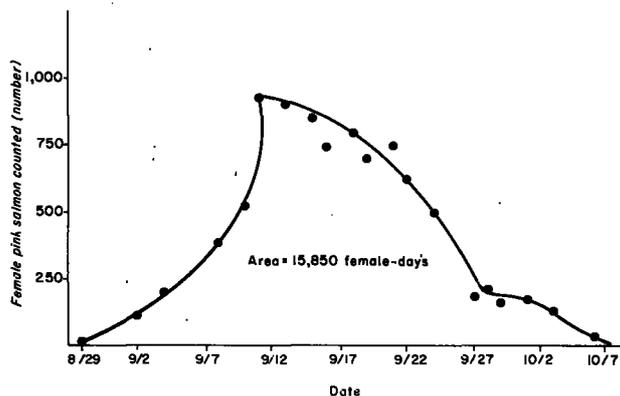


FIGURE 5.—Number of female pink salmon counted within the Harris River sampling area in 1959.

egg deposition (E) within the Harris River sampling area in 1959 was thus estimated to be

$$1,531 \times 1,700 = 2.6 \text{ million.}$$

The use of tagged females to obtain estimates of the average time female pink salmon occupied the spawning bed involved the assumption that tagged females lost no tags. It was assumed also that they behaved in a manner similar to and suffered the same mortality as untagged females, that is, tagged and untagged females reacted the same while on the spawning bed.

Although no attempt was made to measure variance in estimates of potential egg deposition, it is a random variable subject to at least two sources of sampling variability—(1) the estimated number of females spawning and (2) their estimated average fecundity. In the future, studies should be undertaken to evaluate the variance in estimates of each statistic. It would be more satisfactory, however, to conduct mortality studies in streams equipped with weirs for enumeration of adults, making it possible to minimize such sources of variation.

CALCULATION OF TOTAL MORTALITY LEVEL

A confidence interval estimate of total mortality level is calculated from the double inequality.

$$1 - \frac{\bar{a}}{E'} < M_t < 1 - \frac{a}{E'} \quad (5)$$

The values \bar{a} and a are the upper and lower confidence limits of the estimated number of live eggs and larvae per square foot of spawning bed, and E' is the expected number per square foot. Values of \bar{a} and a can be calculated with the t -distribution and the standard error of the mean obtained either from arithmetic counts of live eggs and larvae or from transformed values.

Double inequality (5) is derived in the following manner:

$$\text{Let survival to time } t = \frac{A_t}{E} = 1 - M_t. \quad (6)$$

Let the confidence interval estimate of the number of live eggs and larvae per square foot within a sampling area be represented by the double inequality

$$a < A_t < \bar{a} \quad (7)$$

Dividing (7) by the potential egg deposition, E , gives

$$\frac{a}{E} < 1 - M_t < \frac{\bar{a}}{E} \quad (8)$$

which is equivalent to

$$1 - \frac{\bar{a}}{E} < M_t < 1 - \frac{a}{E} \quad (9)$$

For calculating total mortality, the value E' is substituted for E in double inequality (9). E' is E adjusted to account for the percentage of specimens actually collected within a sampling unit. Tests to determine the percentage collected (tables 1 and 2) suggested that $E' \approx 9/10 E$. This relationship was used to calculate values of E' .

The method of calculating M_t is illustrated with data from Harris River samples collected October 6, 1959. A 90-percent confidence interval estimate of mean number of live eggs per square foot was calculated from the arithmetic counts, giving the following estimate of their abundance:

$$16.0 \text{ eggs/sq. ft.} < A < 35.0 \text{ eggs/sq. ft.}$$

The expected number of eggs per square foot (E') was calculated from the estimated total potential egg deposition, the size of the sampling area (62,640 sq. ft.), and the estimated percentage recovered, i.e.,

$$E' = \left(\frac{9}{10}\right) \left(\frac{2,600,000 \text{ eggs}}{62,640 \text{ sq. ft.}}\right) = 37.4 \text{ eggs/sq. ft.}$$

Using inequality (5) the estimated total mortality was

$$1 - \frac{35.0}{37.4} < M_t < 1 - \frac{16.0}{37.4} \text{ or } 6.4\% < M_t < 57.2\%.$$

The estimated mean mortality was 31.6 percent. For the same sample, M_t was estimated to be only 5 percent.

COMPARING SAMPLES FOR SIGNIFICANT DIFFERENCES

It is not always possible to determine by inspecting confidence limits alone if calculated mean total mortality levels (M_t) differ significantly. The use of confidence limits to detect significant differences implies that assumptions of analysis of variance are satisfied. Furthermore, it is difficult to assign exact levels of significance to confidence

limits. This is due in part to the reduced efficiency of confidence-interval estimates of abundance calculated from arithmetic counts because the distribution of eggs and larvae within the streambed is nonrandom.

Arithmetic counts for calculating confidence-interval estimates of abundance are not always most efficient, but are not too likely to be seriously biased. It should be noted, however, that use of the t-distribution for setting confidence limits requires that sample means from a given population be normally distributed. This assumption can be satisfied for highly skewed population distributions if the sample size is large.

In the discussions that follow, the use of a logarithmic transformation to improve the efficiency of confidence-interval estimates of abundance will be considered. Also described are the uses of single binomial parameters and live-dead ratios to detect changes in total mortality level.

DISTRIBUTION OF EGGS AND LARVAE

The distribution of eggs and larvae within a spawning bed influences the choice of statistical methods to test for sufficient and significant differences among calculated total mortality percentages. Because spawning salmon deposit their eggs in egg pits, eggs are initially clustered. Furthermore, evidence from field sampling indicates that occurrence of mortality does not materially affect the tendency of surviving eggs and larvae to be clustered.

When organisms tend to become clustered, the variance commonly increases as their mean abundance increases. The observed relationship between the mean number of live eggs and larvae collected per square foot of spawning bed and the sample variance is given in table 4. Samples were collected in autumn and winter and were from populations suffering light to heavy mortality. The data from table 4 are plotted in figure 6 to show graphically the relation between mean and variance.

The negative binomial distribution has frequently been fitted to counts of organisms where mean and variance were directly related. Bliss (1953) described several models of the negative binomial. One was derived to describe insect larvae hatching from eggs laid in masses, a condition possibly similar to that found among salmonid eggs and larvae.

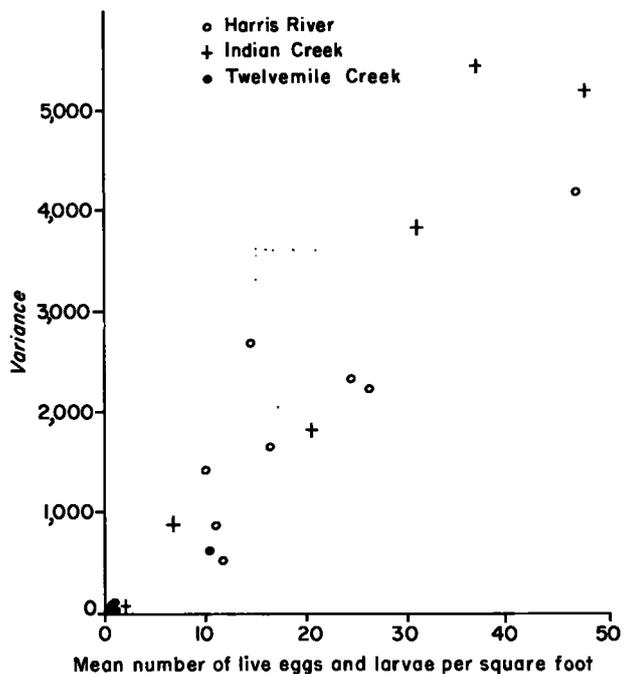


FIGURE 6.—Relation of mean to variance of live eggs and larvae collected per square foot of spawning bed in three southeastern Alaska streams.

TABLE 4.—Means and variances of number of live eggs and larvae collected per square foot of spawning bed in three southeastern Alaska streams

Stream and year class	Collection date	Size of sampling unit (sq.ft.) ¹	Number of sampling units	Mean	Variance	Variance mean
Harris River:						
1957	Apr. 1, 1958	4	74	1.1	41.2	37.5
1958	Sept. 18, 1958	4	34	10.7	878.9	82.1
1958	Nov. 15, 1958	4	32	14.6	2,688.8	184.2
1958	Apr. 5, 1959	4	86	9.9	1,408.7	142.3
1959	Oct. 6, 1959	4	74	24.6	2,338.1	95.0
1959	Oct. 20, 1959	4	43	26.2	2,229.3	85.1
1959	Nov. 16, 1959	4	20	16.3	1,633.0	100.2
1959	Feb. 26, 1960	4	69	11.4	512.2	44.9
1960	Sept. 27, 1960	2	56	47.2	4,157.5	88.1
Indian Creek:						
1958	Nov. 15, 1958	4	50	20.5	1,832.4	89.4
1958	Mar. 28, 1959	4	91	6.8	905.1	133.1
1959	Oct. 10, 1959	4	75	31.0	3,845.0	124.0
1959	Nov. 10, 1959	4	41	47.8	5,192.3	108.6
1959	Feb. 29, 1960	4	70	2.1	70.4	33.5
1960	Sept. 22, 1960	2	89	36.9	5,424.5	147.0
Twelvemile Creek:						
1958	Nov. 30, 1958	4	29	.4	4.2	10.5
1958	Dec. 28, 1958	4	32	.1	.1	1.0
1958	Mar. 24, 1959	4	47	.1	.5	5.0
1959	Oct. 27, 1959	4	77	1.0	68.3	68.3
1959	Feb. 21, 1960	4	56	.04	.07	1.8
1960	Sept. 30, 1960	2	50	10.3	636.1	61.8

¹ Sampling units of 4 square feet were quadrats and sampling units of 2 square feet were circles.

The negative binomial is a unimodal distribution; but bimodal or multimodal distributions may result also from contagion, as, for example

Neyman's contagious distributions which have been studied with regard to their modality and other properties (Beall and Rescia, 1953; Beall, 1954). However, Beall (1954) concluded that, regardless of the form of the distribution, if contagion occurred the empirical relationship between population variance (θ^2) and mean (μ) was

$$\theta^2 = \mu + \beta\mu^2 \quad (10)$$

The β term in equation (10) is a constant. Its value depends upon the degree of contagion—with β increasing with increasing degree of contagion.

Curves of equation (10) are drawn in figure 7 for $\beta=3$ and $\beta=30$.

The variance and mean of samples of live eggs and larvae collected from Harris River are shown in figure 7 as open circles. The plotted points indicated that values of β associated with samples of live eggs and larvae collected in Harris River fell mostly between $\beta=3$ and $\beta=30$. Values of β were also calculated for the Harris River samples from the expected frequency of zero observations in a negative binomial distribution (see Anscombe, 1949, and Bliss, 1953) and values $\beta \geq 2.9$ were obtained by this method for the samples plotted in figure 7.

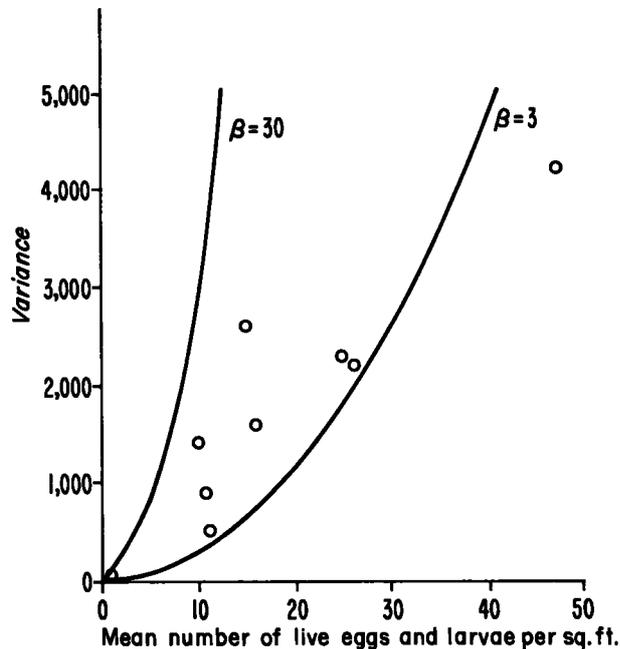


FIGURE 7.—Curves of $\theta^2 = \mu + \beta\mu^2$ for $\beta=3$ and $\beta=30$. Values of variance and mean for samples collected in Harris River are plotted as open circles.

TRANSFORMATION OF COUNTS

A transformation was sought to render variance independent of the mean and to increase efficiency of confidence interval estimates of abundance. Where variance and mean are related according to equation (10), the arc hyperbolic sine transformation is appropriate; but for larger values of β , the transformed values vary almost as the \log^1 of the number of live eggs and larvae in a sample (Beall, 1942). Furthermore, Barnes (1952) showed that the logarithmic was equally as applicable as the more complex arc hyperbolic sine transformation where values of β were large.

Jones (1956) and Taft (1960) used the logarithmic transformation to set confidence limits to estimates of abundance of bottom fish and sardine eggs because mean and variance were directly related. Since field sampling data suggested that the logarithmic transformation was also applicable for pink salmon eggs and larvae, the transformation

$$b_i = \log(n_i + \beta) \quad (11)$$

was tried. In equation (11), n_i is the number of live eggs and larvae per square foot at the i^{th} point and b_i is the transformed variate. A value of β was calculated for each sample from the expected frequency of zero observations in a negative binomial distribution. The technique is described by Anscombe (1949) and Bliss (1953). It requires an iterative solution of the equation

$$\frac{1}{\beta} \log(1 + \beta \bar{n}) = \log\left(\frac{k}{k_0}\right), \quad (12)$$

where k is the total number of observations (sampling units), k_0 is the number of zero observations, and \bar{n} is the sample arithmetic mean.

For samples where $\beta > 3.0$, the logarithmic transformation (equation 11) helped render the variance independent of the mean (see table 5) and improved the efficiency of confidence interval estimates (table 6). However, for samples where $\beta < 3$, there was no apparent improvement in efficiency, and confidence-interval estimates had a significant bias when compared with the arithmetic mean (table 6).

To set confidence limits to estimates of abundance of eggs and larvae with log-transformed data it is first necessary to correct mean log values so

¹In this paper the term "log" refers to the logarithm to the base 10.

TABLE 5.—Comparison of mean and variance of untransformed and log-transformed counts of number of live eggs and larvae per square foot collected in Harris River samples where $\beta > 3.0$

Date of collection	Arithmetic values (N_i)		Log-transformed values ($b_i = \log(n_i + \beta)$)	
	Mean	Variance	Mean	Variance
1958				
Apr. 1.....	1.1	41.2	2.100	<0.001
Sept. 18.....	10.7	878.9	.985	.131
Nov. 15.....	14.6	2,688.8	1.479	.058
Dec. 20.....	3.7	193.6	1.185	.029
1959				
Apr. 5.....	9.9	1,408.7	1.576	.032
Oct. 6.....	24.6	2,338.1	1.057	.292
Oct. 20.....	26.2	2,229.3	1.130	.284
Nov. 16.....	16.3	1,633.0	.949	.231
1960				
Feb. 26.....	11.4	512.2	1.040	.143
1961				
Mar. 7.....	6.6	203.2	.909	.099

TABLE 6.—Ninety-percent confidence interval estimates of mean number of live eggs and larvae per square foot in Harris River calculated from untransformed and log-transformed data

Year class and collection date	Arithmetic mean	Confidence interval estimate of mean	
		Untransformed	Log-transformed
1957			
April 1, 1958.....	1.1	$0 < \mu < 2.3$	$0 < \mu < 2.2$
1958			
September 18, 1958.....	10.7	$2.1 < \mu < 19.3$	$4.5 < \mu < 11.2$
November 15, 1958.....	14.6	$0 < \mu < 30.1$	$4.8 < \mu < 16.6$
December 20, 1958.....	3.7	$0 < \mu < 9.1$	$0.6 < \mu < 6.2$
April 5, 1959.....	9.9	$2.3 < \mu < 17.5$	$4.4 < \mu < 11.3$
1959			
October 6, 1959.....	25.6	$16.0 < \mu < 35.2$	$14.6 < \mu < 26.6$
October 20, 1959.....	26.2	$14.1 < \mu < 39.2$	$13.6 < \mu < 33.9$
November 16, 1959.....	16.3	$0.7 < \mu < 31.9$	$6.1 < \mu < 20.6$
February 26, 1960.....	11.4	$6.9 < \mu < 15.9$	$7.2 < \mu < 12.8$
1960			
September 27, 1960.....	47.2	$32.8 < \mu < 62.6$	$*64.3 < \mu < 131.9$
December 1, 1960.....	27.0	$18.6 < \mu < 35.4$	$*28.4 < \mu < 52.7$
March 7, 1961.....	6.6	$3.8 < \mu < 9.4$	$4.2 < \mu < 7.2$

*Value of $\beta < 3.0$.

that the arithmetic mean will result from the antilog. A correction term is required because the mean of log-transformed data is a geometric rather than an arithmetic mean (Ricker, 1958: ch. 11). Jones (1956) gives the correction term and develops the method used here to calculate confidence limits with log-transformed counts. The equation used to obtain an arithmetic mean (\bar{n}) from the log-transformed counts is

$$n = \text{antilog}(\bar{b} + 1.1518 s_b^2) - \beta \quad (13)$$

where \bar{b} is the logarithmic mean value and s_b^2 is the sample variance of the log-transformed counts. It is necessary to subtract β to correct for its addition to counts before making the transformation (equation 11).

Improvement in efficiency of confidence interval estimates of total mortality percentage calculated with log-transformed data can be shown with the October 6, 1959, Harris River sample considered previously. Ninety-percent confidence limits of M_t set with arithmetic counts were

$$6.4\% < M_t < 57.2\%$$

and the corresponding confidence limits set with log-transformed counts were

$$28.9\% < M_t < 61.0\%$$

TESTS OF PROPORTIONATE FREQUENCIES

Tests of proportionate frequencies are based on the premise that the proportion of points within a spawning bed occupied by eggs and larvae varies with the total mortality level. If no change in mortality occurs, the following conditions will have been satisfied:

1. There will have been no decrease in the fraction of points populated by eggs or larvae ($Pt1 = Pt2 = Pt3 = \dots$).

2. There will have been no decrease in the fraction of points populated by live eggs or larvae ($At1 = At2 = At3 = \dots$).

3. There will have been no increase in the fraction of points populated by dead eggs or larvae ($Dt1 = Dt2 = Dt3 = \dots$).

Each condition was tested separately with chi square. This was done by classifying each point sampled in accordance with the presence or absence of eggs or larvae. In the examples to be given, points containing three or less eggs and larvae per square foot were counted with zeros; hence, the following three conditions were tested:

1. Presence or absence of three or less total eggs and larvae per square foot.
2. Presence or absence of three or less live eggs and larvae per square foot.
3. Presence or absence of three or less dead eggs and larvae per square foot.

One purpose of the classification scheme was to classify jointly all points containing zero or few specimens. The selection of three or less specimens per square foot for joint classification

was arbitrary, however, and the possibility that other criteria for the joint classification of points might improve the tests should not be ignored.

Each of the three conditions was tested by a method described by Bliss and Calhoun (1954: p. 36) and Snedecor (1956: pp. 227-230). Data from the 1959 year class in Harris River are used to illustrate the method in table 7. There was no significant increase in the fraction of points containing three or less total or three or less live eggs and larvae per square foot ($\chi^2=0.85$ and 1.30). There was a significant decrease, however, in the fraction of points containing three or less dead eggs and larvae per square foot ($\chi^2=11.16$).

TABLE 7.—Tests of independence among samples containing three or less eggs and larvae per square foot (Harris River, 1959 year class)

Date of sampling	Number of points sampled	Three or less total		Three or less live		Three or less dead	
		k_o	p_o	k_o	p_o	k_o	p_o
1959							
October 6.....	74	44	0.5946	47	0.6351	72	0.9730
October 20.....	43	25	.5814	26	.6047	38	.8837
November 16.....	20	13	.6500	14	.7000	18	.9000
1960							
February 26.....	69	45	.6522	48	.6957	55	.7971

$$\chi^2 = \frac{\sum k_o p_o - \bar{p}_o \sum k_o}{\bar{p}_o (1 - \bar{p}_o)}, \text{ where } \bar{p}_o = \text{mean of } p_o \text{ values}$$

χ^2 for total = 0.85 (3 degrees of freedom)

χ^2 for live = 1.30 (3 degrees of freedom)

χ^2 for dead = 11.16 (3 degrees of freedom)

These results suggested that the disappearance of eggs and larvae of the 1959 year class may not have been a major factor in this instance; but the increased fraction of points containing dead eggs and larvae indicated that a significant mortality had occurred nevertheless. The next problem was to determine the periods during which mortality levels had changed. This was done by first setting confidence limits to the number of points containing three or less dead eggs and larvae per square foot (k_o). Where the sample size was adequate, the normal approximation of the binomial distribution was used to set confidence limits. In the present study 90-percent confidence limits of k_o were obtained from the roots of equation (14), i.e.:

$$(\bar{k}_o, \underline{k}_o) = k p_o \pm 1.645 [k p_o (1 - p_o)]^{1/2}. \quad (14)$$

Confidence limits of the fraction of points containing three or less eggs and larvae per square

foot (p_0) corresponding to k_0 were obtained by dividing the limits of k_0 by the number of points sampled. Values of k_0 and p_0 for samples of the 1959 year class in Harris River obtained October 6 and 20 and February 26 are given in table 8. Confidence limits were not set to the November 16 sample because of its small size. Inspection of confidence limits of p_0 (table 8) shows that a significant mortality occurred between October 6 and 20 and between October 20 and February 26. Since mortality in these instances was detected with remains of dead eggs and larvae, it was concluded that factors not associated with direct removal of affected specimens from the spawning bed were responsible. If this conclusion is correct then estimates of mortality percentage based on live-dead ratios (M_r) should also indicate that a mortality occurred between October 6 and 20 and between October 20 and February 26. It will be shown shortly that these results are verified by estimates of M_r .

MORTALITY CALCULATED FROM LIVE-DEAD RATIOS

Although estimates of mortality based on ratios of dead eggs and larvae collected in samples (equation 1) are sometimes biased, they do give important evidence of mortality caused by factors not associated with direct removal of affected specimens from spawning beds. Because numbers of eggs and larvae collected from sampling units vary, the necessity of weighting samples for binomial variation before calculating M_r must be considered.

TABLE 8.—Mean and 90-percent confidence limits of estimated number of points with 3 or less dead eggs and larvae per square foot, Harris River, 1959 year class

Date of sample	Points sampled	Points containing 3 or less dead specimens per square foot			
		Points (k_0)		Fraction of points (p_0)	
		Mean	90-percent confidence limits	Mean	90-percent confidence limits
1959	Number		Number		
October 6.....	74	72	±3.2	0.97	±.04
October 20.....	43	38	±3.5	.88	±.08
1960					
February 26.....	69	55	±5.5	.80	±.08

Cochran (1943) has shown that the proper weight applied to each observed fraction of mortality depends on the relative amounts of binomial

and extraneous variation in samples. This question was considered for eggs and larvae collected from Harris River and Twelvemile and Indian Creeks (McNeil, 1962), and it was found that equal weight should be given to sampling units from which 10 or more specimens were collected.

Returning to the Harris River 1959 year class example, we find that estimates of M_r support the conclusion that mortality occurred between October 6 and 20 and between October 20 and February 26 (refer to estimates of p_0 , table 8). For the three samples considered, estimates of M_r and 90-percent confidence limits of the mean were:

	Percent
Oct. 6, 1959.....	$M_r = 5 \pm 5$
Oct. 20, 1959.....	$M_r = 12 \pm 11$
Feb. 26, 1960.....	$M_r = 27 \pm 11$

DISCUSSION AND CONCLUSIONS

The manner in which total mortality estimated from percentages of dead eggs and larvae collected in samples is biased by disappearance of dead eggs and larvae from the population has been shown algebraically. Estimates of mortality based on live-dead ratios ignore completely mortality that is caused by factors inherently associated with the direct removal of affected eggs and larvae from the population. Decomposition and scavenging also introduce bias to mortality estimates based on the percentage of dead eggs and larvae in samples.

Mortality from all causes occurring over any period of the fresh-water life of pink salmon can be assessed from estimates of abundance. By this method, total fresh-water mortality of pink salmon has been determined in a number of streams by enumerating the adults entering, by estimating their average fecundity, and by enumerating the fry departing. Such data have shown rather conclusively that 75 to 99 percent of total deaths within a population commonly occur in fresh water. An important problem requiring solution is to determine the periods of fresh-water residence during which major changes in the mortality rate occur. Solution of this problem is prerequisite to the identification of the major mortality-causing factors.

With the hydraulic sampler, it is possible to estimate quantitatively the abundance of pink salmon embryos and larvae in spawning beds. Results of unpublished studies conducted by the

Bureau of Commercial Fisheries in Sashin Creek, southeastern Alaska, have shown consistent good agreement between the total fresh-water mortality rate of pink and chum (*O. keta*) salmon estimates by sampling with the hydraulic sampler just prior to emergence of fry and by enumerating fry at a weir.

In Sashin Creek potential egg deposition for the stream as a whole is calculated from the number of adult females enumerated at the weir and their average fecundity. Under some circumstances, however, it may be desirable or necessary to estimate spawning densities within defined segments of the spawning ground. A method of estimating density of females spawning by visual foot survey censuses has been described, but the technique requires further evaluation to determine variability and bias in estimates. The Bureau of Commercial Fisheries is making comparisons between the number of females spawning (estimated by censuses taken on foot surveys) and the number counted at the weir in Sashin Creek. Preliminary unpublished results of these comparisons are not inconsistent with the hypothesis that estimates from foot surveys are essentially unbiased estimates of the true population at spawning densities similar to those observed in Harris River and Indian and Twelvemile Creeks.

Estimates of egg and larval abundance determined from sampling spawning beds are not always as efficient as an investigator might desire. High variability in estimates of abundance and mortality is due primarily to clustering of eggs and larvae in spawning beds. Clustering causes the variance and mean to increase dependently; and confidence limits of estimates of abundance may be widely separated, even with relatively intensive sampling. There is no evidence of reduced tendency of larvae to be clustered, suggesting little if any horizontal scattering of young pink salmon within spawning beds.

Three statistics useful for evaluating mortality in spawning beds have been considered. Total mortality (M_t) is least sensitive as a measure of change in the mortality rate, but it is most useful in determining the magnitude of mortality from all causes. The single binomial parameters of presence or absence of live or dead eggs and larvae at sampling points (p_o) are helpful in two ways. They provide a basis for identifying the periods during which total mortality increased significantly

and for determining whether or not such mortality was associated with disappearance of eggs or larvae from the spawning bed. Mortality estimated from live-dead ratios (M_r) is a useful statistic for evaluating mortality caused by factors not associated with the direct removal of dead eggs and larvae from the spawning bed. M_r is biased by the disappearance of dead eggs and larvae from decomposition and scavenging, however. By sampling spawning beds randomly with the hydraulic sampler, the field data can be evaluated by the three independent methods described.

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LITERATURE CITED

- ANSCOMBE, F. J.
1949. The statistical analysis of insect counts based on the negative binomial distribution. *Biometrics*, vol. 5, No. 2, pp. 165-173.
- BARNES, H.
1952. The use of transformations in marine biological statistics. *Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil*, vol. 18, No. 1, pp. 61-71.
- BEALL, GEOFFREY.
1942. The transformation of data from entomological field experiments so that the analysis of variance becomes applicable. *Biometrika*, vol. 32, pp. 243-262.
1954. Data on binomial and near binomial distribution. In O. Kempthorne, T. A. Bancroft, J. W. Cowen, and J. L. Lush (editors), *Statistics and mathematics in biology*, pp. 295-302. The Iowa State College Press, Ames.
- BEALL, GEOFFREY, and RICHARD R. RESCIA.
1953. A generalization on Neyman's contagious distributions. *Biometrics*, vol. 9, No. 3, pp. 354-386.
- BLISS, C. I.
1953. Fitting the negative binomial distribution to biological data. *Biometrics*, vol. 9, No. 2, pp. 176-200.
- BLISS, C. I., and D. W. CALHOUN.
1954. An outline of biometry. Yale Co-operative Corporation, New Haven, Connecticut, 272 pp. [Processed.]
- BRIGGS, JOHN C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. *California Department of Fish and Game, Fish Bulletin No. 94*, 62 pp.

- CAMERON, W. M.
1940. The efficiency of fertilization in the natural spawning of Pacific salmon. Fisheries Research Board of Canada, Progress Reports of the Pacific Biological Station and Pacific Fisheries Experimental Station, No. 45, pp. 23-24.
- COCHRAN, WILLIAM G.
1943. Analysis of variance for percentages based on unequal numbers. American Statistical Association Journal, vol. 38, pp. 287-301.
- DAVIDSON, F. A., AND S. J. HUTCHINSON.
1942. Natural reproduction of pink salmon studied at Little Port Walter, Alaska. Ecology, vol. 23, No. 2, pp. 234-235.
- FOERSTER, RUSSELL E., AND ANDREW L. PRITCHARD.
1941. Observations on the relation of egg content to total length and weight in the sockeye salmon (*Oncorhynchus nerka*) and the pink salmon (*O. gorbuscha*). Transactions of the Royal Society of Canada, vol. 35, section 5, pp. 51-60.
- HATCH, RICHARD W.
1957. Success of natural spawning of rainbow trout in the Finger Lakes region of New York. New York Fish and Game Journal, vol. 4, No. 1, pp. 69-87.
- HOBBS, DERISLEY F.
1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. New Zealand—Marine Department, Fisheries Bulletin No. 6, 104 pp.
1940. Natural reproduction of trout in New Zealand and its relation to density of populations. New Zealand—Marine Department, Fisheries Bulletin No. 8, 93 pp.
- HUNTER, J. G.
1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada, vol. 16, No. 6, pp. 835-886.
- HUTCHINSON, S. J., and R. F. SHUMAN.
1942. Reproduction of pink salmon at Little Port Walter, 1941-42. Pacific Fisherman, vol. 40, December 1942, pp. 29-31.
- JONES, R.
1956. The analysis of trawl haul statistics with particular reference to the estimation of survival rates. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 140, part 1, pp. 30-39.
- MARTIN, JOHN W. (editor)
1959. Stream catalog of eastern section of Ketchikan Management District of Southeastern Alaska U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 305, 379 pp.
- MATHISEN, OLE A.
1962. The effect of altered sex ratios on the spawning of red salmon. In Ted S. Y. Koo (editor), Studies of Alaska red salmon, pp. 137-246. University of Washington, Seattle, Publications in Fisheries, vol. 1.
- MCNEIL, WILLIAM JOHN.
1962. Mortality of pink and chum salmon eggs and larvae in Southeast Alaska streams. Ph. D. Thesis, University of Washington, Seattle, 270 pp.
- MERRELL, T. R., JR.
1962. Freshwater survival of pink salmon at Sashin Creek, Alaska. In N. J. Wilimovsky, editor, Symposium on pink salmon, pp. 59-72. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- NEAVE, FERRIS.
1953. Principles affecting the size of pink and chum salmon populations in British Columbia. Journal of the Fisheries Research Board of Canada, vol. 9, No. 9, pp. 450-491.
1958. Stream ecology and production of anadromous fish. In P. A. Larkin (editor), The investigation of fish-power problems, pp. 43-48, Institute of Fisheries, University of British Columbia, Vancouver, H. R. MacMillan Lectures in Fisheries.
- PRITCHARD, A. L.
1948. Efficiency of natural propagation of the pink salmon, (*Oncorhynchus gorbuscha*) in McClinton Creek, Masset Inlet, B.C. Journal of the Fisheries Research Board of Canada, vol. 7, No. 5, pp. 224-236.
- RICKER, W. E.
1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, vol. 11, No. 5, pp. 559-623.
1958. Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin No. 119, 300 pp.
- SNEDECOR, GEORGE A.
1956. Statistical methods, 5th ed. Iowa State College Press, Ames, 534 pp.
- TAFT, BRUCE, A.
1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. Limnology and Oceanography, vol. 5, No. 3, pp. 245-264.

MERISTIC VARIATION IN THE HEXAGRAMMID FISHES

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ABSTRACT

Meristic characters of 300 to 800 specimens of eight hexagrammid fish species are examined for geographic and local variation, and the characters are analyzed for relative variation within and between species. Significant geographic variation occurs frequently and generally is most pronounced in those species with extensive north-south distributions. Sample variation, as measured by the coefficient of variation, is quite consistent for each character both within and between species. Frequency distributions of coefficients enable

a general ranking of the characters, with counts of total vertebrae showing the lowest variation and counts of gill rakers the highest. Character variation is comparable with that reported in the literature for other fishes. Geographic variation, where pronounced, appears to be positively correlated with local variation. Character variation probably is affected both by time of embryonic fixation and structural peculiarities of the part.

Students of variation in fishes have usually described, for each population, the fluctuations in range, mode, or mean that are correlated with changes in such environmental factors as geography, temperature, and salinity. A few students have analyzed the correlation between variation of different characters within populations of a species. Both approaches have yielded valuable information. A third approach has been neglected; prior to this study, little attempt has been made to measure the variation of meristic characters within regional samples for the purpose of comparing fish species or populations of fishes. For works of this nature, one must turn to such papers as those on ammonites (Simpson, 1953) and on oreodonts (Baker, 1955).

The term "meristic" has at least two interpretations in the ichthyological literature. A general usage is synonymous with "numerical" or "capable of being counted." A restricted usage applies to those countable characters that

appear to be anatomically associated with body somites. Gill raker counts are "meristic" in the general sense, but not in the restrictive. In this paper the more general usage is employed except where otherwise stated.

Data utilized in my analysis became available during taxonomic studies on the nine extant species of the family Hexagrammidae. The family is allied to the Cottidae, and is in the same percoid suborder, Cottoidei. Distributions of the nine species fall within an arc of the North Pacific Ocean above lat. 30° N. (fig. 1). Only eight species are analyzed for geographic variation because insufficient material is available to analyze the ninth species, the Atka mackerel (*Pleurogrammus monoptygius*). The adults of all but one species are demersal and frequent rocky areas to depths of 60 m. or more. The adults of *P. monoptygius* appear largely to have retained the pelagic existence that characterizes hexagrammid larvae.

The three subfamilies that the family may be divided into are the Hexagramminae and the

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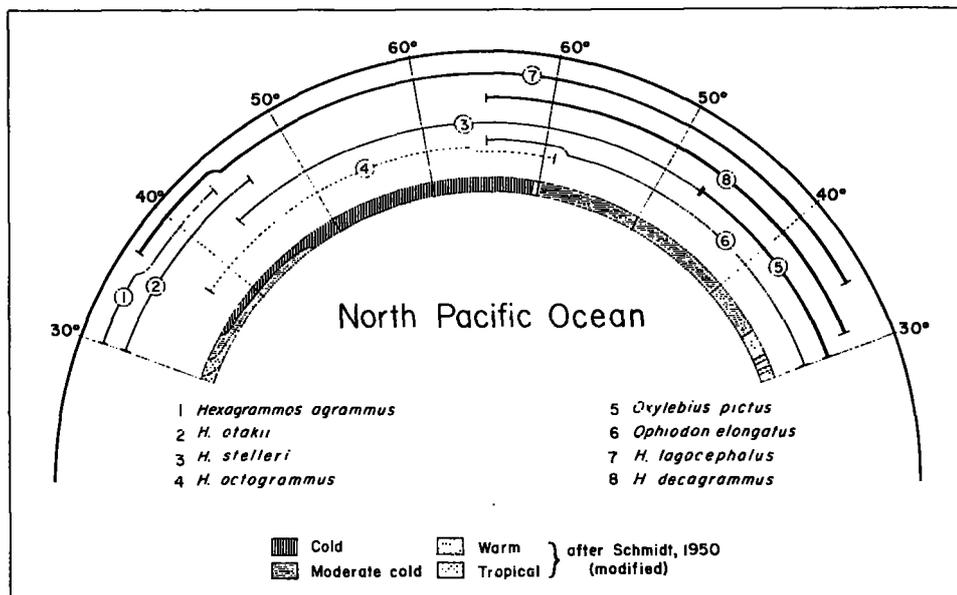


FIGURE 1.—Schematic diagram of geographic ranges in the hexagrammids that are analyzed for geographic variation. Numbers outside the semicircle indicate intersections of lines of latitude with the coastline. Species distributions are indicated by numbered arcs, and the weight of each line is roughly proportional to the degree of geographic variation (as indicated by analyses in figures 2 and 11 and discussed in the text) shown by the species. Limited inshore regions of colder upwelled water are indicated for some lower latitudes of the eastern Pacific Ocean. (Temperature data from Schmidt (1950); slightly modified.)

monotypic Oxylebiinae and Ophiodontinae. The convictfish (*Oxylebius pictus*), sole representative of the Oxylebiinae, is judged to be the most primitive member of the family because of its low meristic counts and the absence of specializations that characterize other representatives of the family. Almost all of the Hexagramminae have multiple lateral lines. In general, the evolutionary trend in the family has been toward the occupation of cold-water niches.

The names of two species depart from conventional usage, in accordance with Quast (1960): *Agrammus agrammus* is called *Hexagrammos agrammus*, and *Hexagrammos superciliosus* is synonymized with its Oriental counterpart, *H. lagocephalus*.

The family Hexagrammidae was judged ideal for meristic analysis because of the limited number of species and the high degree of overlap in their ranges, the ease with which the species could be arranged in phyletic sequence, the meristic diversity of the species, and the relative abundance of specimens in collections.

MATERIAL AND METHODS

The analysis is based on counts of vertebrae, fin rays, lateral line scales, and gill rakers of between 300 and 800 specimens, depending on the character involved. To facilitate comparisons, the geographic ranges are divided arbitrarily, and meristic data from individual localities are lumped for each division. Nearly all specimens available were examined. In most instances the collection localities range over the divisions, and in only a few are divisions represented by a single locality. A detailed listing of collection localities appears in the taxonomic section of Quast (1960). Other than gill rakers in *Ophiodon elongatus*, discussed below, there appears to be no association of meristic number with sex or size.

The methods of counting are usually those described by Hubbs and Lagler (1949). Terminal dorsal and anal rays are counted as recommended by these authors except for rare specimens that have the last two elements separated by a space

at their base approximately equal to the spacing of the preceding rays; in these, a count one unit higher is assigned. Pectoral rays and lateral line pored scales are counted on the left side unless that side is damaged. Pores in the skin over the cleithrum and pored scales on the caudal fin posterior to the hypural fan are excluded from the counts of lateral line pored scales. Gill rakers are counted on the first arch of the right side and include rudimentary rakers. (In *Ophiodon elongatus* the anteriormost rakers on the hypobranchial become so indistinct with fish growth that they cannot be counted accurately.) In vertebral counts the urostyle is included as one element, and the first caudal vertebra is identified on X-ray pictures as the anteriormost centrum with a simple haemal spine.

In regard to the analysis of meristic data, frequency distributions approximated the normal in nearly all instances. Cochran's test (Dixon and Massey, 1951) was used for general evaluation of homogeneity of variance for the *t* and analysis of variance tests. The variances appeared excessively different in an insignificant percentage of the comparisons.

GEOGRAPHIC VARIATION IN THE MEANS OF COUNTS

The means of counts (figs. 2 to 11)¹ vary geographically to some degree in all eight of the hexagrammid species examined. Of 73 species characters analyzed, approximately one-half show geographic variation. The three species with extensive north-south distributions, *Oxylebius pictus*, *Hexagrammos lagocephalus*, and *H. decagrammus*, show the greatest geographic variation both on the criterion of degree of change of counts (discussed in the section on within-sample variation) and on the criterion of the proportion of the counts that vary (fig. 1). Probably *Ophiodon elongatus* also should be included with these species because considerable geographic variation is shown despite

¹ In figures 2 to 11 the number of specimens in each sample follows the geographic designation. The mean of each sample is bracketed by a black bar that indicates its 95-percent confidence interval (with *t* correction). The light bar on each side of the mean indicates one standard deviation; the range of counts is given by the heavy lower line. Probabilities shown to the right of each species character are obtained by a *t*-test where two samples are compared, or by analysis of variance where more than two samples are compared. Coefficients of variation for the samples are indicated in the right-hand column. In the discussion, deviations between paired samples are termed "prominent" when the sample mean with the smaller confidence interval falls outside the 95-percent confidence interval of the mean for the distribution with the larger confidence interval.

only a partial sampling of its range. The other species, which have restricted Oriental distributions or distributions limited to an arc across the North Pacific, show considerably less geographic variation.

In general, the number of meristic elements declines to the south, in agreement with the latitudinal trends commonly reported for fishes in the literature. Numerous deviations from consistent geographic gradients may be noted, however, and the proportions of exceptions vary considerably from species to species.

In *Oxylebius pictus* the highest average for pre-caudal vertebrae is in the sample from northern and central California, the middle of the geographic range (fig. 2). The average for the northernmost sample is prominently (see footnote 1 for explanation of term) lower than that for the central sample, but the aggregate variation among the samples does not test as significant. The highest average for caudal vertebrae is in the northernmost sample, which is responsible for the high statistical significance of the caudal comparison; and no important differences are apparent between the two southern samples (fig. 3). Similarly, the highest average for total vertebrae occurs in the northernmost sample (fig. 4), where the high average for caudal vertebrae more than compensates for the relatively low average for pre-caudal vertebrae. No important differences in total vertebrae are demonstrated between the two southern localities. Dorsal fin spines show a definite cline of decreasing counts to the southward (fig. 5). The Puget Sound-Washington sample averages are prominently higher, and the southern-Baja California averages prominently lower than the intermediate samples. A similar trend is shown in the averages of dorsal soft rays (fig. 6), and the trends in spinous and soft rays summate to produce a very definite cline of decreasing total counts to the southward (fig. 7). The northernmost sample of anal fin rays gives the highest count, but the remaining samples show no important differences (fig. 8). Counts of lateral line pored scales shift to lower averages to the south, but the trend is slight and of borderline significance (fig. 9). Counts of pectoral rays show no definite geographic variation in means, but the southern samples appear to have greater ranges (fig. 10). Counts of gill rakers also show no definite geographic variation in means, although the range in

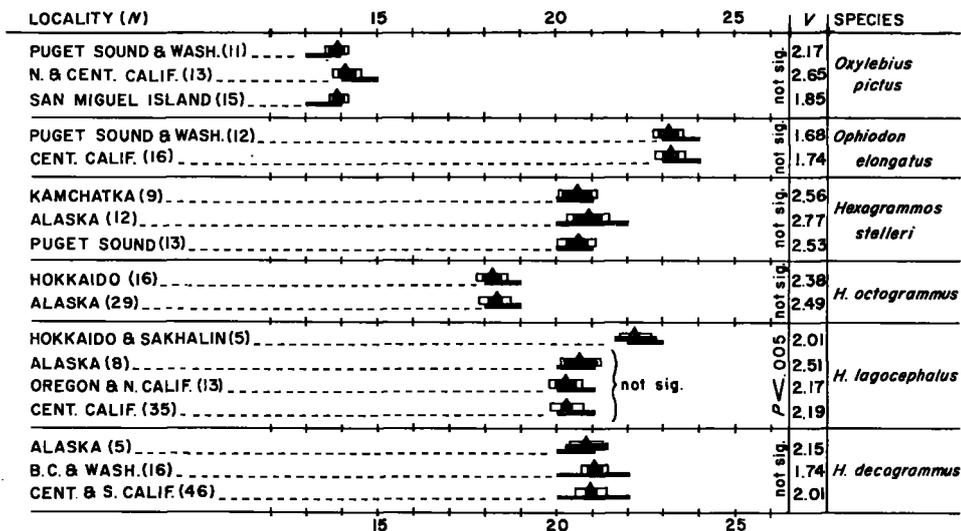


FIGURE 2.—Geographic variation in precaudal vertebrae.

counts is greater in the southern samples (fig. 11).

In *Ophiodon elongatus* no geographic trends are indicated for precaudal, caudal, or total vertebra counts (figs. 2, 3, 4). In contrast, total dorsal ray counts decrease to the southward (fig. 7), apparently because of the decrease in the soft ray portion between the northern and central samples (fig. 6) (where spine counts remain constant) and the decrease in the spinous portion between the central and southern samples (fig. 5) (where soft ray counts remain practically constant). The anal rays follow the pattern of the dorsal fin spines, and a southward decrease in counts is limited to the

southern part of the range (fig. 8). No geographic variation is apparent for the averages of lateral line pored scales, but the sample from the central portion of the range is the most variable (fig. 9)—the reverse of the situation for anal rays. Pectoral rays show no important variation. Gill raker variation is not assessed because gill raker counts change with growth in this species.

Specimens of *Hexagrammos agrammus* were available in limited quantity, and the samples are lumped into two groups. Vertebral comparisons are not made. Counts of spinous dorsal rays are prominently higher in specimens from the

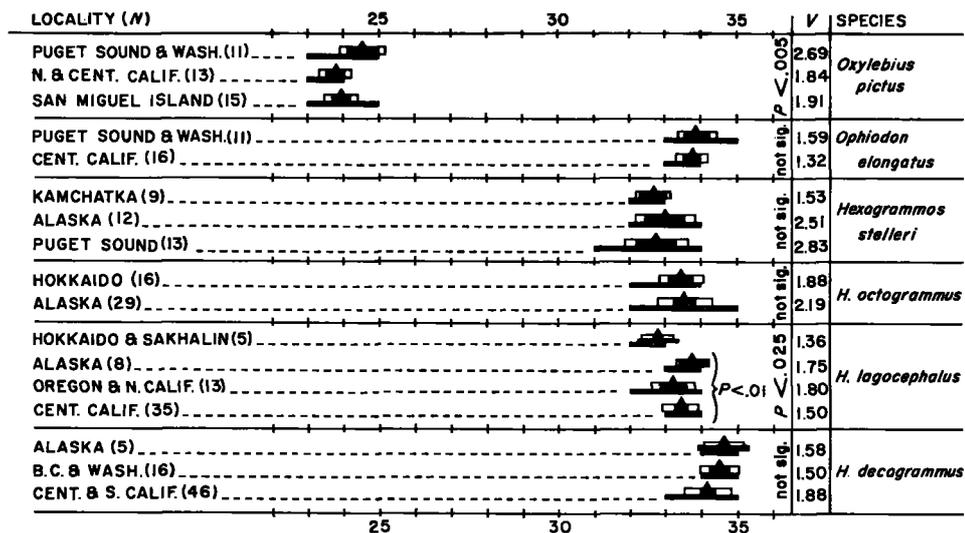


FIGURE 3.—Geographic variation in caudal vertebrae.

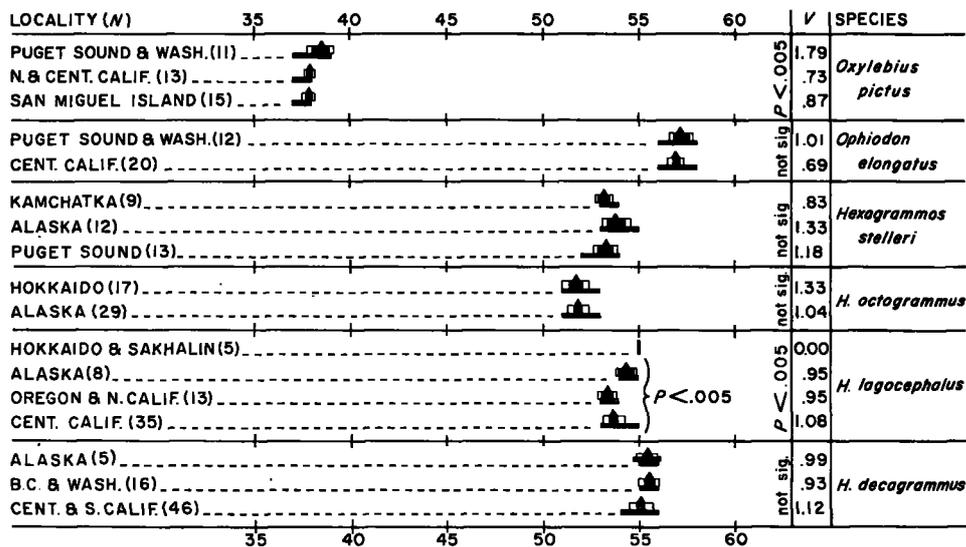


FIGURE 4.—Geographic variation in total vertebrae.

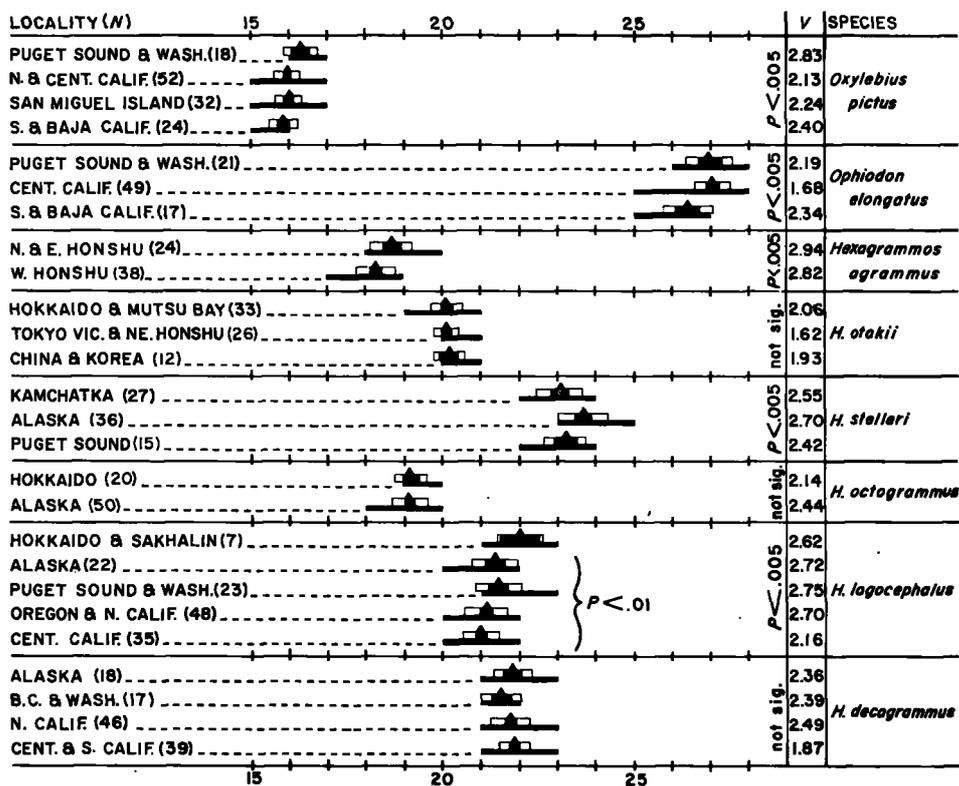


FIGURE 5.—Geographic variation in dorsal fin spinous rays.

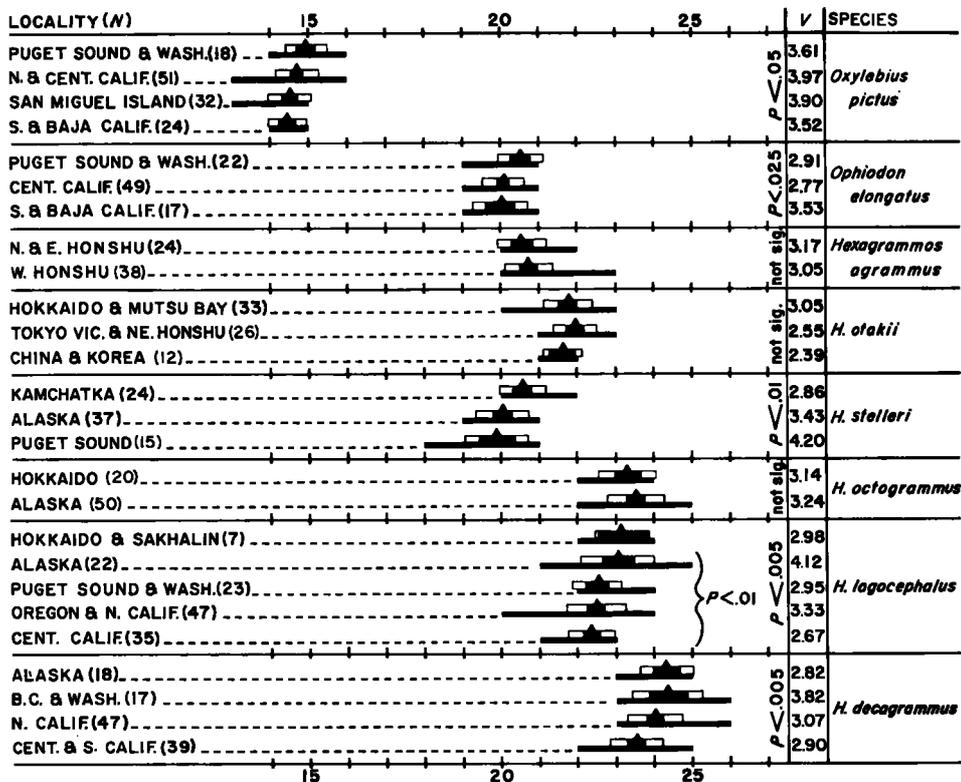


FIGURE 6.—Geographic variation in dorsal fin soft rays.

oceanic side of Honshu (fig. 5), but no differences of corresponding magnitude are apparent for dorsal soft rays or total dorsal rays (figs. 6, 7). Although anal rays are more numerous in the sample from the oceanic side (fig. 8), the difference is not significant. Counts of pectoral rays are prominently lower on the oceanic side of Honshu (fig. 10). No important variation is indicated for lateral line pored scales (fig. 9) or for gill rakers (fig. 11).

Vertebral comparisons are omitted also for *H. otakii*. Counts of dorsal fin rays show no variation worthy of note (figs. 5, 6, 7). Counts of anal rays show significant variation, however, and the mean for counts from the eastern coast of Honshu is prominently higher than the mean for Hokkaido or the mainland (fig. 8). (Although similar in mean value, the counts from the mainland and Hokkaido differ markedly in coefficient of variation.) Lateral line pored scales show a definite shift toward lower counts in the regions from Hokkaido through Honshu to China and southern Korea (fig. 9). Counts of pectoral rays show no significant differences (fig. 10). Counts of gill

rakers are prominently higher in the Hokkaido-Mutsu Bay sample than in the northeastern Honshu sample (fig. 11).

The three geographic samples of *H. stelleri* differ relatively little in latitude. No significant overall differences are indicated for counts of precaudal, caudal, or total vertebrae (figs. 2, 3, 4), although the total counts for Alaska average prominently higher than those for Kamchatka and Puget Sound. Averages for counts of total dorsal fin rays from Kamchatka and Alaska (fig. 7) are similar, although there are prominently opposing trends in spines and soft rays between the two localities (figs. 5, 6). The Puget Sound sample has prominently lower total dorsal ray counts than either Kamchatka or Alaska. No important differences are evident in the averages for anal fin rays or lateral line pored scales (figs. 8, 9). In pectoral rays, the Alaska sample has the prominently highest average (fig. 10). Gill raker counts are prominently lower in the Alaska sample than in the one from Kamchatka, but the three samples of this character do not differ significantly in the aggregate (fig. 11).

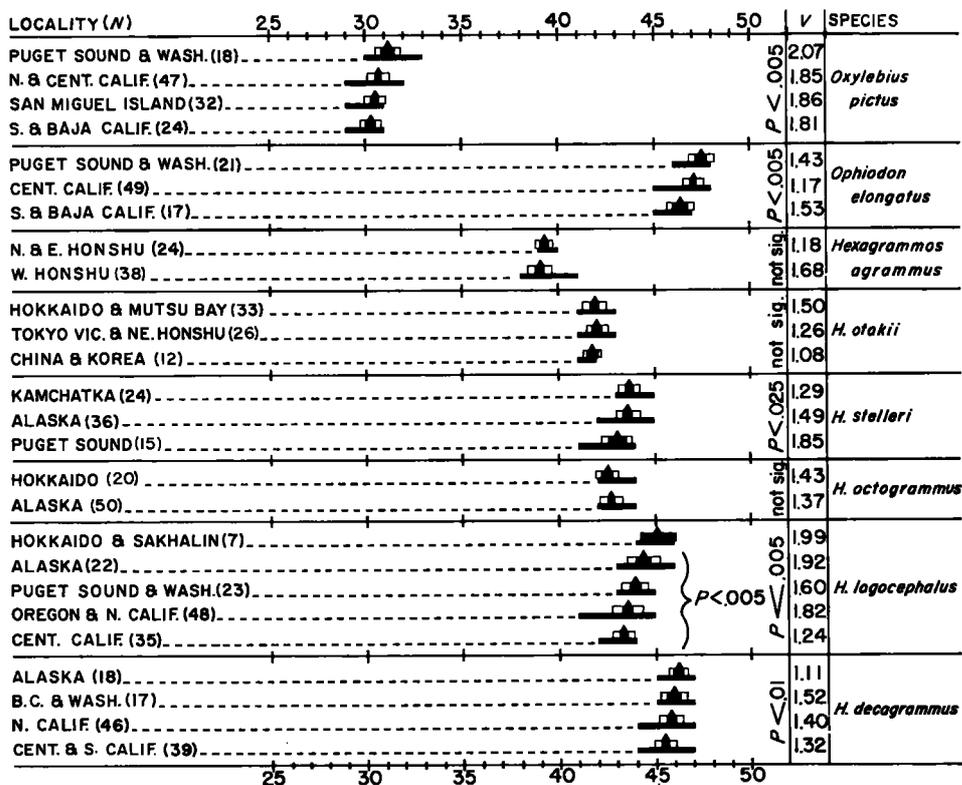


FIGURE 7.—Geographic variation in total dorsal rays.

Samples of *H. octogrammus* from the Orient and Alaska show few important meristic differences. Average counts for vertebrae (figs. 2, 3, 4), dorsal fin rays (figs. 5, 6, 7), lateral line pored scales (fig. 9), and gill rakers (fig. 11) are quite similar in the two samples. Only counts of anal and pectoral rays show differences of possible significance, and the Oriental sample gives the highest average in each instance (figs. 8, 10).

In *H. lagocephalus*, a sharp discontinuity is shown between samples of counts of precaudal vertebrae from Hokkaido-Sakhalin and Alaska (fig. 2). The dramatic difference may warrant subspecific recognition of the eastern and western Pacific representatives. Adequate data are not available from intermediate points, however, and a cline actually may exist between the two regions. In contrast, no important differences are apparent between samples of precaudal counts from the northeastern Pacific. A reciprocal relationship between precaudal and caudal counts, similar to that noted for *Oxylebius pictus*, is apparent in the Oriental and eastern Pacific samples (figs. 2, 3). Prominent differences exist between all samples of

total vertebral counts, with the Oriental counts the highest and the Alaskan specimens second highest (fig. 4). Definite clines of decreasing counts from Hokkaido to central California are apparent in dorsal fin rays (figs. 5, 6, 7), and the clines remain significant whether the Oriental samples are included or not. Anal fin rays show a similar cline except for a slight increase in means between the Oregon-northern California sample and the central California sample (fig. 8); the variation in anal fin rays is also significant whether the Oriental sample is considered or not. Averages for lateral line pored scales show a variation pattern similar to that of anal fin rays, with the highest average in the Orient (fig. 9). Pectoral rays also have the highest average in the Oriental sample, and the Oriental counts are nearly disjunct from the distributions obtained from the eastern Pacific, where no variation is apparent (fig. 10). Little variation is visible in the numbers of gill rakers (fig. 11).

In *H. decagrammus* vertebral counts show a low degree of geographic variation, but caudal and total vertebral counts are prominently lower from

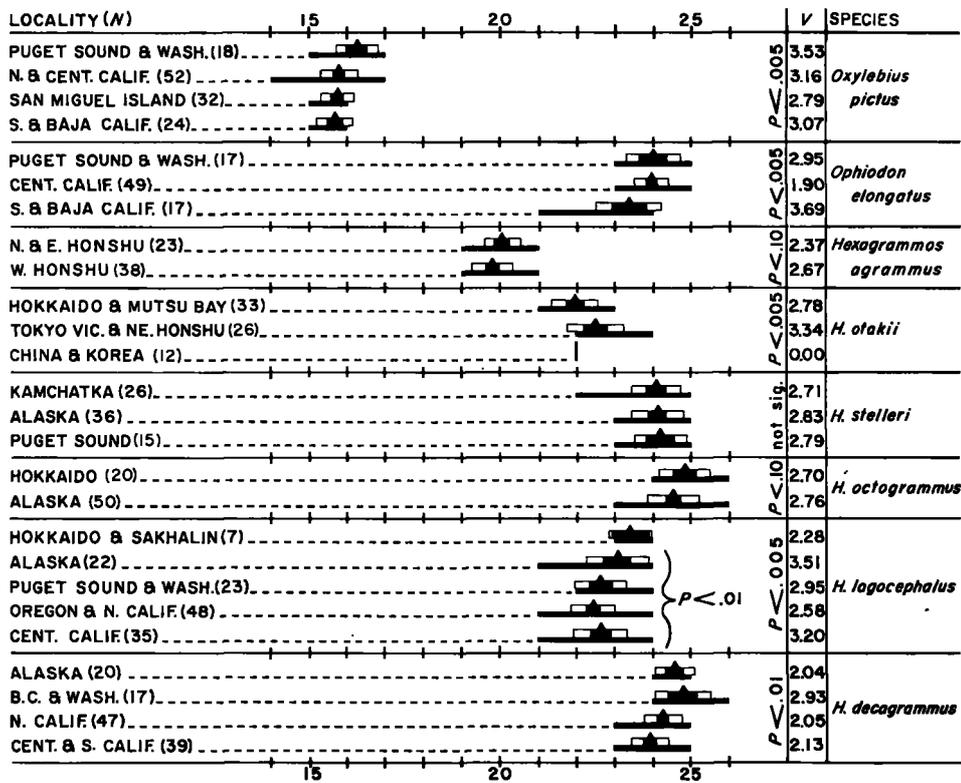


FIGURE 8.—Geographic variation in anal fin rays.

California than from British Columbia and Washington (figs. 2, 3, 4). Numbers of dorsal fin spinous rays show no differences worthy of emphasis, but the dorsal soft rays show a prominent decrease in number in the southern part of the species geographic range (figs. 5, 6). Total dorsal fin ray counts show a cline of numerical decrease to the south (fig. 7); the shift apparently is caused by a slight decline in spinous ray counts in the northern part of the geographic range (where soft ray counts remain constant) and a prominent decrease in soft ray counts in the southern part (where the shift in spinous counts opposes but does not completely compensate for the shift in the number of soft rays). Anal fin rays follow the dorsal soft ray pattern and show a decrease in counts only in the southern half of the geographic range (fig. 8). A general north-south cline of decreasing numbers of lateral line pored scales is evident, although the differences between adjacent samples are slight (fig. 9). Similar clines are noticeable in numbers of pectoral rays and gill rakers, but the aggregate variation in gill rakers does not test as significant (figs. 10, 11).

The foregoing examination of meristic variation in the hexagrammids demonstrates that the manifestation of this variation is quite complex and that shifts in means and ranges of counts between geographic samples are not always predictable. The tendency for meristic counts to be greater in the more northern and more western Pacific localities is obvious. Sampling error may be responsible for some of the contradictory trends noted between neighboring samples and, in part, for the poor correspondence in details of variation found between the species over shared portions of their geographic ranges. Numerous instances of poor correspondence between trends in counts of total elements and the numbers of elements in their sections also are noted. For example, a southward decrease in total vertebrae in *Oxylebius pictus* over the two northernmost localities (fig. 4) reflects a considerable decrease in the average number of caudal vertebrae (fig. 3), and the average number of precaudal vertebrae may actually vary in the opposite direction over the same region (fig. 2). As a corollary, the apparent lack of geographic variation in a total count may mask

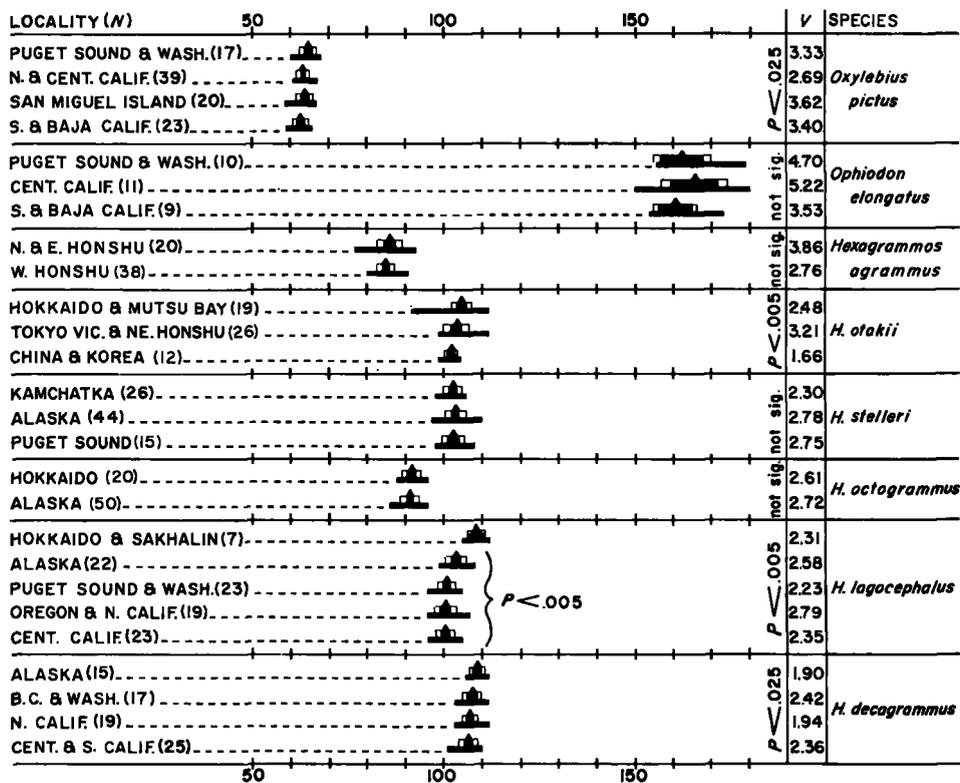


FIGURE 9.—Geographic variation in lateral line pored scales.

significant opposing geographic trends in its sections such as, for example, the pattern of dorsal fin variation in *H. stelleri* between Kamchatka and Alaska (figs. 5, 6, 7). Significant geographic variation is most frequent in the dorsal fin, second most frequent in the anal fin, and least frequent in the gill rakers.

WITHIN-SAMPLE VARIATION OF MERISTIC CHARACTERS

In addition to the mean, a measure of dispersion is necessary to characterize fully a normal frequency distribution, and the study of variation in organisms is not complete without some such estimate of the variation of characters about their sample averages. This estimate provides an index to the stability of the processes that lead to the mean values of anatomical features used to characterize populations or species. Statistics on meristic characters in fishes have the advantage that these characters are easily counted and their frequency distributions commonly approximate normal.

Simpson (1953) raised an important question

concerning the role of variation in evolution without arriving at any definite conclusions. He asked whether a highly variable population would offer more materials for evolution of new species than one that is less variable. This and other questions regarding variation in phyletic lines of animals are responsible for the following analysis. In order to examine the hexagrammid fishes in this respect, coefficients of variation are calculated for meristic characters from the available geographic samples of the species. This coefficient gives the standard deviation of a sample as a percentage of the mean. For a discussion of its use, see Simpson, Roe, and LeWontin (1960).

Interspecific and Intraspecific Similarities in Variation Coefficients of a Character

A comparison of the character coefficients of variation for all hexagrammid samples (see figs. 2 to 11 and table 1) demonstrates that for each character (e.g. total vertebral count) there is a remarkable consistency in the degree of variation shown (1) between geographic samples of a species and (2) between the species themselves. Also,

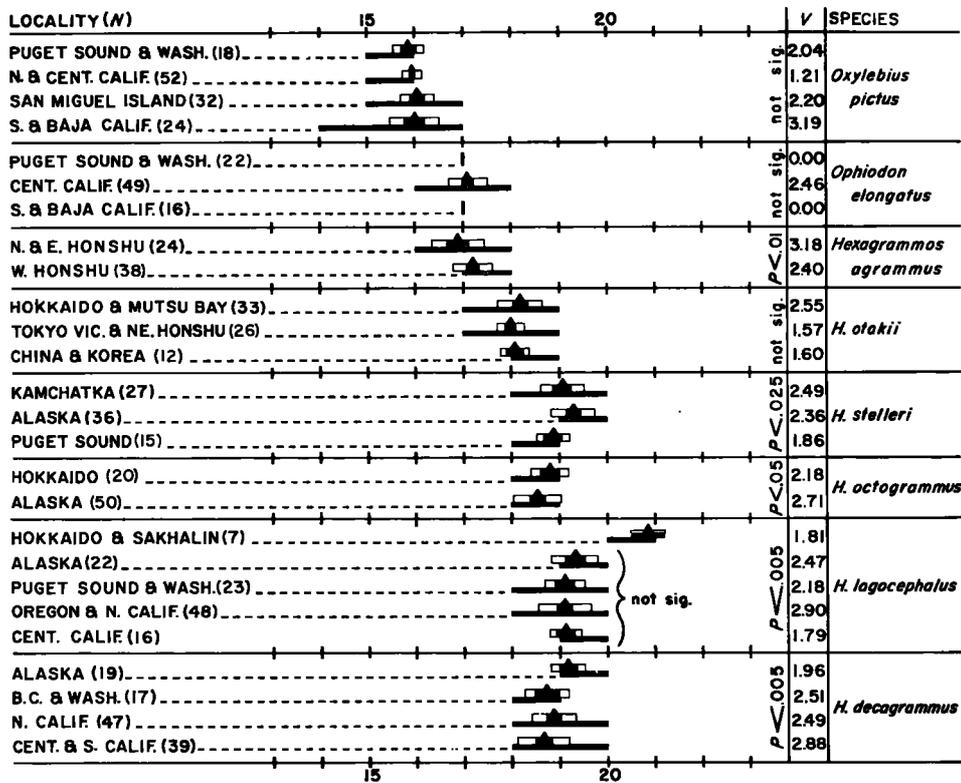


FIGURE 10.—Geographic variation in pectoral rays.

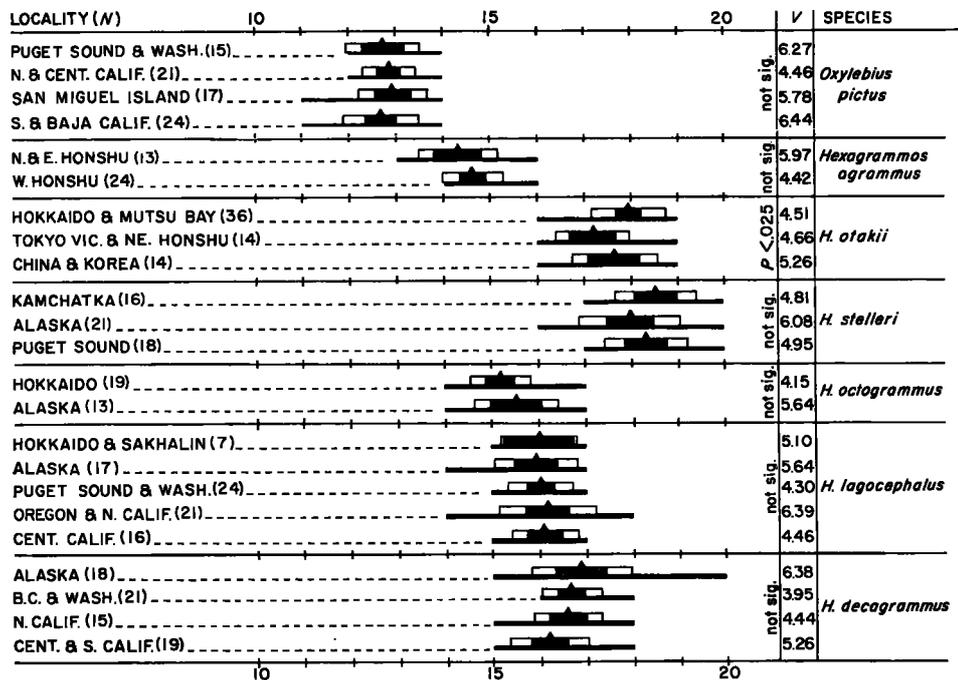


FIGURE 11.—Geographic variation in gill rakers.

each of the characters (e.g. number of anal fin rays, number of caudal vertebrae) appears to have a characteristic modal value for variation that usually differs in some degree from that for each of the other characters. Because of the consistency in variation between similar counts and the difference in variation between different counts, the samples form a hierarchical pattern when plotted on a frequency diagram (fig. 12). Similar results are obtained by ranking for each species, in order of numerical value, the averages of each set of character coefficients. In nearly all rankings, vertebral values are lowest, and total dorsal rays adjoin; whereas gill raker values are consistently highest.

The study shows an interesting relationship between the variation of entire counts, namely total dorsal spines and total vertebrae, and that of their serial components. In each comparison of this type (fig. 12), the range of coefficients for the whole count is distinctly lower than for either of its sections. The greater variation shown by components of the whole counts may be explained in part by an apparent variability in the developmental fate of the transitional elements; that is, whether a given element will develop into the type characteristic of the anterior or the posterior section. This instability, mentioned above as introducing some exceptions to the general geographic trends of the means, is presumably not linked to body metamerism, but rather to the processes that influence the fate of the boundary

TABLE 1.—Variation data on hexagrammid species not presented in figures 2 to 11¹

Species and character	Number	Mean and range of counts	Coefficient of variation
<i>Hexagrammos agrammus:</i>			
Precaudal vertebrae.....	32	18.81 (18-20)	2.84
Caudal vertebrae.....	32	29.22 (28-30)	2.26
Total vertebrae.....	32	48.03 (46-50)	1.45
<i>Hexagrammos otaki:</i>			
Precaudal vertebrae.....	32	20.08 (20-21)	1.44
Caudal vertebrae.....	12	31.58 (31-33)	1.63
Total vertebrae.....	12	51.67 (51-52)	0.95
<i>Pleurogrammus monopterygius:</i>			
Dorsal spines.....	34	22.18 (24-29)	3.42
Dorsal soft rays.....	33	26.61 (24-29)	3.75
Total dorsal rays.....	33	48.79 (47-50)	1.43
Total anal rays.....	31	26.10 (25-27)	2.68
Pectoral rays.....	34	25.09 (24-26)	2.67
Precaudal vertebrae.....	8	26.62 (26-27)	1.95
Caudal vertebrae.....	8	33.62 (33-35)	2.21
Total vertebrae.....	8	60.25 (60-61)	0.77
Lateral line pored scales.....	38	152.08 (139-166)	4.13
Gill rakers.....	31	24.90 (22-27)	4.79

¹ Data are from collections from single geographic locations only: *Hexagrammos agrammus*, Kyogo Misaki, Japan; *H. otaki*, "Tokyo," Japan; *Pleurogrammus monopterygius*, Alaska.

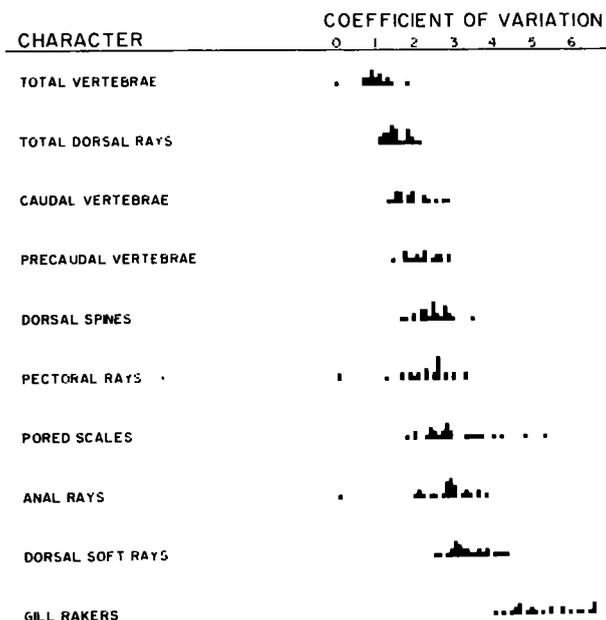


FIGURE 12.—Frequency diagram of variation coefficients for samples of hexagrammid meristic counts. Characters arranged in order of increasing variability.

elements. Although according each section of entire counts high values for variation, the instability of transitional elements has no effect on the variability of entire counts because the total number of elements is not affected. As an example, the frequency with which a boundary element becomes either a dorsal spine or a dorsal soft ray, or a precaudal or a caudal vertebra, has no effect on the total number of elements in the dorsal fin or in the vertebral column. Gosline (1947) described a negative correlation between the number of anterior and posterior elements for *Etheostoma exile*, and Hubbs and Hubbs (1954) described it for the kelp perch, *Brachyistius frenatus*.

The values for the variation of meristic characters of the same body region are not necessarily similar. Although the caudal vertebrae and the anal and soft dorsal fins are of similar extent and occupy the same body region in hexagrammid fishes, an overall comparison of the frequency distributions of the character variation coefficients (fig. 12) demonstrates that variation in the numbers of caudal vertebrae throughout the family generally is less than in anal rays and dorsal soft rays.

Meristic Variation of Hexagrammids Compared With That of Other Fishes

In general, meristic variability in characters of the hexagrammid fishes agrees with or is lower than that for the same characters in fishes of several other families and orders randomly selected from the literature (table 2). Coefficients of variation (V) for vertebral counts are relatively uniform and low among all samples of the various families, with two exceptions: In *Fundulus*, especially in laboratory-reared samples, and in some samples of the flatfish *Parophrys vetulus*, the coefficients are unusually high. Variation in the number of dorsal spines, as compared with the hexagrammids, is lower in five families and higher in two. The range of coefficients for numbers of dorsal fin soft rays in hexagrammids approximates that of herring, flatfishes, some scorpaenids, one cottid, and one goby, but is considerably lower than that of one serranid, two percids, and two scorpaenids. Variation in numbers of anal rays, lateral line pored scales, pectoral rays, and gill rakers in hexagrammids generally is below that of the other examples.

Overall Variation in the Hexagrammids and Its Relationship to Evolution Within the Family

A crude estimate of general meristic variability was attempted for each of the nine species of Hexagrammidae by calculating character by character the number of positive and negative deviations of all samples of each species from the family averages for variation. It was assumed that any species having overall high or low values for variation also will have unusually high or low totals of values above or below the family means. When the frequencies of positive and negative deviations were tested with the chi-square distribution, a significant departure from the distribution of values expected in a homogeneous sample was found at the 95-percent level, indicating that some species probably have greater allotments of variation coefficients above or below the family means than would be expected by chance alone. The data indicate that the values for *Oxylebius pictus* and *Hexagrammos decagrammus* are in large part responsible for the high chi-square value. The two species depart strongly from the family averages for meristic variation, but in different directions: In *O. pictus*, 12 out of 15 coefficients are above the family means; in *H. decagrammus*, 13 out of 15 coefficients are below.

Because the average counts for meristic characters in the two species are markedly dissimilar, another interpretation of the differences in variation between the two species, as indicated by V , would be necessary if the standard deviations of character samples of *O. pictus* and *H. decagrammus* were the same. In this instance, the divisor of the variation equation would be larger for characters of *H. decagrammus* because of the higher counts in this species, and hence would accord this species lower values for variation. The data disclose, however, that the standard deviations for characters of *O. pictus* are not the same as for those of *H. decagrammus*, and that the latter are consistently higher (table 3). The lower values for V in *H. decagrammus* are the result of the disproportionate differences in means and standard deviations of the two species: the increase in standard deviations of character samples between *O. pictus* and *H. decagrammus* does not quite keep pace with that of the mean values of their meristic characters.

The differences in variation between *O. pictus* and *H. decagrammus* suggest that the more highly evolved form may be less variable. *Oxylebius pictus* is interpreted as being the most primitive living species in the family because of its low meristic counts and single lateral line. In contrast, *H. decagrammus* has these characters in an apparently more derived condition. However, since it is not known to what extent the differences in variability between the two species are due to environmental rather than to genetic causes, the significance of the differences is questionable. In addition, other hexagrammid species that contrast nearly as strongly in subjective estimates regarding their evolutionary status show no corresponding general differences in their variation. It must be concluded that any relationships between variation and evolution in the Hexagrammidae are too subtle or too complex to be reliably indicated by such gross numerical analyses.

Relationship Between Variation Within Samples and Geographic Variation of a Character

Considerable taxonomic significance may pertain to the possible relationships between the variation within regional or local samples of a character, as measured by the coefficient of variation, and the variation between samples taken over the entire geographic range of a species. A

TABLE 2.—Comparison of coefficients of variation (V) for hexagrammids with those for other fishes, as calculated from data randomly selected from the literature

Character, family, and species	Samples (specimens)	Sample averages	Range of V
Vertebral elements:			
Hexagrammidae:-----	20 (327)	38-60	0.7-1.8
Clupeidae:			
<i>Clupea pallasii</i> (Hubbs, 1925).....	5 (847)	52-53	1.2-1.5
<i>Sardinops caerulea</i> (Hubbs, 1925).....	2 (494)	52	1.1-1.2
Engraulidae:			
<i>Engraulis mordax</i> (Hubbs, 1925).....	2 (729)	46	1.3-1.5
Cyprinodontidae:			
<i>Fundulus heteroclitus</i> (Gabriel, 1944):			
Laboratory-reared specimens.....	3 (932)	32-33	2.3-2.9
Wild population.....	1 (105)	32	2.0
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (1,988)	37-38	.9-1.8
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	15 (1,486)	43	.8-1.9
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (266)	52	1.2-1.7
<i>Parophrys vetulus</i> (Taylor, 1957).....	27 (2,130)	42-44	1.1-2.8
Percidae:			
Fourteen species (Bailey and Gosline, 1958).....	14 (405)	36-43	.7-1.5
<i>Etheostoma exile</i> (Bailey and Gosline, 1958).....	1 (1,000)	37	1.9
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,938)	36-38	1.1-1.8
Dorsal spines:			
Hexagrammidae:-----	27 (799)	16-27	1.6-3.4
Serranidae:			
<i>Roccus saxatilis</i> (Raney, 1957).....	12 (1,320)	9	3.0-6.0
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	10	7.9
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,720)	12	4.1-5.9
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	15-16	3.4
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	12	.7-1.4
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,754)	7-8	4.6-8.6
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	4-5	.9-1.2
Dorsal soft rays:			
Hexagrammidae:-----	27 (795)	14-27	2.4-4.2
Clupeidae:			
<i>Clupea pallasii</i> (Hubbs, 1925).....	2 (390)	18	3.7-4.1
Serranidae:			
<i>Roccus saxatilis</i> (Raney, 1957).....	4 (294)	11	4.3-5.0
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	11	6.0
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,698)	11-12	4.2-6.1
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (2,268)	82-88	2.5-5.8
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	16 (1,337)	90-93	2.2-3.4
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (255)	103-105	3.2-4.6
<i>Parophrys vetulus</i> (Taylor, 1957).....	27 (2,083)	77-83	3.2-5.6
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	8-9	5.6-7.7
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	10	.7-3.4
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,753)	16-18	3.0-4.0
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	16-17	3.0-3.6
Anal rays, total or soft rays only:			
Hexagrammidae:-----	27 (816)	16-26	1.9-3.7
Clupeidae:			
<i>Clupea pallasii</i> (Hubbs, 1925).....	2 (390)	16-17	5.0-5.4
Cyprinodontidae:			
<i>Fundulus</i> , 2 spp. (Brown, 1958).....	15 (368)	10	2.6-6.1
Serranidae:			
<i>Roccus saxatilis</i> (Raney, 1957).....	4 (294)	10-11	3.8-5.0
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	8	8.6
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (2,265)	63-70	2.1-4.1
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	15 (1,331)	70-73	2.6-5.4
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (258)	85-87	3.3-4.5
<i>Parophrys vetulus</i> (Taylor, 1957).....	27 (2,058)	57-62	3.1-6.0
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	6	5.7-6.4
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	5	2.3-2.4
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (1,752)	15-18	3.1-4.1
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	16	3.5-3.8

TABLE 2.—Comparison of coefficients of variation (V) for hexagrammids with those for other fishes as calculated from data randomly selected from the literature—Continued

Character, family, and species	Samples (specimens)	Sample averages	Range of V
Blenniidae:			
<i>Istiblennius edentulus</i> (Strasburg, 1955).....	3 (280)	22	2.2-2.8
Acanthuridae:			
Three species (Randall, 1955, 1956).....	6 (249)	20-26	2.0-3.0
Lateral line scales or pored scales:			
Hexagrammidae:-----	27 (620)	63-165	1.7-5.2
Cyprinidae:			
<i>Notropis spilopterus</i> (Gibbs, 1957a).....	16 (1,157)	36-39	1.7-2.7
<i>Notropis venustus</i> (Gibbs, 1957b).....	19 (1,149)	30-42	1.7-4.3
Percidae:			
<i>Etheostoma exile</i> (Gosline, 1947).....	1 (1,000)	53	5.1
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,745)	52-63	4.1-6.1
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	15	6.9-11.6
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (278)	25-26	5.2-5.4
Pectoral rays:			
Hexagrammidae:-----	27 (803)	16-25	1.2-3.2
Cyprinidae:			
<i>Notropis spilopterus</i> (Gibbs, 1957a).....	22 (2,757)	14	3.0-6.1
<i>Notropis venustus</i> (Gibbs, 1957b).....	23 (2,575)	14-16	3.1-8.8
Percidae:			
<i>Percina nigrofasciata</i> (Crawford, 1956).....	19 (1,702)	28-29	2.5-4.5
Bothidae:			
<i>Citharichthys stigmaeus</i> (Taylor, 1957).....	25 (2,330)	11-12	4.6-7.2
Pleuronectidae:			
<i>Eopsetta jordani</i> (Taylor, 1957).....	16 (1,441)	12-13	2.3-7.9
<i>Microstomus pacificus</i> (Taylor, 1957).....	5 (272)	10	5.8-7.9
<i>Parophrys vetulus</i> (Taylor, 1957).....	21 (1,704)	12	4.3-7.1
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (75)	12	2.6-3.7
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (278)	22	2.7
Cottidae:			
<i>Leptocottus armatus</i> (Hubbs and Hubbs) ¹	12 (4,256)	18-19	2.5-3.2
Gobiidae:			
<i>Clevelandia ios</i> (Prasad, 1958).....	4 (188)	19	3.6-4.9
Gill rakers:			
Hexagrammidae:-----	24 (611)	13-25	3.9-6.4
Scorpaenidae:			
<i>Ocosia</i> , 2 spp. (Matsubara, 1943).....	2 (65)	8-10	10.8-13.1
<i>Setarches</i> , 2 spp. (Matsubara, 1943).....	2 (283)	13	5.5-6.9

¹ Hubbs, Carl L., and L. C. Hubbs. Analysis of meristic variation in *Leptocottus armatus*, a fish of western North America. Manuscript being prepared for publication, Scripps Institution of Oceanography, La Jolla, Calif.

character that varies little within regional or local samples assumes greater significance when associated with extensive geographic variation. An index of variation within samples of species characters is available in the form of averaged coefficients of variation of the samples. An index of geographic variation may be obtained by dividing the maximum difference between sample means of a species character by the midrange of the character means. The value obtained, like the coefficient of variation, expresses the difference as a percentage of the mean or central value. To determine what relationships may exist between these two types of variation, averaged values of the coefficient of variation were compared with the index of geographic variation for each of nine strictly meristic counts in the four species that display marked geographic variation—*Oxylebius*

TABLE 3.—A comparison of mean values for the standard deviation in samples of *Oxylebius pictus* and *Hexagrammos decagrammus*

Character	<i>O. pictus</i>			<i>H. decagrammus</i>			Proportionate increase	
	Standard deviation		Mid-range of count	Standard deviation		Mid-range of count	Standard deviation	Mid-range of count
	Number	Mean		Number	Mean			
Dorsal spines.....	4	0.387	16.0	4	0.487	22.0	1.26	1.37
Dorsal soft rays.....	4	.550	14.5	4	.760	24.0	1.38	1.65
Total dorsal rays.....	4	.585	31.0	4	.612	45.5	1.05	1.47
Anal rays.....	4	.498	15.5	4	.560	24.5	1.12	1.68
Pectoral rays.....	4	.341	15.5	4	.462	19.0	1.35	1.23
Precaudal vertebrae.....	3	.310	14.0	3	.407	21.0	1.31	1.60
Caudal vertebrae.....	3	.520	24.0	3	.470	34.0	1.09	1.42
Total vertebrae.....	3	.430	38.0	3	.564	55.0	1.31	1.45
Lateral line pored scales.....	4	2.060	63.5	4	2.310	107.5	1.11	1.69
Gill rakers.....	4	.735	12.5	4	.832	17.5	1.13	1.40
Average increase.....							1.21	1.47

pictus, *Ophiodon elongatus*, *Hexagrammos lagocephalus*, and *H. decagrammus* (table 4). The comparison by means of the rank-correlation test (Dixon and Massey, 1951) indicates a probable positive correlation between the two types of variation for *H. decagrammus* and *Ophiodon elongatus*, and *H. lagocephalus* if the Oriental sample is excluded. A positive correlation may also exist in *Oxylebius pictus*. The pooled data for all four species show a high level of significance. It seems, therefore, that the two types of variation are positively associated in the hexagrammid fishes and that characters exhibiting the greatest shift in means geographically, by the above criteria, also tend to have the highest average values for the coefficient of variation in the regional samples. This conclusion suggests that the other species of hexagrammids, whose characters exhibit comparable variation on a local basis, have a potential for geographic variation that is unrealized.

The eight species contrast markedly in the total amount of geographic variation they demonstrate relative to their local variation. A comparison is possible if the index of geographic variation of each species character is divided by the corresponding index of local variation and all the quotients are averaged for each species (table 5). The four species with extensive north-south distribution, *Oxylebius pictus*, *Ophiodon elongatus*, *Hexagrammos lagocephalus*, and *H. decagrammus*, generally show the highest values for character

TABLE 4.—Rank correlation between local and geographic variation in meristic characters in four species of *Hexagrammidae*

[Meristic characters are ranked for both types of variation (see text) within the four species and also over the four species (overall ranking in parentheses). Highest values represent lowest ranks. Significance levels of within-species data: 5-percent=0.600; 1-percent=0.783. Significance levels of overall data: 5-percent=<0.306; 1-percent=<0.432. (From Dixon and Massey, 1951)]

Character	<i>Oxylebius pictus</i>		<i>Ophiodon elongatus</i>		<i>Hexagrammos lagocephalus</i>		<i>Hexagrammos decagrammus</i>	
	Local	Geographic	Local	Geographic	Local	Geographic	Local	Geographic
Precaudal vertebrae....	5(17)	7(25)	5(26)	9(36)	6(18)	1(1)	6(23)	8(31)
Caudal vertebrae.....	7(20)	3(12)	6(29)	7(34)	8(28)	9(17)	7(27)	7(29)
Total vertebrae.....	9(32)	8(28)	8(34)	8(35)	9(38)	8(16)	9(33)	9(32)
Dorsal spines.....	4(13)	6(18)	4(22)	5(23)	3(10)	4(4)	4(15)	6(27)
Dorsal soft rays.....	1(2)	2(11)	2(7)	3(21)	1(4)	7(10)	1(5)	2(9)
Total dorsal rays.....	8(24)	5(15)	7(30)	4(22)	7(26)	6(6)	8(31)	5(26)
Anal rays.....	3(6)	1(7)	3(9)	2(20)	2(8)	5(5)	3(14)	1(8)
Pectoral rays.....	6(19)	9(30)	9(35)	8(33)	5(16)	2(2)	2(11)	3(19)
Lateral line pored scales.....	2(3)	4(13)	1(1)	1(14)	4(12)	3(3)	5(21)	4(24)
Rank correlation coefficient within species.....	0.567		0.683		0.300 ¹		0.800	
Rank correlation coefficient over the four species.....	0.598							

¹ Rank correlation coefficient=0.783 if Oriental sample is excluded.

variation geographically. This finding is schematized in figure 1. The ranking of species is similar whether the sectional counts are used or not. The variation data for *H. lagocephalus* emphasize, once again, the meristic differences between representatives from the eastern Pacific (formerly *H. superciliosus*) and those from the Orient (table 5). East-west variation accounts for much of the very high values attributed to *H. lagocephalus*, and the values correspond much more closely to those of the other species when the Oriental sample is excluded.

DISCUSSION

Meristic variation in fishes apparently has its basis in a number of processes, the relationships between some of which are not clear. Variations in the process of body segmentation during ontogeny are probably the basic source of variation in those counts that may be termed meristic in the strict sense. Vertebrae are laid down relatively early in life and are subject to fewer extraneous influences than meristic characters fixed later in ontogeny. Counts of total vertebrae, therefore, reasonably may be expected

TABLE 5.—Geographic variation relative to local variation for all hexagrammid species assessed

[Degree of geographic variation relative to local variation averaged over all characters of each species (see text). Data for total counts column excludes the sectional counts (precaudal and caudal vertebrae; dorsal spines and soft rays). I=index of geographic variation for each species character divided by the corresponding index of local variation]¹

Species	All counts				Total counts only			
	Z I	Number characters	Average I	Rank	Z I	Number characters	Average I	Rank
<i>Oxylebius pictus</i>	10.27	10	1.03	2	5.95	6	0.99	3
<i>Ophiodon elongatus</i>	6.82	9	.76	4	4.52	5	.90	4
<i>Hexagrammos agrammus</i>	3.56	7	.51	7	2.50	5	.50	6
<i>H. otakii</i>	4.96	7	.71	5	4.24	5	.85	5
<i>H. stelleri</i>	5.87	10	.59	6	2.94	6	.49	7
<i>H. octogrammus</i>	2.86	10	.29	8	2.11	6	.35	8
<i>H. lagocephalus</i> ²	24.09	10	2.41	1	15.22	6	2.54	1
<i>(H. lagocephalus)</i> ³	(8.21)	(10)	(.82)	(3)	(4.69)	(6)	(.78)	(5)
<i>H. decagrammus</i>	9.43	10	.94	3	6.44	6	1.07	2

¹ Arrangement of species-character indices about the median for all indices in a 2 x 8 table indicates that the species distributions are highly unlikely on the basis of chance (chi square=27.4; 99.5 percentile=20.3) and that ranking is justified. Rank correlation analysis between the arrays in the columns all counts and total counts only indicates close correlation ($r_s=0.96$; 1 percent critical value=0.53). (Tests and confidence levels from Dixon and Massey, 1951.)

² All samples.

³ Oriental sample excluded.

to be the least variable of the meristic characters, a conclusion borne out not only by the hexagrammid variation coefficients (fig. 12) but also by the comparison of hexagrammid coefficients with those for fishes in other families and orders (table 2).

Hubbs (1926) suggested that increased meristic counts in northern representatives of fishes of the northern hemisphere could be caused by dissimilar effects of low temperatures on embryonic rates of growth and differentiation. He theorized that both rates were slowed by lower temperatures but that differentiation was slowed more than growth, with the result that the embryo was larger at the time that differentiation of the counts took place. In later papers Hubbs theorized that a larger number of meristic elements result in the organs of such an embryo because of the greater amount of actual tissue space available when the meristic elements are formed. This explanation is contingent on the assumption that the meristic elements are of roughly the same size in embryos developing at colder temperatures or, as stated by Hubbs and Hubbs (1945, p. 268), "that meristic elements such as vertebrae, scales, and fin rays are laid down at a relatively constant distance apart, in absolute terms, and that the number of

elements depends on the space available, up to the time when development stops."

A large number of papers have been published on the subject since Hubbs proposed his theory (for a review see Gordon, 1957), but to my knowledge no one has tested Hubbs' theory by measuring the developing segments in groups of fish embryos that have developed under differing environmental conditions. Another pertinent question is whether meristic variation finds its expression in the entire series of a meristic count or whether it is concerned mainly with variation in the occurrence of terminal elements, as indicated by Hubbs and Hubbs (1945) and McHugh (1950). Ford (1937) believed that variation in the ultimate centra in the vertebral column was the usual cause of variation in vertebral count, but he also cited some examples of variation in vertebrae at the beginning of the column, implying that in some perciform species the centra may be added either at its beginning or at its end. Seymour (1959), however, found nearly equal frequencies of abnormal vertebrae in both caudal and precaudal regions of experimentally reared chinook salmon (*Oncorhynchus tshawytscha*).

The relationship between changes in numerical counts through variation and their changes through evolution should be a fertile field for study. The hexagrammid species form a series in which increase in meristic count parallels habitation of colder waters, both intraspecifically and interspecifically. Neither interspecific increase in vertebral counts through geographic variation nor intraspecific variation in these counts is confined to the posterior region of the vertebral column. It seems likely that several processes, at least, are involved in meristic variation as expressed by vertebral number, and that the addition or loss of vertebrae through the fusion of elements at the ends of the vertebral column may sometimes be but an environment-induced change that takes place when the embryo is not developing under environmental conditions to which the population is genetically adjusted.

It appears that the variation of samples may be of value as an index of the degree to which a population has adapted to local conditions. In two examples, at least, fish populations reared in artificial situations were more variable than those reared in natural situations. In both *Fundulus*

heteroclitus (table 2) and *Etheostoma exile*,² vertebral variation was considerably higher in samples from modified environments than it was in samples of the same or closely related species from natural situations. Further support for the use of variation as an index to adaption may be found in the data of Seymour (1959). Although Seymour did not analyze his data from the standpoint of variation, such an analysis definitely indicates that batches of chinook salmon eggs reared at temperatures above or below those at which the eggs normally develop produce embryos with significantly increased variation in number of vertebrae (fig. 13).

In accordance with the large proportion of the data reported in the literature, it appears that the intraspecific geographic variation in the Hexagrammidae is temperature correlated. In general, water temperatures decline northward along the eastern and western coasts of the North Pacific Ocean and are lowest in the Bering Sea and in the Sea of Okhotsk (U.S. Navy Hydrographic Office, 1944). In some eastern temperate coastal regions, particularly off northwest-southeast coastlines and south of projecting headlands, this pattern is disturbed somewhat by the upwelling of colder waters and by the local warming of partly enclosed waters. The geographic variation in the meristic characters of the hexagrammids usually parallels this general geographic gradient in ocean temperatures, and the four species with the most extensive north-south distributions show the largest differences in their counts. Conclusive evidence of temperature-correlated variation in this family is still lacking, however, because little is known about the natural range of temperatures at which hexagrammid eggs develop. At present it only may be surmised that more northerly representatives of the species undergo lower temperatures at sensitive periods of development, such as those described by Tåning (1952). The environmental factors of salinity, oxygen tension, and carbon-dioxide tension, as listed by Gordon

² Bailey and Gosline (1955) did not refer to the artificial circumstances involved in the rearing of the *Etheostoma exile* population that they cite. These vertebral data are included in a long list of similar data on populations of other percid species that, presumably, were taken in the field. However, the *E. exile* data are the same as those analyzed by Gosline for an earlier paper (1947), and were taken on specimens (called *Poecilichthys exilis* at that time) which had been reared in a hatchery pond that was protected from predators. Gosline stated that the population was possibly not a natural one and that an unusually high percentage of abnormal specimens had been found. The unusually high variation values that I calculated from Gosline's data (table 2) support this supposition.

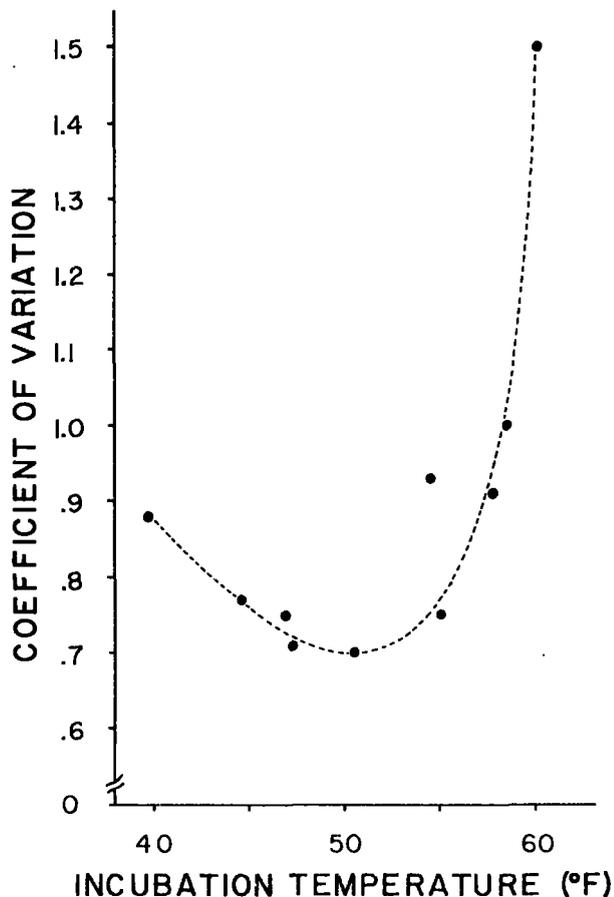


FIGURE 13.—Vertebral variation in batches of chinook salmon, *Oncorhynchus tshawytscha*, reared at different temperatures. Above and apparently below the middle range of temperatures (from 45° to 55° F.), variation increased markedly in the surviving young. Data fitted by eye. (Calculated from Seymour, 1959.)

(1957), probably can be eliminated as a cause of the variation observed in hexagrammids. Available information indicates that the larvae are pelagic and that juveniles and adults occupy rocky open-coast intertidal and subtidal habitats, both of which probably are quite uniform in salinity and dissolved gases, regardless of latitude. If temperature is proved to be directly or indirectly responsible for much of the intraspecific meristic variation in the Hexagrammidae, its role in the interspecific meristic differences in the family should also be investigated. It is possible that a part of the important meristic differences that characterize hexagrammid species also is due,

again directly or indirectly, to the range of temperatures at which a particular species develops.

Geographic variation in the Hexagrammidae differs in at least one important aspect from experimental results reported by Molander and Molander-Swedmark (1957) and Tåning (1952). These authors indicated that for a trout and a flatfish species respectively the means of all meristic counts do not vary in the same direction with higher or lower temperatures. Molander and Molander-Swedmark found that the means of vertebrae are lower in batches of larvae raised at 8° C. than in batches raised at 6° C., which is the opposite of the trend of variation in dorsal ray and anal ray means over this temperature range. Similarly, vertebra and fin ray means vary in opposite directions in Tåning's experiments. In contrast, the direction of geographic variation of these characters in the Hexagrammidae is largely consistent between characters. Similar results are reported by Hubbs and Hubbs³ in their extensive analysis of geographic variation in the cottid *Leptocottus armatus* in which the means for all meristic counts also decline toward the south. The general trend of geographic variation exemplified by the hexagrammids and *L. armatus* is commonly observed but is not universal. For example, the pattern of geographic variation reported for *Gobius* by Johnsen (1936) shows opposing trends between the means of total dorsal rays and total vertebrae on the one hand and those of pectoral counts and total vertebrae on the other. Such an inverse relationship between the total counts was shown in only one instance among the hexagrammids (pectoral and anal rays in *H. agrammus*), and the relationship may be fortuitous.

Little is known about the causal mechanism behind variation. It appears, however, that numerical characters other than somites and their functionally associated vertebrae probably have at least two sources of variation in addition to those to which vertebrae are subject. On the one hand, these characters follow the vertebrae in time of differentiation, and the formative tissues are therefore susceptible to environmental influence for a greater period of time before the number

of elements is fixed. As an extreme example, the number of gill rakers, which appears to be the latest count to be fixed in many fishes (and rakers may continue to be added or lost with growth into adult life), is the most variable numerical character assessed in the Hexagrammidae. On the other hand, variability of a count also seems highly dependent on the anatomical relationships of the elements making up the count. The relationship seems somewhat analogous to the statistical concept of degrees of freedom. The number of vertebral elements corresponds closely to the number of somites and may be described as having but one source of variation (with the somites), or one degree of freedom. The total count of dorsal rays has additional possible sources of freedom in many perciform fishes because elements may be either added or lost at both the anterior and posterior ends of the fin. In the hexagrammid fishes, however, the dorsal fin gains only one degree of freedom over the vertebrae, because the fin spines and their inter-neurals occupy all available spaces at the insertion of the fin, and the number of spines corresponds closely to the number of anterior interneural spaces. In these fishes there is little opportunity for variation at the fin's anterior insertion. Similarly, the hexagrammids show no variation in addition or loss of fin elements with respect to the number of vertebral elements within the fin (in *Ophiodon elongatus* one element seems to be consistently lacking). The one additional source of variation in number of total dorsal elements over number of vertebrae in these fishes lies in the addition or deletion of elements at the posterior end of the fin. The total elements in the dorsal fin of hexagrammids thus may be characterized as having two degrees of freedom. Because of the variable fate of adjoining rays separating the spinous and soft portions, the spinous dorsal fin of these fishes also has two degrees of freedom. The soft-rayed fin, however, like the anal fin, probably is able to gain or lose elements at either end, and thus may be characterized as having three degrees of freedom.

Hubbs and Hubbs (1945) held that the pectoral rays vary entirely at the lower part of the fin in *L. armatus*. Carl L. Hubbs states (personal communication, 1961), "I believe that it is usually not true that elements may be added at both ends, as in the dorsal and anal. It does

³Hubbs, Carl L., and L. C. Hubbs. Analysis of meristic variation in *Leptocottus armatus*, a fish of western North America. Manuscript being prepared for publication, Scripps Institution of Oceanography, La Jolla, Calif.

seem that this does occur in the first dorsal of darters (as *E. exile*), in which the front of the fin slopes down, with no specialized elements But usually the front ray(s) is (are) specialized and fixed as in an anal fin with I, II, or III spines (depending on the species) or in the pectoral fin with the uppermost ray specialized (one short; the next long, thick, unbranched). The anal fin is usually fixed in front of the posterior of the anus and by vertebral connections." He adds. "If the variation in pectoral rays was at either end, then it wouldn't be the almost universal rule that the lowest (i.e., morphologically most posterior) ray is the shorter on the side with the higher number of rays." However, an unstable forward position of a fin's anterior formative tissue may have little to do with the later formation of the specialized anterior fin elements, which merely will appear one or more somites removed from their usual position. The insertions of dorsal and anal fins certainly have changed materially in the evolution of the various perciform fishes; a strong argument that the somites of insertion are subject to variation as well as the other morphological characteristics of fishes. Furthermore, specialized elements such as anal fin spines do vary in number in some perciform fishes, in eight of nine hexagrammid species, for example, anal spines vary over two or three units. Also, the variation in the number of the first vertebral element bearing the first haemal spine (presumably one cause of reciprocal variation in numbers of precaudal and caudal vertebrae) argues against the specialized anterior portion of the anal fin being fixed completely serially in respect to the vertebral column. Although Hubbs' argument concerning the last element in the pectoral fins seems persuasive, it applies mainly to the length of the formative tissue at the time of meristic differentiation and may have little to do with whether the formative tissue is shifted forward or backward one or two somites or whether the tissue is "longer" because the tissue for additional elements is added anteriorly, posteriorly, or medially.

The methods of variation study utilized in my paper are admittedly crude in comparison with refinements that would have been possible were the study more limited in scope and more specimens available. It is evident from the data presented that the variation in samples is influenced by the type of sample chosen and that a hierarchy

of values may be constructed from data obtained by different sampling methods. If geographic variation occurs, it is the same as saying that the value for the variation of all samples of a character, when lumped, is greater than the variation in regional samples, which, in turn, should exceed that of local samples. Local samples should be less variable than regional assortments because the geographic component of variation should decrease as the samples are limited to a narrower geographic range. Theoretically, further reduction of variation by more restrictive sampling is possible. Local samples drawn from a single year class should reduce the amount of variation over samples drawn from several year classes, especially where environmental conditions change appreciably from year to year. In a single instance of this type available among the hexagrammids, a large sample of a single year class of *Ophiodon elongatus* from San Francisco Bay (figs. 2 to 11) yielded considerably lower values for variation in most of its meristic elements than mixed samples taken elsewhere along the species range.⁴ Even further reductions in the variation of samples may occur with more selective sampling. Significant differences between meristic counts in samples of a year class taken from individuals spawned early and late in the spawning season have been reported for numerous fishes from both fresh-water habitats (Hubbs, 1922 and 1924) and salt-water habitats (Hubbs, 1925, and Hubbs and Hubbs, 1954). Even the variation in a sample of fish spawned at the same time and place may be lessened. Mottley (1934 and 1937) demonstrated lower values for variation in samples of siblings of *Salmo* spp. than in samples of a single year class from mixed parentage. In conclusion, because of this hierarchy of values for character variation that depends on the type of sample chosen, it is important that the sampling method be kept in mind when comparisons of variation are being made.

It is difficult to assess what relationship, if any, exists between the number of lateral line pored scales and the number of somites; and the hexagrammids are not analyzed in this regard. Scales are laid down late in ontogeny, and their number is subject to an undetermined set of influences

⁴ However, the year-class differences in variation are nearly restricted to the characters that also show geographic variation (dorsal spines, dorsal soft rays, total dorsal rays, and total anal rays). This adds weight to the foregoing observations concerning a positive relationship between local and geographic variation.

after the fixation time of the somites, with the result that nearly all mechanical correspondence between the two meristic series, such as that described for fin rays and vertebrae, may be lost.

SUMMARY AND CONCLUSIONS

The following conclusions are based on all available samples of the species. While the specimens are numerous in the aggregate, some samples were necessarily small and inadequate for conclusive testing of the hypotheses. Therefore these are provisional conclusions that must await intensive examination of large series of specimens for final substantiation.

1. There is significant geographic variation in the means of some meristic counts in all eight of the hexagrammid species investigated.

2. The species differ in the number of meristic characters that vary geographically; even similar species differ in this respect in overlapping portions of their geographic ranges.

3. Geographic variation in meristic counts probably is related directly or indirectly to environmental temperatures over the geographic ranges.

4. Geographic variation in the number of gill rakers does not appear to be correlated with the variation of those characters associated with the body somites.

5. The variation shown by meristic characters is remarkably consistent for each character, not only for the different regions occupied by a single species but also between the eight hexagrammid species studied.

6. Meristic variation in the Hexagrammidæ usually is as low as or lower than that calculated from the data for other fishes randomly selected from the literature.

7. Despite the general consistency of variation shown by each character within and between hexagrammid species, two species differ significantly in overall variation (as measured by the coefficient of variation) from the family averages. The most primitive representative, *Oxylebius pictus*, generally is the most variable, whereas the highly specialized *Hexagrammos decagrammus* is less variable than the average of species of the family in 13 out of 15 characters. However, no other examples of correlation were found between overall variation in the hexagrammid

species and subjective estimates of their specializations.

8. In species exhibiting marked geographic variation, the variation of different meristic characters within regional samples is positively correlated with the degree of geographic variation.

9. The coefficient of variation may be of some value in assessing how well fish populations are adapted to environmental conditions during embryonic stages.

10. The hypothesis is presented that both the time of fixation and the structural relations of the meristic parts are operative in creating differences in variation in meristic characters.

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LITERATURE CITED

- BADER, ROBERT S.
1955. Variability and evolutionary rate in the oreodonts. *Evolution*, vol. 9, No. 2, pp. 119-140.
- BAILEY, REEVE M., AND WILLIAM A. GOSLINE.
1955. Variation and systematic significance of vertebral counts in the American fishes of the Percidae. University of Michigan, Ann Harbor, Museum of Zoology, Miscellaneous Publication 93, 44 pp.
- BROWN, JERRAM L.
1958. Geographic variation in southeastern populations of the cyprinodont fish, *Fundulus notti* (Agassiz). *American Midland Naturalist*, vol. 59, No. 2, pp. 477-488.
- CRAWFORD, RONALD W.
1956. A study of the distribution and taxonomy of the percid fish, *Percina nigrofasciata* (Agassiz). Tulane University, New Orleans, Tulane Studies in Zoology, vol. 4, No. 1, 55 pp.
- DIXON, WILFRID J., AND FRANK J. MASSEY, JR.
1951. Introduction to statistical analysis. McGraw-Hill Book Company, Inc., New York, 370 pp.
- FORD, E.
1937. Vertebral variation in teleostean fishes. *Journal of Marine Biological Association of the United Kingdom*, vol. 22, No. 1, 60 pp.
- GABRIEL, MORDECAI L.
1944. Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*. *Journal of Experimental Zoology*, vol. 95, No. 1, pp. 105-147.

- GIBBS, ROBERT H., JR.
 1957a. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. II. Distribution and variation of *Notropis spilopterus*, with the description of a new subspecies. *Lloydia*, vol. 20, No. 3, pp. 186-211.
 1957b. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. III. Variation and subspecies of *Notropis venustus* (Girard). Tulane University, New Orleans, Tulane Studies in Zoology, vol. 5, No. 8, pp. 175-203.
- GORDON, MYRON.
 1957. Physiological genetics of fishes. In the physiology of fishes. Margaret E. Brown (editor), vol. 2. Academic Press, New York, 526 pp.
- GOSLINE, WILLIAM A.
 1947. Some meristic characters in a population of the fish *Poeciliichthys exilis*: their variation and correlation. University of Michigan, Ann Arbor, Museum of Zoology, Occasional Papers, No. 500, 23 pp.
- HUBBS, CARL L.
 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. *American Naturalist*, vol. 56 (July-August), pp. 360-372.
 1924. Seasonal variation in the number of vertebrae of fishes. *Papers of the Michigan Academy of Science, Arts, and Letters*, vol. 2 (1922), pp. 207-214.
 1925. Racial and seasonal variation in the Pacific herring, California sardine and California anchovy. State of California Fish and Game Commission, Fish Bulletin No. 8, 23 pp.
 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. *American Naturalist*, vol. 60 (January-February), pp. 57-81.
- HUBBS, CARL L., AND LAURA C. HUBBS.
 1945. Bilateral asymmetry and bilateral variation in fishes. *Papers of the Michigan Academy of Science, Arts, and Letters*, vol. 30, 310 pp.
 1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an embiotocid fish of the Californias. *California Fish and Game*, vol. 40, No. 2, pp. 183-198.
- HUBBS, CARL L., AND KARL F. LAGLER.
 1949. Fishes of the Great Lakes region. Cranbrook Institute of Science, Bloomfield Hills, Mich., 186 pp.
- JOHNSON, SIGURD.
 1936. On the variation of fishes in relation to environment. Bergens Museums Årbok Naturvidenskapelig Rekke, 4 hefte, 26 pp.
- MATSUBARA, KIYOMATSU.
 1943. Studies on the scorpaenoid fishes of Japan (II). *Transactions of Sigenkagaku Kenkyusyo*, No. 2, pp. 171-486.
- McHUGH, JOHN L.
 1950. Variations and populations in the clupeoid fishes of the North Pacific. Ph.D. Thesis, University of California at Los Angeles, 116 pp.
- MOLANDER, ARVID R., AND MARTHA MOLANDER-SWEDMARK.
 1957. Experimental investigations on variation in plaice (*Pleuronectes platessa* Linne). Reports Lysekil Institute of Marine Research (Biology) No. 7, 44 pp.
- MOTTLEY, C. McC.
 1934. The effect of temperature during development on the number of scales in the Kamloops trout, *Salmo kamloops* Jordan. *Contributions to Canadian Biology and Fisheries* (A, general, No. 41), vol. 41, No. 8, pp. 255-263.
 1937. The number of vertebrae in trout (*Salmo*). *Journal of Biological Board of Canada*, vol. 3, No. 3, pp. 169-176.
- PRASAD, RAGHU R.
 1958. Racial analysis of *Clevelandia ios* (Jordan and Gilbert) in California waters. *American Midland Naturalist*, vol. 59, No. 2, pp. 465-476.
- QUAST, JAY C.
 1960. The fishes of the family Hexagrammidae: their classification, variation, and osteology. Ph.D. Thesis, University of California at Los Angeles, 380 pp.
- RANDALL, JOHN E.
 1955. A revision of the surgeon fish genus *Ctenochaetus*, family Acanthuridae, with descriptions of five new species. *Zoologica*, vol. 40, part 4, pp. 149-166.
 1956. A revision of the surgeon fish genus *Acanthurus*. *Pacific Science*, vol. 10, No. 2, pp. 159-235.
- RANEY, EDWARD C.
 1957. Subpopulations of the striped bass, *Roccus saxatilis* (Walbaum), in tributaries of Chesapeake Bay. In U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, John C. Marr (editor), No. 208, pp. 85-107.
- SCHMIDT, P. U.
 1950. Fishes of the Sea of Okhotsk. *Akademiia Nauk, SSSR, Moscow*, 370 pp.
- SEYMOUR, ALLYN.
 1959. Effects of temperature upon the formation of vertebrae and fin rays in young chinook salmon. *Transactions of the American Fisheries Society*, vol. 88, No. 1, pp. 58-69.
- SIMPSON, GEORGE GAYLORD.
 1953. The major features of evolution. Columbia University Press, New York, 434 pp.
- SIMPSON, GEORGE GAYLORD, ANNE ROE, AND RICHARD D. LEWONTIN.
 1960. Quantitative zoology. Harcourt, Brace and Company, Burlingame, New York, 440 pp. [Revised edition.]
- STRASBURG, DONALD W.
 1955. North-south differentiation of blennioid fishes in the central Pacific. *Pacific Science*, vol. 9, No. 3, pp. 297-303.

TÅNING, Å. VEDEL.

1952. Experimental study of meristic characters in fishes. Biological Reviews of the Cambridge Philosophical Society, vol. 27, No. 2, pp. 169-193.

TAYLOR, FREDERICK H. C.

1957. Variations and populations of four species of

Pacific Coast flatfish. Ph.D. Thesis, University of California at Los Angeles, 351 pp.

UNITED STATES NAVY HYDROGRAPHIC OFFICE.

1944. World atlas of sea surface temperatures.

Publication 225, 2d edition.

MOVEMENTS, GROWTH, AND RATE OF RECAPTURE OF WHITEFISH TAGGED IN THE APOSTLE ISLANDS AREA OF LAKE SUPERIOR

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ABSTRACT

A total of 1,303 whitefish were marked with spaghetti streamer tags in Wisconsin waters of Lake Superior in November of 1959, 1960, and 1961 and June–July 1960. The fish tagged in June–July 1960 were mostly undersized (less than 17 inches long) whereas those captured on the spawning grounds and tagged in November 1959–61 were almost all legal size. Of the 374 recoveries (28.7 percent), nearly all were made during the first 2 years after tagging. The earliest returns were from fish which were among the largest when tagged. Over one-half of the recoveries were made within 5 miles of the tagging site; the greatest distance traveled by an

individual was 25 miles. The fish tagged in June–July 1960 grew 1.6 inches the first season and 1.2 the second. Of 27 whitefish recaptured within 6 months from the November 1959–61 group, 17 (63 percent) had lost length (range from decrease 0.1 to 1.4 inches). Whitefish of the June–July group recaptured during the second growing season after tagging gave an exploitation rate of 22.6 percent. First-year returns from the November 1959–61 tagging gave an exploitation rate of 20.5 percent. The true exploitation rate probably is higher since no allowance has been made for tagging mortality, loss of tags, or unreported recaptures.

The production of whitefish, *Coregonus clupeaformis* (Mitchill), in the U.S. waters of Lake Superior declined from over 4½ million pounds in 1885 to 113,000 pounds in 1913, the lowest production recorded. Since 1913 the catch has fluctuated widely; the take exceeded 1 million pounds in 1948–50 and 1954–55 but dropped to 284,000 pounds in 1960.

The production of whitefish in Wisconsin waters of Lake Superior has contributed about 35 percent to the total U.S. output in the lake over the past 50 years. The Apostle Islands region provides nearly all of Wisconsin's production.

The progressive decline of the lake trout (*Salvelinus namaycush*) since 1955, followed by the complete closure of the lake trout fishery in 1962, has made the whitefish of increased importance to the economy of Wisconsin commercial fishermen. Sound management and rational exploitation should be based on a thorough knowledge of the

species. The present paper is a contribution to this knowledge.

The first tagging study of whitefish in Lake Superior was in 1951 when staff members of the Fish and Wildlife Service marked 208 undersized (then less than 2 pounds) whitefish with nylon-streamer tags off Bete Grise, Mich. Only 23 fish (11 percent) were recaptured, all within 2 months after tagging. Except for one fish which had traveled 40 miles, all recoveries were made within 20 miles of the tagging site.

In 1955–59, the Wisconsin Conservation Department tagged 2,400 whitefish in the Apostle Islands region. Only 78 recoveries (3.3 percent) were reported, nearly all within 1 year after tagging. All of the recaptured fish were reported from the Apostle Islands region.

The limited recovery of the whitefish tagged by Wisconsin personnel was believed to reflect a high rate of tag loss. The tag used in this earlier experiment was a streamer-type attached to the

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body of the fish posterior to the dorsal fin. Nylon thread (No. 69 Nylac) was used in 1955-57, and polyethylene thread was used in 1958-59. The difference between the percentage returns of tags held by the two types of thread was negligible.

Evidence that these types of tags are lost was given by Eschmeyer (1959), who found that only 1 of 200 streamer tags attached to lake trout with No. 34 or 46 nylon thread remained intact at the end of 1 year. Budd (1957) estimated that the loss of streamer tags on whitefish tagged in South

Bay (Lake Huron), Ontario, was about 10 percent per year.

The present study is an extension of the earlier work of the Wisconsin Conservation Department. We wished to learn more about the migratory habits, growth, and exploitation rate of the Apostle Islands whitefish.

MATERIALS AND METHODS

A total of 1,303 whitefish were tagged in the Apostle Islands area during November 1959-61

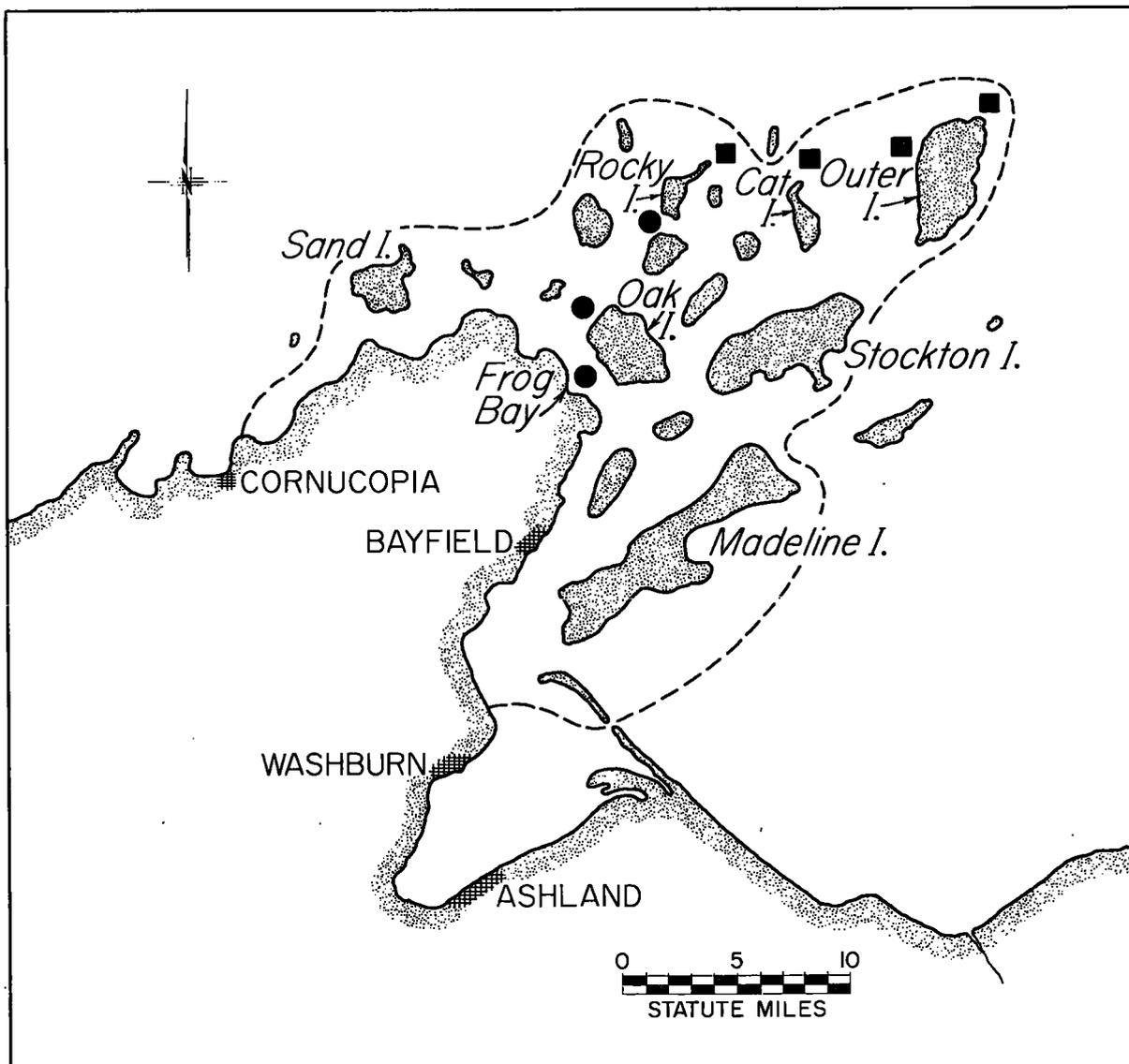


FIGURE 1.—Apostle Islands region of Lake Superior. The dots represent locations where whitefish were tagged in June-July 1960 and the squares show locations of the November 1959-61 tagging. All recoveries were made within the dotted line.

TABLE 1.—Number of whitefish tagged in the Apostle Islands region according to location and date, and the number and percentage of recaptures from each tagging, 1959-61

Item	Tagging locality						Length when tagged	
	Rocky Island	Oak Island	Frog Bay	Cat Island	Outer Island	All locations	Average	Range
June-July 1960:								
Number tagged.....	455	563	104	-----	-----	1,122	Inches 15.4	Inches 10.6- 17.4
Number recaptured.....	139	169	21	-----	-----	329	-----	-----
Percentage recaptured.....	30.5	30.1	20.2	-----	-----	29.3	-----	-----
November 1959-61:								
Number tagged.....	73	-----	-----	96	12	181	18.8	16.0- 23.7
Number recaptured.....	20	-----	-----	20	5	45	-----	-----
Percentage recaptured.....	27.4	-----	-----	20.8	41.7	24.9	-----	-----
All dates:								
Number tagged.....	528	563	104	96	12	1,303	15.9	10.6- 23.7
Number recaptured.....	159	169	21	20	5	374	-----	-----
Percentage recaptured.....	30.1	30.0	20.2	20.8	41.7	28.7	-----	-----

and June-July 1960 (table 1, fig. 1). The 1,122 fish tagged in June-July 1960 were collected in commercial pound nets (50-70 feet deep, 4¼-inch-mesh pot); the remaining 181 whitefish came from large-mesh gill nets (from 4½- to 5½-inch mesh) fished on the whitefish spawning grounds from the Bureau of Commercial Fisheries research vessel *Siscowet*. One purpose of tagging spawning-run fish was to detect possible "homing" behavior.

The tag—a spaghetti streamer—used in this experiment was a modification of the type used by Wilson (1953) for marking tuna. It consisted of a vinyl plastic tube (outside diameter, 0.094 inch) with a yellow plastic disc attached to one end. A stainless steel tube served as a needle for piercing the back of the fish just posterior to the dorsal fin. The tubing was placed inside the steel needle; as the needle passed through the fish, the tag was carried through with it. The ends of the plastic tubing were joined by a small metal clamp, similar to a bird band. No reward was offered for the return of the tags. Although the inscription on the plastic disc instructed that the tags be forwarded to the Bureau's Biological Laboratory in Ann Arbor, Mich., most were sent directly to the field station at Ashland, Wis.

The whitefish tagged from pound nets in the summer of 1960 ranged from 10.6 to 17.4 inches long (average, 15.4 inches). The spawning-run

fish tagged aboard the *Siscowet* were considerably larger (16.0-23.7 inches; average, 18.8 inches).

Most of the returns (296) came from the intensive summer pound net fishery, and the remainder (78) from large-mesh gill nets fished under the ice during the winter. The percentage of recoveries from the various tagging locations and dates varied little. Among groups of 40 or more fish tagged at one location, the percentage return ranged from 20.2 to 30.5. The total percentage return was 28.7 for all tagging combined.

The number of tag returns used for various phases of this study varies according to the information received with the tags. Complete data, i.e., date and location of capture and length of the fish were reported with most of the returns. Some reports, however, were incomplete and their usefulness was limited according to the information received. Because reports of recoveries declined sharply in the summer of 1962 the study was terminated December 31, 1962. I felt that the few additional returns that might be reported after this date would not influence the results appreciably.

TIME BETWEEN TAGGING AND RECOVERY

The time between tagging and recovery for Apostle Islands whitefish was influenced by seasonal fishing pressure and by the size of the fish when tagged. The recaptures from the group tagged in June-July 1960 were highest during the summer pound net fishery of 1961. Since whitefish tagged in June-July 1960 were mostly undersized and returned to the lake if captured, returns from them were few during the first several months out.

The percentage of whitefish recaptured from the June-July 1960 group (table 2) increased from 6.3 percent during the first 10 months (July-April) to 19.8 percent during the 11- to 22-month (May-April) period. The cumulative percentage recovered was 26.1 percent at the end of 22 months, only 3.3 percent below the final percentage (29.4 percent) at the end of 29 months. Of the 37 recoveries made after 22 months, only 4 were reported later than 24 months. The percentage of the total number recaptured was also highest (67.3 percent) during the 11- to 22-month period and the cumulative percentage of the total stood at 88.8 percent at the end of 22 months.

TABLE 2.—Recoveries of whitefish tagged in June–July 1960 according to length of time at liberty

Item	Time out (months)		
	<11	11–22	23–29
Number recaptured.....	71	222	37
Percentage recaptured.....	6.3	19.8	3.3
Cumulative percentage.....	6.3	26.1	29.4
Percentage of total recoveries.....	21.5	67.3	11.2
Cumulative percentage.....	21.5	88.8	100.0

Of the 43 returns from fish tagged during the fall spawning season (November) in 1959–61 (table 3), all but 5 were reported during the first 12 months (20 were taken during the first 5 months in the winter fishery, and 18 in the following 12 months). No recoveries were made after 20 months. The cumulative percentage of recapture was 20.9 percent at the end of 12 months, only 2.8 percent below the total percentage return of 23.7. The percentage of the total recaptured was highest during the first 5 months, and the cumulative percentage stood at 88.4 percent at the end of 12 months.

The small number of returns after the first year for fish tagged in November 1959–61 and after the second year for the June–July 1960 group suggests either a high rate of tag loss or a heavy natural mortality.

DISTANCES TRAVELED

The distances traveled by tagged whitefish were relatively small regardless of the time between tagging and recapture. Of the small whitefish tagged in June–July 1960, 142 fish (64.6 percent of the total recoveries) were recaptured at distances less than 5 miles from the tagging site (table 4). Only 19 fish (8.6 percent) had traveled more than 10 miles, and the greatest distance traveled by an individual was 17 miles.

More than half (56.5 percent) of the recoveries of the larger whitefish tagged during the fall spawning seasons were within 5 miles of the tagging site, but 26.1 percent (6 fish) traveled more than 10 miles. The greatest distance traveled by a whitefish tagged during the spawning run was 25 miles. The *Siscowet* recovered only one whitefish which had returned to spawn on the same grounds where it was tagged.¹

¹ Since the completion of this report the Wisconsin Conservation Department has given me records of the recapture in 1963 of six whitefish from the spawning grounds on which they were tagged.

TABLE 3.—Recoveries of whitefish tagged in November 1959–61 according to length of time at liberty

Item	Time out (months)		
	<6	6–12	>12
Number recaptured.....	20	18	5
Percentage recaptured.....	11.0	9.9	2.8
Cumulative percentage.....	11.0	20.9	23.7
Percentage of total recoveries.....	46.5	41.9	11.6
Cumulative percentage.....	46.5	88.4	100.0

TABLE 4.—Recoveries of tagged whitefish according to distance traveled from tagging site

Tagging period and item	Distance traveled (miles)			
	<5	5–10	>10	Greatest distance
June–July 1960:				
Number recaptured.....	142	59	19	17
Percentage of total recaptures.....	64.6	26.8	8.6	-----
Cumulative percentage.....	64.6	91.4	100.0	-----
November 1959–61:				
Number recaptured.....	13	4	6	25
Percentage of total recaptures.....	56.5	17.4	26.1	-----
Cumulative percentage.....	56.5	73.9	100.0	-----

Since the major portion of the pound net fishery in the Apostle Islands is concentrated within a 20-mile radius of Bayfield, Wis., it was to be expected that most of the recoveries would come from that area. Gill nets, on the other hand, are fished along the entire south shore of Lake Superior. Had the whitefish migrated greater distances, recoveries should have been made outside the Apostle Islands region.

The lack of recoveries from outside the Apostle Islands region supports Dryer's (1963) suggestion, based on growth data, that the whitefish in the Bayfield region are one of a number of distinct stocks in Lake Superior. These stocks of fish have characteristic growth rates (Apostle Islands and Munising Bay stocks grow extremely slowly in comparison with those from Marquette and Whitefish Bay).

Smith and Van Oosten (1940) reported that of 101 returns from 457 whitefish tagged in Lake Michigan, only 4 were recovered at distances greater than 25 miles. They further indicated that no correlation could be found between distances traveled and time out. Budd (1957) reported that one whitefish had traveled 150 miles from the tagging site in South Bay, Lake Huron. His tag returns suggested, however, that the South Bay stock retains its identity and that fish return to South Bay during the winter or early spring.

It is, of course, impossible to determine the distance traveled before an individual was recaptured. A whitefish recaptured 2 years after tagging at a point only 5 miles from the tagging site certainly could have moved extensively at some time during the 2-year interval.

GROWTH OF TAGGED WHITEFISH

The data on growth in length of tagged whitefish are summarized according to group of fish tagged and the number of growing seasons completed before recapture. Since the growth rates and recapture dates for whitefish tagged in June-July 1960 differed from those for fish tagged during the November spawning season in 1959-61, the two groups are kept separate for the discussion of growth in length.

The number of growing seasons completed for recaptured whitefish was determined as follows: fish from the June-July 1960 group which were recovered during the following November-June (5-12 months out) were considered to have completed 1 growing season; those fish which were out 17-24 months after tagging had completed 2 growing seasons. Since annulus formation occurs in mid-June for Lake Superior whitefish (Dryer, 1963), some of the fish conceivably may have completed a small amount of the current season's growth before they were tagged. This small growth, if any occurred, should not seriously impair the data on the first year's growth.

The estimates of growth of individual whitefish are the differences between lengths at recapture reported by commercial fishermen and lengths at tagging, measured by staff members. The measurements at tagging may be considered accurate within the normal limits of error common to field operations. The dependability of measurements by commercial fishermen doubtless varies from individual to individual. Many fishermen do not carry a ruler or yardstick but have a board with a mark at 17 inches, the minimum legal length for both whitefish and lake trout. The distance between this mark and the end of the tail probably was estimated for many fish to obtain the reported length. Other fish probably were measured closely. The fishermen's measurements must be recognized as less accurate than the measurements at tagging but they give a reasonably dependable estimate of average if not of individual growth.

Growth was relatively slow for the whitefish recaptured from those tagged in June-July 1960 (table 5). The increments ranged from -1.4 to 3.9 inches for fish recaptured after 1 year and from 0.9 to 7.4 inches for those recaptured after 2 growing seasons. The average increment of length was 1.6 inches for fish out 1 growing season and 2.8 inches for those out 2 growing seasons.

Since most of the whitefish tagged in June-July 1960 were undersized (average length, 15.4 inches), few returns from them were expected until they reached the legal size of 17 inches.² It was expected further that the first returns would come from the larger fish since they would be the first to reach legal size. The average length at tagging was 15.9 inches for fish out 5-10 months, 15.5 inches for those out 12 months, and 15.1 inches for those out 24 months. Smith and Van Oosten (1940) also found that the first recoveries of tagged whitefish in Lake Michigan were from fish which were among the largest when tagged.

TABLE 5.—Distribution of length increments of tagged whitefish recovered in the Apostle Islands region by time tagged and number of growing seasons.

Increment of total length	Period of tagging and number of growing seasons		
	June-July 1960		November 1959-61
	1 season	2 seasons	<1 season
<i>Inches</i>			
7.0-7.4.....		1	
5.0-5.4.....		1	
4.5-4.9.....		2	
4.0-4.4.....		3	
3.5-3.9.....	1	3	
3.0-3.4.....	2	4	
2.5-2.9.....	16	2	
2.0-2.4.....	33	10	
1.5-1.9.....	67	4	
1.0-1.4.....	56	5	1
.5-.9.....	23	2	1
.1-.4.....	4		4
0. 0.....	1		4
-.1-.4.....	1		10
-.5-.9.....	2		6
-.1-1.4.....	1		1
Number of fish.....	207	37	27
Average length when tagged.....	15.7	15.2	18.6
Average length when recaptured.....	17.3	18.0	18.5
Average increment.....	1.6	2.8	-.1

Nearly all of the recoveries (for which length data are available) from fish tagged in November 1959-61 were made before the start of the following growing season (less than 8 months out). Many of the spawning-run whitefish recaptured during the following December-June showed a loss

² Fishermen reported releasing many undersized tagged whitefish from their pound nets during the summer of 1960.

EXPLOITATION RATE

of length. Of the 27 whitefish recaptured, 17 (63 percent) had lost length (range, from -0.1 to -1.4 inches) and 4 had the same length as at tagging. Six of the fish put on growth over the winter; the largest increase was 1.4 inches. Only 4 fish for which appropriate data are available were taken after completion of 1 growing season. The average growth for these fish was 0.9 inch (range, 0.3–2.5 inches).

Carbine and Applegate (1948) reported that 50 percent of the tagged northern pike (*Esox lucius*) recovered by anglers from Houghton Lake and Muskegon River, Mich., showed "negative growth." They considered the data erroneous and excluded them from their discussion of growth. Eschmeyer and Jones (1941) also found that fish recaptured soon after tagging in Norris Reservoir, Tenn., often had lost several millimeters in length.

Some animals can, of course, lose considerable length. Sea lampreys with their cartilaginous skeleton, for example, shrink considerably between December and the following spring (Parker and Lennon, 1956). Shrinkage offers a more difficult problem for those organisms which have an osseous axial skeleton; any loss of length of necessity is accommodated by a reduction in the distance between the successive vertebrae. Also to be considered in the apparent shrinkage in length is whether or not the fish is alive at the time of measurement after recapture. Measurements made several hours after recapture would undoubtedly reflect the normal shrinkage which occurs after death. Shetter (1936b) found that brook trout shrink about 2.6 percent due to rigor mortis.

Little doubt exists that the growth rate of fish is retarded by tags. The extent of retardation in growth depends on such factors as type of tag, location of the tag on the fish, and the species of fish tagged. Eschmeyer and Crowe (1955) reported that the annual length increments of walleyes bearing jaw tags averaged less than two-thirds those of untagged fish. Smith, Krefling, and Butler (1952) determined that walleyes bearing jaw tags had not formed an annulus in 2 years after tagging and that growth was negligible. Eschmeyer (1959) stated that the growth of lake trout in a rearing pond was retarded about 25 percent when the fish were tagged with Petersen, cheek, and lower-jaw tags.

Estimates of exploitation rates based on tagging studies may be prejudiced by various factors. The principal difficulties originate in four major sources of bias: loss of tags; tagging mortality; unreported returns; and increased vulnerability of tagged fish to fishing gear.

The first three sources of bias lead to underestimates of exploitation rates, and bias through increased vulnerability of tagged fish to fishing gear leads to overestimates. When estimates are based on the ratio of the number of fish returned to the number tagged, it is assumed implicitly that all of the tags remained intact, that all of the recaptures were reported, and that tagging did not cause mortality or increase vulnerability.

Tag loss and mortality from tagging are probably the most serious deterrents to the quantitative interpretation of data from any tagging study. Various experiments (Snyder, 1932; Markus, 1933; Shetter, 1936a; and Eschmeyer, 1959) have revealed losses with various types of tags ranging from 40 to 100 percent within 1 year after tagging. Data are not available on the percentage loss of the spaghetti tags used in this study but I believe it is less than that for jaw and streamer tags.

The extent of mortality caused by tagging depends on the type of tag, the hardiness of the species tagged, the condition of the fish at tagging, the method of handling the fish during tagging, and probably on other factors as well. Eschmeyer (1959) lost only 9 lake trout of 600 held in a rearing pond and tagged with Petersen, cheek, jaw, and streamer tags. The mortality of whitefish tagged with spaghetti tags is unknown.

No method exists for judging the number of tagged fish recaptured but not reported. Most fishermen intend to report tagged fish but sometimes, through neglect, they forget to return the tag. A few deliberately withhold information on tag returns.

Information is lacking also on the effect of the tag on the vulnerability of the whitefish to commercial gear. Buettner (1961) found that returns from lake trout tagged with Petersen tags were 2.6 times greater than those from fish bearing tags of other types. He concluded that the high rate of returns of Petersen-tagged fish

was due to entanglement of the tags in the webbing of the gill nets. Eschmeyer, Daly, and Erkkila (1953) also suggested that fish tagged with Petersen tags were far more vulnerable to the fishery than were fish bearing other types of tags. The relative vulnerability of fish tagged with these other types of tags is not fully known, but it seems reasonable to assume that the presence of any external tag would increase the chance of capture in certain gears, particularly gill nets.

The effect of the increased vulnerability of the tagged whitefish to the fishing gear may not be great in this study since nearly all (92 percent) of the returns of fish used for inquiry into exploitation rates came from pound nets. The heavy twine of pound nets rarely gills or otherwise entangles whitefish. Tags may, nevertheless, cause pound nets to hold a few fish that otherwise might slip through the meshes.

Even though the effect upon the data from loss of tags, unreported returns, and tagging mortality may be offset in some measure by compensating increased vulnerability of tagged fish to the fishing gear, I believe that the compensation was only partial and that data on exploitation rate offered later in this section are in fact underestimates—possibly severe ones. I have not, however, undertaken any arbitrary adjustment such as that of Smith and Van Oosten (1940) who based their estimation of fishing intensity on various species in Lake Michigan on the assumption that 50 percent of the fish had lost their tags.

Since nearly all of the 1,122 whitefish tagged in June–July 1960 were undersized at tagging, the first-year returns were so few that the rate of exploitation for them could not be estimated over the first year of freedom. The rate of exploitation was estimated from second-year returns, however, by the following procedure: the average growth in length of the tagged whitefish recaptured after completion of 1 growing season (1.6 inches—table 5) was added to each of the lengths of whitefish tagged in June–July 1960 to determine the number of tagged fish that would have reached legal size at the beginning of the second fishing season (May 1, 1961); the number of fish which would have reached legal size at the beginning of the second year (737) was reduced by 59, the number taken as legal-size fish during the first year of freedom, to obtain the adjusted number of

678 actually available; the 153 fish recaptured during the second growing season gave an estimated exploitation rate of $100 \times \frac{153}{678}$ or 22.6 percent.

The rate of exploitation for Apostle Islands whitefish was also estimated from first-year returns of the legal-size fish tagged in November 1959–61. Of the 171 legal-size fish tagged, 35 (20.5 percent) were recaptured during the following 12 months (December–November) after tagging.

The close agreement between estimates of exploitation rates of the November 1959–61 fish (20.5 percent) and the June–July 1960 group (22.6 percent) strongly suggests that the system for estimation of the exploitation rate of the latter group was reasonably sound.

Annual exploitation rates a little above 20 percent cannot be termed excessive. These estimates almost surely are minimal, and as was brought out in earlier discussions, they may be far below the true value. Strong evidence of extremely heavy exploitation of whitefish in the Apostle Islands area was given by Dryer (1963), who found that the intensive summer pound net fishery selected the legal-size whitefish from the population early in the season, leaving mostly the undersized, slowly growing members of an age group during late season. The average size of the age groups declined progressively through the summer.

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LITERATURE CITED

- BUDD, JOHN.
1957. Movements of tagged whitefish in northern Lake Huron and Georgian Bay. *Transactions of the American Fisheries Society*, vol. 86, for the year 1956, pp. 128–134.
- BUETTNER, HOWARD J.
1961. Recoveries of tagged, hatchery-reared lake trout from Lake Superior. *Transactions of the American Fisheries Society*, vol. 90, No. 4, pp. 404–412.

- CARBINE, WILLIAM F., AND VERNON C. APPLGATE.
1948. The movement and growth of marked northern pike (*Esox lucius* L.) in Houghton Lake and the Muskegon River. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 32, for the year 1946, pp. 215-238.
- DRYER, WILLIAM R.
1963. Age and growth of the whitefish in Lake Superior. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 63, No. 1, pp. 77-95.
- ESCHMEYER, PAUL H.
1959. Survival and retention of tags, and growth of tagged lake trout in a rearing pond. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 21, No. 1, pp. 17-21.
- ESCHMEYER, PAUL H., AND WALTER R. CROWE.
1955. The movement and recovery of tagged walleyes in Michigan, 1929-1953. Michigan Department of Conservation, Institute for Fisheries Research, Miscellaneous Publication No. 8, pp. 1-32.
- ESCHMEYER, PAUL H., RUSSELL DALY, AND LEO F. ERKKILA.
1953. The movement of tagged lake trout in Lake Superior, 1950-1952. Transactions of the American Fisheries Society, vol. 82, for the year 1952, pp. 68-77.
- ESCHMEYER, R. W., AND ALDEN M. JONES.
1941. The growth of game fishes in Norris Reservoir during the first five years of impoundment. Transactions of the Sixth North American Wildlife Conference, pp. 222-240.
- MARKUS, HENRY C.
1933. The effects of tags upon fresh water fishes. Transactions of the American Fisheries Society, vol. 63, pp. 319-325.
- PARKER, PHILLIP S., AND ROBERT E. LENNON.
1956. Biology of the sea lamprey in its parasitic phase. U.S. Fish and Wildlife Service, Research Report 44, pp. 1-32.
- SHETTER, DAVID S.
1936a. The jaw-tag method of marking fish. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 21, for the year 1935, pp. 651-653.
1936b. Shrinkage of trout at death and on preservation. Copeia, 1936, No. 1, pp. 60-61.
- SMITH, LLOYD L., LAURITS W. KREFTING, AND ROBERT L. BUTLER.
1952. Movements of marked walleyes, *Stizostedion vitreum vitreum* (Mitchill), in the fishery of the Red Lakes, Minnesota. Transactions of the American Fisheries Society, vol. 81, for the year 1951, pp. 179-196.
- SMITH, OLIVER H., AND JOHN VAN OOSTEN.
1940. Tagging experiments with lake trout, whitefish, and other species of fish from Lake Michigan. Transactions of the American Fisheries Society, vol. 69, for the year 1939, pp. 63-84.
- SNYDER, J. P.
1932. Tagged smallmouth black bass in Lake Ontario, New York. Transactions of the American Fisheries Society, vol. 62, pp. 380-381.
- WILSON, ROBERT C.
1953. Tuna marking, a progress report. California Fish and Game, vol. 39, No. 4, pp. 429-442.

AGE, GROWTH, SEX RATIO, AND MATURITY OF THE WHITEFISH IN CENTRAL GREEN BAY AND ADJACENT WATERS OF LAKE MICHIGAN

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ABSTRACT

This study is based on 1,023 whitefish, *Coregonus clupeaformis* (Mitchill)—819 in seven samples from five localities in central Green Bay in 1948-49 and 1951-52 and 204 in a single 1948 collection from northwestern Lake Michigan proper.

Records of age indicated unusual strength for only one year class—1943 which strongly dominated the 1948 sample from Lake Michigan and the 1949 sample from Green Bay and was well represented in the 1948 collection from Green Bay. Collections of 1951-52 without exception were dominated by age group III.

Length distributions of samples varied widely according to the age composition. Among fish more than 2 years old, the length distributions of age groups overlapped broadly. Several 1-inch intervals included fish of four age groups.

The length-weight relation varied considerably among central Green Bay samples, but differences among localities were nearly equalled by the year-to-year difference at a single locality. Lake Michigan whitefish were generally lighter than those from Green Bay. Weight increased to the 3.386 power of length in Green Bay (combined samples) and the 3.359 power in Lake Michigan.

Growth in length, calculated by direct proportion from diameter measurements of growth fields on scales, differed among localities in central Green Bay and between samples of different years at a single locality. If permanent locality differences exist they are not

large and can be obscured by the evident annual fluctuations of growth. The grand average calculated length of Green Bay whitefish (combined collections) exceeded that of Lake Michigan fish in all years of life. The advantage was greatest (2.2 inches) at 3 years (calculated lengths of 16.0 and 13.8 inches) and subsequently declined to 0.5 inch at 9 years (lengths of 24.6 and 24.1 inches). Both groups reached the minimum legal length of 17 inches during the fourth growing season. Green Bay whitefish also had the larger calculated weights. The advantage reached 9.3 ounces in 3 years (calculated weights of 22.4 and 13.1 ounces). In years of life 4-9, the weight advantage over Lake Michigan fish ranged from 8.7 ounces, (seventh year; weights of 74.4 and 65.7 ounces) to 12.2 ounces (ninth year; weights of 96.2 and 84.0 ounces).

Comparison of growth of whitefish at four localities in northern Lake Michigan indicates that fastest growth is in central Green Bay and slowest near the Fox Islands. Growth is intermediate and similar in northwestern Lake Michigan proper and northern Green Bay.

Youngest mature male whitefish in Green Bay belonged to age group II and youngest mature females to age group III. All IV-group fish were mature. Shortest mature males were at 14.5-14.9 inches and shortest mature females at 16.5-16.9 inches. All males longer than 17.9 inches and all females longer than 18.4 inches were mature.

The whitefish, *Coregonus clupeaformis* (Mitchill), long has been a major commercial species in the Great Lakes. It occurs in all five lakes. Publications on Great Lakes whitefish include: Hart (1931), Lake Ontario; Van Oosten and Hile (1949),

Lake Erie; Van Oosten (1939), Lake Huron; Roelofs (1958), Lake Michigan; and the most recent studies in Lake Superior by Edsall (1960) and Dryer (1963).

Some of these studies revealed the existence of populations with greatly different growth characteristics within the same lake and separated by

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only relatively short distances. The present paper discloses a similar situation between central Green Bay waters of Lake Michigan and the adjacent area of the lake proper. The knowledge of the existence and location of the various separate populations of whitefish is valuable to the sound management and commercial exploitation of the species.

MATERIALS AND METHODS

This study is based on 1,023 whitefish collected in six areas of central Green Bay and adjacent waters of Lake Michigan from 1948 through 1952 (fig. 1; table 1). The numbers of fish in individual samples ranged from 204 from the Europe Bay area of Lake Michigan to 80 at Peshtigo. The 230 fish at Minneapolis Shoals (131 on July 31, 1952, and 99 on September 16, 1952) had such

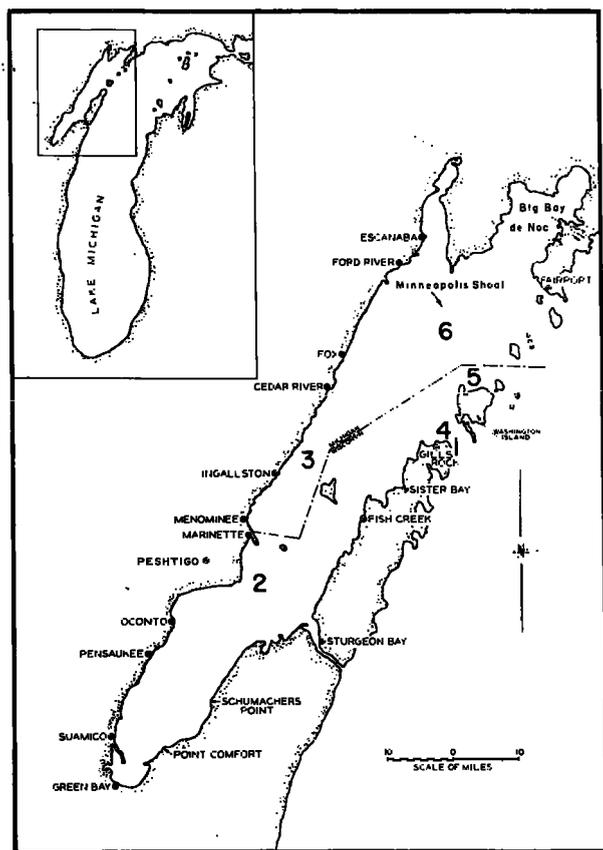


FIGURE 1.—Localities at which whitefish were collected in Lake Michigan proper and central Green Bay. The locality numbers are used in table 1 to identify individual samples.

closely similar growth and size that they were treated as a single collection. All collections were complete catches from the nets.

Several other samples of selected fish, or samples too small to be used effectively for comparison with the larger collections, were employed in the section on the length-weight relation.

TABLE 1.—Locality, gear, and date of capture of whitefish from Lake Michigan and central Green Bay

[Figures in parentheses are used to identify localities in figure 1]

Date of capture	Locality	Gear	Number of fish
1948			
Oct. 14...	Lake Michigan (1)....	4½-inch-mesh pound net.....	204
Oct. 13...	Peshtigo (2).....	4¾- to 5-inch mesh gill net.....	80
1949			
May 18...	Cedar River (3).....	5-inch-mesh pound net.....	182
1961			
June 15...	Cedar River (3).....	4½-inch-mesh pound net.....	85
June 11...	Gills Rock (4).....	4½-inch-mesh pound net.....	129
1962			
Feb. 14...	Washington Island (5)...	4½-inch-mesh gill net.....	113
July 31...	Minneapolis Shoals (6).....	5-inch-mesh pound net.....	131
Sept. 16...	Minneapolis Shoals (6).....	5-inch-mesh pound net.....	99

All available data have been applied to each matter under consideration. As a result, certain discrepancies appear in numbers of fish. For example, a table giving the length-frequency distribution or the length-weight relation for an entire sample may be based on more fish than a table of age composition for the same sample. The latter table, of necessity, excludes those fish for which scales could not be read.

Scales were removed from the left side of the fish between the lateral line and the middle of the base of the dorsal fin. Total lengths (tip of the head to the tip of the tail, lobes compressed) were measured to the nearest 0.1 inch. Weights were determined with spring balances and recorded to the nearest quarter or half ounce. All records were later converted to the nearest 0.1 ounce. The sex was determined for all fish but maturity data were lacking or incomplete for all but the Minneapolis Shoals collections.

Scale impressions were made in cellulose acetate (Smith, 1954) and examined by means of a microprojector at a magnification $\times 44$ (Moffett, 1952). Diameters of scales and of growth fields within

were measured to the nearest 0.1 inch along a line through the focus that approximately bisected the anterior field.

Since the data in this study were not adequate for a precise determination of the body-scale relation all calculations of length were by direct proportion. A plot of the available data did indicate a straight line with an intercept value near zero. This observation disagrees with that of Edsall (1960) who found the relation for Munising Bay (Lake Superior) whitefish to be linear with an intercept of 1.486 inches on the axis of fish length. It agrees, however, with the finding of Van Oosten (1923) for whitefish reared in the New York Aquarium and of Dryer (1963) for Lake Superior whitefish from the Apostle Islands region.

All fish were considered to become a year older on January 1; an annulus was credited at the edge of the scale from that date until the current-season annulus was completed. Age groups are designated by Roman numerals corresponding to the number of annuli.

None of the fish collected in spring or early summer had started growth. At Minneapolis Shoals, growth was in progress in July and September but no difficulty was encountered in locating the outermost annulus.

Growth of the Lake Michigan and Peshtigo samples collected in mid-October 1948 has been assumed to be complete for the year. The lengths at capture of age groups in these samples as well as in samples taken in the spring or early summer are therefore treated also as calculated lengths.

On the basis of findings detailed in later text sections it was determined desirable to treat the sample from the Europe Bay area of Lake Michigan separately from the central Green Bay collections; fish from Europe Bay have been designated "Lake Michigan." The collections made within Green Bay are identified by actual locality of capture or labeled collectively as "Central Green Bay."

In the presentation of data, the collections are arranged in the order of capture with two exceptions. The Lake Michigan collection always appears first despite its collection a day later than the one from Peshtigo because the fish are distinct from the central Green Bay fish; again in 1951 the Cedar River sample is placed in tables in advance of the Gills Rock collection to take

advantage of ready comparisons of the Cedar River collections of 1949 and 1951—the only two collections from the same locality.

AGE COMPOSITION

The records of age composition point clearly to the presence of only one exceptionally strong year class of whitefish—that of 1943 (table 2; fig. 2). It was strongly dominant as the V group in the Lake Michigan sample in 1948 (52.7 percent) and as the VI group at Cedar River (65.2 percent) in 1949. It was also abundant (38.7 percent) at Peshtigo in 1948 although outnumbered by the IV group (49.4 percent). It had disappeared, however, by 1951.

The collections of 1951 and 1952 from Cedar River, Gills Rock, Washington Island, and Minneapolis Shoals were all dominated by age group III (fig. 2). Roelof's (1958) data showed that age group III provided 85 to 90 percent of the annual commercial catch in Big Bay de Noc waters of Lake Michigan in 1951–54. The author believed that mortality was extremely high from age group III to age group IV.

The use of two types of gear (gill and pound nets) to catch fish made it possible to study their effect on age composition in the samples. The gill net is designed to catch fish above a certain size but does not catch the largest fish. The pound net is not so selective, as the effect of its leaders and the mechanical action of lifting the net frequently result in the capture of small fish. Although many more of these smaller fish escape than are actually caught, some do mill around and avoid escape through the larger side meshes until they are trapped during lifting and are retained. It was this fishing action that permitted the capture of six I-group fish by pound nets; no fish of that age appeared in gill net samples. The pound net also can take the larger fish which cannot be caught readily in a gill net.

The Washington Island gill net sample showed that these various gear effects did not alter the basic composition of dominance by III-age fish during 1951–52. The Peshtigo sample did have fewer V-group fish than would be expected on the basis of the strong dominance of the 1943 year class in the Lake Michigan collection of 1948 and the Cedar River collection of 1949. The Peshtigo sample was small (only 80 fish), however,

TABLE 2.—Age and year-class composition of samples of whitefish from Lake Michigan and central Green Bay

Locality, year of capture, and item	Year class												Average or total ¹
	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	
Lake Michigan, 1948:													
Age group.....	VIII		VI	V	IV	III	II	I					4.0
Number.....	1		3	106	20	27	40	4					201
Percentage.....	0.5		1.5	52.7	10.0	13.3	20.0	2.0					
Peshtigo, 1948:													
Age group.....				V	IV	III							4.3
Number.....				29	37	9							75
Percentage.....				38.7	49.4	11.9							
Cedar River, 1949:													
Age group.....	IX	VIII	VII	VI	V	IV	III	II					5.2
Number.....	2	2	2	114	3	15	34	3					175
Percentage.....	1.1	1.1	1.1	65.2	1.7	8.6	19.5	1.7					
Cedar River, 1951:													
Age group.....						V	IV	III					3.1
Number.....						7	70	70					78
Percentage.....						1.3	8.9	89.8					
Gills Rock, 1951:													
Age group.....							IV	III	II	I			2.7
Number.....							5	78	41	1			125
Percentage.....							4.0	62.4	32.8	0.8			
Washington Island, 1952:													
Age group.....									IV	III			3.2
Number.....									21	89			110
Percentage.....									19.1	80.9			
Minneapolis Shoals, 1952:													
Age group.....									IV	III	II	I	2.8
Number.....									5	182	59	1	227
Percentage.....									2.2	71.4	26.0	0.4	

¹ The first of each pair of figures is the average number of annuli.

and may not have been fully representative of the local stock.

The average number of annuli in the 1948-49 samples ranged from 4.0 to 5.2 as compared to 2.7 to 3.2 in the 1951-52 samples (table 2). This difference in average age is traceable to the great strength of the 1943 year class at ages V and VI.

The 1943 year class of whitefish was abundant in Lake Huron as well as in Lake Michigan. Saginaw Bay of Lake Huron, for example, showed an average commercial production of 26,000 pounds during 1938-45, an increase to an average of 807,000 pounds during 1946-48, and a decline to an average of 17,000 pounds during 1949-56 (Hile and Buettner, 1959).

The effect of the 1943 year class of whitefish on the commercial production from the Wisconsin waters of Lake Michigan and the Michigan waters of Lakes Michigan and Huron is shown by the records of catch for 1940-51 (table 3—data from Baldwin and Saalfeld, 1962).

Production in all three areas showed a marked increase in 1946, reached peaks in 1947 or 1948 and thereafter declined to the level of the early 1940's. A feature of the record is the longer period of high catch in Michigan waters of Lake Michigan than in the other two waters; the bulk of this production came from Green Bay.

The same year also saw a strong year class of another coregonine, the lake herring, *Coregonus artedii*, in Green Bay. Following low production over the period 1939-44 (high of 697,000 pounds in 1939 and a low of 285,000 pounds in 1942) the commercial take of lake herring in State of Michigan waters of Green Bay rose to 2,668,000 pounds in 1948 (Hile, Lunger, and Buettner, 1953).

TABLE 3.—Production (thousands of pounds) of whitefish in Wisconsin and Michigan waters of Lake Michigan and Michigan waters of Lake Huron, 1940-51

Year	Lake Michigan		Lake Huron, Michigan
	Wisconsin	Michigan	
1940.....	197	754	188
1941.....	401	896	114
1942.....	279	1,061	95
1943.....	254	1,152	149
1944.....	343	1,403	185
1945.....	331	1,326	181
1946.....	735	1,822	545
1947.....	1,807	4,018	3,023
1948.....	985	4,263	2,972
1949.....	485	3,007	530
1950.....	259	2,102	114
1951.....	242	971	143

Coregonines were not alone in the production of strong 1943 year classes in Lakes Michigan and Huron, as the commercial production of walleye, *Stizostedion vitreum*, likewise rose impressively. This increase was most dramatic in State of Michigan waters of Green Bay, where it rose from

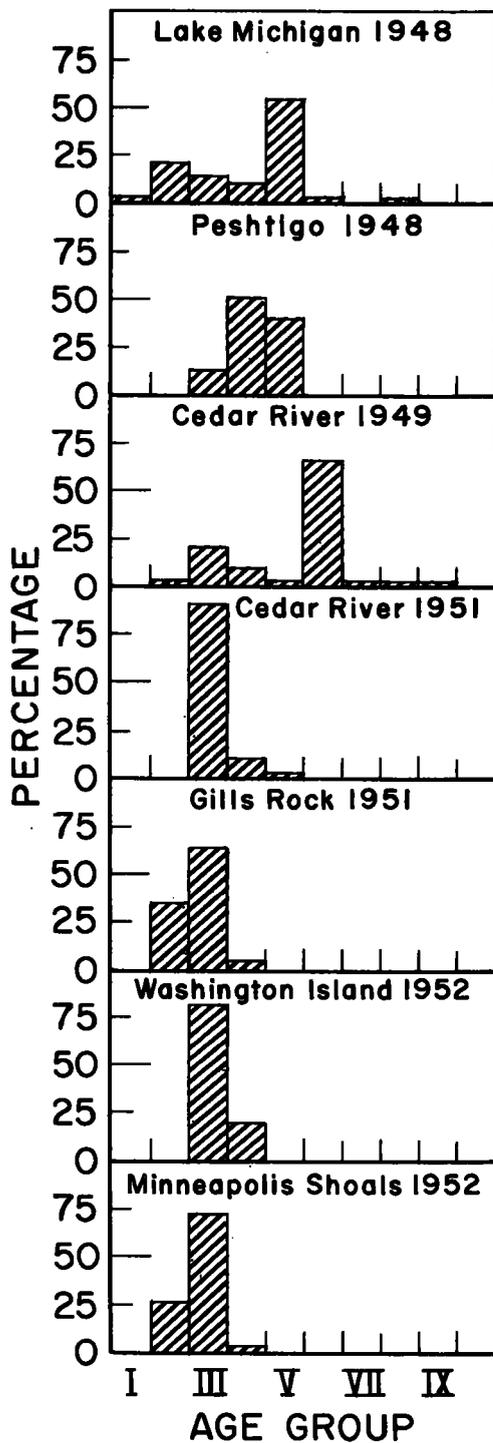


FIGURE 2.—Age composition of whitefish from Lake Michigan and central Green Bay.

the 1929-43 mean of 51,000 pounds to 1,063,000 pounds in 1949 (Hile, Lunger, and Buettner, 1953). Hile (1950) showed that 93.6 percent of

a sample of 109 fish taken in the spring of 1949 were 6 years old, and Pycha (1961) gave a complete history of the 1943 year class.

The walleye production in Saginaw Bay, Lake Huron, experienced a rapid decline from an all-time high commercial production of over 2 million pounds in 1942. This decrease was interrupted, however, by a temporary rise in 1946. Hile and Buettner (1959) stated "The recovery of walleyes in 1946 can be attributed to the great strength of the 1943 year class (unpublished records of age)."

LENGTH DISTRIBUTION

No single sample of whitefish in this study is truly suitable for demonstrating a "typical" distribution of the catch of commercial gear. As is common among the coregonines, one age group strongly dominated each sample (see previous section on age composition). This dominance caused individual samples to have a relatively tight length distribution with high modes.

The range of length, mean length, position and relative height of mode, and the percentage of legal-size whitefish varied greatly from collection to collection (table 4), but the seven samples fell clearly into two generally similar groups—the three samples of 1948-49 and the four of 1951-52.

The 1948-49 samples showed high mean lengths (18.9-20.1 inches), high modal lengths (19-21 inches), and high percentages of legal fish (68-96). Dominance or great abundance of the 1943 year class at a time its members had completed 6 growing seasons caused these high values.

The 1951-52 samples were all dominated by III-group fish; consequently the mean lengths (15.6-17.5 inches), the modal lengths (16 or 17 inches), and the percentages of legal fish (41-67) were all lower than in the other group.

The records of table 4 give evidence that pound nets capture more smaller whitefish than do gill nets. Neither of the gill net samples (Peshtigo and Washington Island) included fish shorter than 15.0 inches, whereas four of five pound net samples included smaller fish—some in considerable numbers. Particularly striking is the contrast between the Peshtigo and Lake Michigan samples which were collected on consecutive days.

The individual collections were poorly suited also to show the length distribution of age groups. A single collection usually yielded dependable data on the length distribution of only one age group.

TABLE 4.—Distribution of total length of whitefish from Lake Michigan and central Green Bay

[Includes a small number of fish for which ages could not be determined; asterisks indicate modes]

Length interval	Location and year of collection						
	Michigan (1948)	Peshigo (1948)	Cedar River (1949)	Cedar River (1951)	Gills Rock (1951)	Washington Island (1952)	Minneapolis Shoals (1952)
Inches	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish
7.0-7.9					1		
8.0-8.9							
9.0-9.9	1						
10.0-10.9	2				4		
11.0-11.9	1				8		1
12.0-12.9	3		3		13		
13.0-13.9	17		1		14		4
14.0-14.9	17		3		2		25
15.0-15.9	12	1	13	2	5	9	30
16.0-16.9	12	2	16	26	29	*55	35
17.0-17.9	5	9	8	*43	*45	28	*96
18.0-18.9	7	16	10	7	5	10	34
19.0-19.9	8	*20	6	4	2	5	3
20.0-20.9	*52	19	25	1	1	5	2
21.0-21.9	47	13	*58				
22.0-22.9	14		25			1	
23.0-23.9	5		9	1			
24.0-24.9			5	1			
25.0-25.9							
26.0-26.9	1						
Number of fish	204	80	182	85	129	113	230
Percentage at mode	25.5	25.0	31.9	50.6	34.9	48.7	41.7
Average length	18.9	19.4	20.1	17.5	15.6	17.2	16.8
Percentage legal ¹	68.2	96.2	80.2	67.0	41.1	43.4	58.6

¹ Total length, 17 inches or longer; actually, the size limit in State of Michigan waters was not changed from 2 pounds (round) to 17 inches until 1953.

The pooling of length data for fish of corresponding age in different samples, because of annual differences and possible local differences in growth, extends the range somewhat beyond that which would be expected in a single sample of fish of that age and broadens the modal region but does provide a useful idea of the general range and distribution.

Records obtained by the pooling of collections from central Green Bay (table 5) yielded fairly good information on the length distribution of whitefish that had completed 2-6 growing seasons and some data on lengths at other ages. In order to describe the distribution of total lengths in terms of completed growing seasons of the whitefish from central Green Bay, the Minneapolis Shoals collection was not included. Omission of this group, the only one in which growth was in progress when the samples were collected, made it possible to give lengths in terms of completed seasons without the use of any calculated lengths.

If length intervals with only one fish are excluded, length ranges of fish that had completed

2-6 seasons of growth were 5 inches for all but the 6-season fish, which had a range of 6 inches. When all fish are considered, the greatest range was 9 inches (15.0-23.9 inches) for fish that had completed 5 growing seasons. Overlap of lengths for growing seasons 3 through 6 was substantial. Fish 17.0-19.9 inches long could have completed 3, 4, 5, or 6 growing seasons. Every 1-inch length interval above 14 inches included fish of at least 2 ages and usually 3 or 4.

TABLE 5.—Distribution of total length of whitefish from central Green Bay that had completed one to nine growing seasons

[Asterisks indicate modes; the lower half of the broad mode at two growing seasons is the one nearer the mean]

Length interval	Completed growing seasons								
	1	2	3	4	5	6	7	8	9
Inches	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish	Number of fish
7.0-7.9	1								
8.0-8.9									
9.0-9.9									
10.0-10.9		4							
11.0-11.9		8							
12.0-12.9		*15							
13.0-13.9		15							
14.0-14.9		2							
15.0-15.9			2			1			
16.0-16.9			*120	3	1				
17.0-17.9			109	13	4	1			
18.0-18.9			11	*23	11	2			
19.0-19.9				1	11	*15	5		
20.0-20.9				1	6	4	37		
21.0-21.9						4	*65		
22.0-22.9					1		24	1	
23.0-23.9						1	9		
24.0-24.9								1	2
Number of fish	1	44	271	57	41	143	2	2	2
Average length	7.1	12.4	16.7	18.5	19.2	21.2	23.8	24.6	24.5
Percentage legal ¹	.0	.0	44.7	94.7	95.2	100.0	100.0	100.0	100.0

¹ Total length, 17 inches or longer; actually, the size limit in State of Michigan waters was not changed from 2 pounds (round) to 17 inches until 1953.

LENGTH-WEIGHT RELATION

Whitefish from central Green Bay exhibited considerable sample-to-sample differences in the length-weight relation but the data gave no reason for a conclusion that stocks with different length-weight relations exist in the area (table 6). The Cedar River samples of 1949 and 1951 (both collected in late spring) showed an annual difference as great or nearly as great (3.9 ounces at 17.2 inches; 3.7 ounces at 18.2 inches; and 7.3 ounces at 18.7 inches) as is found between samples from different locations (2.9 ounces at 17.2 inches between Gills Rock and Washington Island; 5.8 ounces at 18.2 and 18.7 inches between Washing-

ton Island and Minneapolis Shoals). The pooling of all the central Green Bay samples therefore gives the most useful length-weight information.

The annual weight differences as demonstrated by the Cedar River samples are comparable to fluctuations described for other coregonines (Deason and Hile, 1947, for the kiyi, *Coregonus kiyi*; Van Oosten and Hile, 1949, for the Lake Erie whitefish; Morawa, 1960, whose data showed that adult *Coregonus fera* in Lake Geneva, Switzerland, could lose 25 percent of their weight and 63 percent of their fat between summer and the fall spawning season).

TABLE 6.—Length-weight relation of whitefish from Lake Michigan and central Green Bay collections

Total length ¹	Location and year of collection						
	Michigan (1948)	Peshigo (1948)	Cedar River (1949)	Cedar River (1951)	Gills Rock (1951)	Washington Island (1952)	Minneapolis Shoals (1952)
Inches	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces	Ounces
7.2					1.6		
7.7							
8.2							
8.7							
9.2							
9.7							
10.2	4.0				5.6		
10.7	4.0				6.0		
11.2	6.5				7.0		6.5
11.7	8.0				8.2		
12.2	8.5		9.3		9.3		
12.7	9.1		12.0		10.6		
13.2	11.6				12.2		
13.7	12.9				13.5		12.8
14.2	15.2				17.0		14.2
14.7	15.8		18.0		18.0		16.5
15.2	18.0		20.8			25.0	18.2
15.7	19.7	25.0	22.3	22.5	20.3	24.0	20.4
16.2	22.1		25.2	22.7	23.9	28.3	23.0
16.7	26.0	26.5	27.2	24.3	26.8	29.7	24.6
17.2	26.0	34.5	30.7	26.8	29.1	32.0	27.0
17.7	35.4	36.5	34.5	29.9	28.6	32.8	29.8
18.2	32.7	38.8	34.4	30.7	35.7	38.0	32.2
18.2	37.5	43.5	40.8	33.5	42.5	40.5	34.7
18.2	38.8	43.4	38.8	39.5	40.0	40.1	
19.2	42.7	48.0	46.4	42.7	49.0		43.7
20.2	47.7	53.7	48.8	47.5	52.0	48.7	49.0
20.7	52.7	53.6	54.2			53.0	54.0
21.2	56.3	59.1	56.4				
21.7	61.2	65.2	61.5				
22.2	67.7		64.6			70.5	
22.7	65.8		69.6				
23.2	73.8		77.2				
23.7	85.9		79.2	79.5			
24.2			78.0				
24.7			93.1				
25.2							
25.7							
26.2	100.0						

¹ Midpoints of 0.5-inch intervals.

The Lake Michigan sample of 1948 is held to be different from the central Green Bay fish on the basis of mean weights much lighter than those of the Peshtigo fish collected only a day earlier (26.0 and 34.5 ounces at 17.2 inches; 32.7 and 38.8 ounces at 18.2 inches; 38.8 and 43.4 ounces at 19.2 inches); the Lake Michigan fish furthermore

were generally lighter than those of other Green Bay samples (table 6).

A length-weight equation, to be most useful, should include fish of both sexes, sampled at various times of the year over a period of years. Bias from annual and seasonal variations, sex differences, and maturity and state of sex organs is minimized by this procedure. The resulting general curve, though not exactly descriptive of fish collected at any given time and considerably different from those of some samples, produces the most usable record.

The samples from central Green Bay meet the above-stated requirements fairly well because both sexes are represented and collection dates covered all seasons—the Peshtigo sample in mid-October 1948; the Cedar River samples in May 1949 and June 1951, the Gills Rock sample in June 1951, the Washington Island sample in February 1952, and the Minneapolis Shoals sample in July and September 1952. Selected fish taken at other times were also used to provide more small individuals. Effects of annual and seasonal fluctuations on determination of the length-weight relation were therefore lessened to a fair degree in central Green Bay. The Lake Michigan data, on the other hand, are based on a single October sample.

Length-weight equations were derived for the Lake Michigan sample and the central Green Bay samples by fitting straight lines by least squares to the logarithms of the lengths and weights. The curves in figure 3 are the graphs of the following equations:

Lake Michigan

$$W = 1.9422 \times 10^{-3} L^{3.35903}$$

Central Green Bay

$$W = 1.8756 \times 10^{-3} L^{3.38647}$$

where

W = weight in ounces,

and

L = total length in inches.

The weight of the Lake Michigan whitefish increased as the 3.35903 power of the length, and the weight of the central Green Bay fish as the 3.38647 power of the length. The difference between the exponents cannot be considered great. Both equations show a substantial departure from the cube relation; plumpness increases considerably with increase of length.

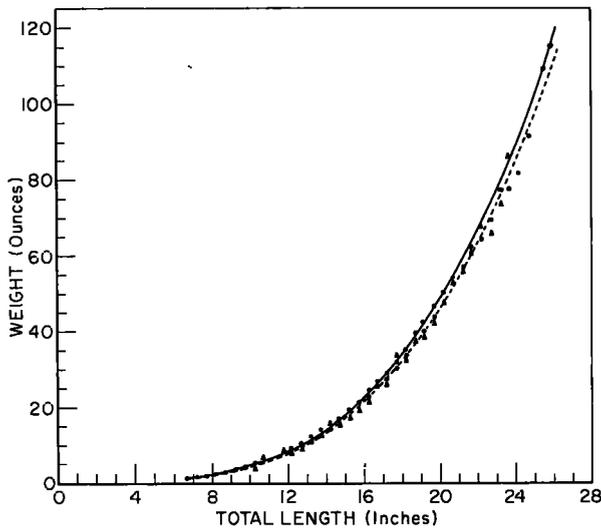


FIGURE 3.—Length-weight relation of whitefish from Lake Michigan and central Green Bay. The broken line represents the calculated weights and the triangles the empirical weights of the Lake Michigan fish; the solid line and dots represent the central Green Bay fish.

Agreement of empirical and calculated weights of the Lake Michigan whitefish (table 7; fig. 3) varied considerably according to length and number of fish. Over the length range, 20.2–22.2 inches, where the fish were most plentiful, the empirical weights were all higher than the calculated weights by 0.6–3.1 ounces. The length range, 9.7–19.7 inches, had empirical weights both greater and smaller than the calculated weights. The maximum deviation of empirical weight below the calculated was 1.4 ounces at 17.2 inches, and the maximum deviation above the calculated weight was 3.1 ounces at the next interval, 17.7 inches. At 11 lengths the empirical weight was less than the calculated, and at 8 it was greater. The greatest disagreement over the entire length range was 12.8 ounces at 26.2 inches (only one fish).

The empirical weights of the Green Bay fish were below the calculated weights at lengths above 21.2 inches; the discrepancies ranged from a low of 1.0 ounce at 21.7 inches to a high of 9.5 ounces at 24.2 inches. Over the remainder of the length range (6.7–20.7 inches) empirical and calculated weights were the same at 4 lengths, differed by only 0.1 or 0.2 ounce at 14 and disagreed by 0.5–1.8 ounces at 10. At 16 of the 24 lengths where the two weights differed, the empirical weight was less than the calculated weight.

TABLE 7.—Length-weight relation of whitefish from Lake Michigan and in the combined collections from central Green Bay

[Calculated weights from equations given in text]

Total length ¹	Lake Michigan		Central Green Bay			
	Number of fish	Weight		Number of fish	Weight	
		Calculated	Empirical		Calculated	Empirical
<i>Inches</i>		<i>Ounces</i>	<i>Ounces</i>		<i>Ounces</i>	<i>Ounces</i>
6.7		1.1		6	1.1	1.3
7.2		1.4		15	1.6	1.6
7.7		1.9		27	1.9	2.0
8.2		2.2		26	2.3	2.4
8.7		2.8		12	2.8	2.7
9.2		3.3		5	3.5	3.5
9.7	1	4.0	4.0	4	4.2	4.2
10.2	1	4.8	4.0	8	4.8	5.0
10.7	1	5.5	6.5	10	5.8	5.6
11.2		6.4		11	6.7	7.7
11.7	1	7.6	8.0	19	7.7	9.1
12.2	1	8.6	8.0	15	8.9	9.1
12.7	2	9.9	9.1	12	10.3	10.5
13.2	6	11.3	11.6	13	11.6	12.2
13.7	11	12.8	12.9	9	13.3	13.1
14.2	7	14.5	15.2	17	14.9	14.4
14.7	10	16.1	15.8	16	16.9	17.0
15.2	7	18.2	18.0	33	18.8	19.5
15.7	5	20.2	22.1	42	21.1	21.1
16.2	6	22.5	22.1	81	23.4	24.9
16.7	6	24.9	22.0	89	25.9	26.7
17.2	3	27.4	26.0	133	28.7	28.6
17.7	2	30.3	33.4	89	31.6	30.6
18.2	3	33.3	32.7	56	34.7	33.8
18.7	4	36.7	37.5	27	38.0	39.8
19.2	4	39.7	38.8	22	41.6	41.5
19.7	4	43.3	42.0	14	45.4	46.5
20.2	23	47.1	47.7	20	49.3	50.7
20.7	29	51.2	52.7	29	53.7	53.9
21.2	25	55.4	52.7	39	58.2	57.0
21.7	22	59.9	61.2	32	62.9	61.9
22.2	11	64.6	67.7	17	68.0	64.7
22.7	3	69.7	65.3	12	73.3	69.4
23.2	3	74.9	73.8	5	78.9	77.2
23.7	2	80.6	85.9	10	84.9	77.8
24.2		86.8		2	91.0	81.5
24.7		92.8		5	97.6	91.9
25.2		99.0			104.5	
25.7		105.7			111.6	
26.2	1	112.8	100.0		119.1	

¹ Midpoint of 0.5-inch intervals.

CALCULATED GROWTH IN LENGTH

The records of sex for all fish made it possible to study sex difference in growth rate. No difference was found in four of the seven collections; females grew slightly faster in two and males in one. Because sex differences were nil or small, and did not favor either males or females, separation of the sexes was not justified. The growth of whitefish at each locality was described by combining the data for males and females. The mean calculated length at the end of each year of life was determined for each age group of the various samples (tables 8–14).

The calculated lengths of the whitefish in the various collections give little evidence of "Lee's phenomenon" of decrease of growth rate with increase in the age of the fish for which lengths are computed. Among the collections in which

TABLE 8.—Calculated total length of whitefish taken from Europe Bay area of Lake Michigan, October 14, 1948

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life								
		1	2	3	4	5	6	7	8	9
I.....	4	Inches 6.5	Inches *10.5	Inches						
II.....	40	6.4	10.6	*14.1						
III.....	27	5.7	10.2	13.9	*18.5					
IV.....	20	5.9	9.7	14.7	18.0	*20.1				
V.....	106	5.1	9.5	13.4	17.0	19.4	*21.1			
VI.....	3	6.3	10.1	14.9	18.5	20.6	23.2	*23.2		
VIII.....	1	5.5	12.2	16.3	19.2	21.5	23.1	24.2	25.2	*26.0
Grand average calculated length.....		5.6	9.8	13.8	17.1	19.5	21.2	23.4	25.2	26.0
Increment of average.....		5.6	4.2	4.0	3.3	2.4	1.7	2.2	1.8	0.8
Grand average increment of length.....		5.6	4.2	4.0	3.4	2.4	1.6	1.1	1.0	0.8
Sum of average increments.....		5.6	9.8	13.8	17.2	19.6	21.2	22.3	23.3	24.1

TABLE 9.—Calculated total length of whitefish taken at Peshtigo, October 13, 1948

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life					
		1	2	3	4	5	6
III.....	9	Inches 5.8	Inches 11.5	Inches 15.6	Inches *18.0	Inches	Inches
IV.....	37	6.1	10.8	14.8	17.6	*19.0	
V.....	29	6.4	11.7	15.2	17.7	19.3	*20.5
Grand average calculated length.....		6.2	11.2	15.0	17.7	19.1	20.5
Increment of average.....		6.2	5.0	3.8	2.7	1.4	1.4
Grand average increment of length.....		6.2	5.0	3.8	2.7	1.5	1.2
Sum of average increments.....		6.2	11.2	15.0	17.7	19.2	20.4

TABLE 10.—Calculated total length of whitefish taken at Cedar River, May 18, 1949

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life								
		1	2	3	4	5	6	7	8	9
II.....	2	Inches 7.0	Inches *12.6	Inches						
III.....	34	6.5	11.6	*16.1						
IV.....	15	5.9	10.7	15.3	*18.3					
V.....	3	5.9	10.7	15.3	17.9	*19.1				
VI.....	114	5.8	11.0	15.1	18.3	20.2	*21.6			
VII.....	2	8.3	12.9	17.5	20.1	21.7	22.8	*23.8		
VIII.....	2	7.8	13.8	17.4	20.3	21.6	22.7	23.1	*24.5	
IX.....	2	7.7	10.5	15.9	18.9	20.6	21.9	23.1	23.8	*24.5
Grand average calculated length.....		6.0	11.1	15.4	18.3	20.3	21.7	23.3	24.1	24.5
Increment of average.....		6.0	5.1	4.3	2.9	2.0	1.4	1.6	0.8	0.4
Grand average increment of length.....		6.0	5.1	4.3	3.2	1.9	1.4	0.9	1.0	0.7
Sum of average increments.....		6.0	11.1	15.4	18.6	20.5	21.9	22.8	23.8	24.5

TABLE 11.—Calculated total length of whitefish taken at Cedar River, June 15, 1951

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life				
		1	2	3	4	5
III.....	70	Inches 6.8	Inches 12.3	Inches *17.1	Inches	Inches
IV.....	7	5.9	10.7	15.4	*18.5	
V.....	1	7.5	13.4	17.3	21.2	*23.6
Grand average calculated length.....		6.8	12.1	16.9	18.8	23.6
Increment of average.....		6.8	5.3	4.8	1.9	4.8
Grand average increment of length.....		6.8	5.3	4.8	3.2	2.4
Sum of average increments.....		6.8	12.1	16.9	20.1	22.5

TABLE 12.—Calculated total length of whitefish taken at Gills Rock, June 11, 1951

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life			
		1	2	3	4
I.....	1	Inches *7.1	Inches	Inches	Inches
II.....	41	7.1	*12.4		
III.....	78	6.9	12.3	*16.9	
IV.....	5	7.4	10.9	14.8	*18.2
Grand average calculated length.....		7.0	12.2	16.7	18.2
Increment of average.....		7.0	5.2	4.5	1.5
Grand average increment of length.....		7.0	5.2	4.5	3.4
Sum of average increments.....		7.0	12.2	16.7	20.1

TABLE 13.—*Calculated total length of whitefish taken north of Washington Island, February 14, 1952*

[Asterisks indicate length at time of capture]

Age group	Number of fish	Calculated length at end of year of life			
		1	2	3	4
III	89 21	<i>Inches</i> 7.4	<i>Inches</i> 12.5	<i>Inches</i> *16.6	-----
IV		6.5	12.0	16.2	*19.1
Grand average calculated length	-----	7.3	12.4	16.6	19.1
Increment of average	-----	7.3	5.1	4.2	2.5
Grand average increment of length	-----	7.3	5.1	4.2	2.9
Sum of average increments	-----	7.3	12.4	16.6	19.5

TABLE 14.—*Calculated total length of Whitefish taken at Minneapolis Shoals, July 31 and September 16, 1952*

Age group	Number of fish	Length at capture	Calculated length at end of year of life			
			1	2	3	4
I	1	<i>Inches</i> 11.2	<i>Inches</i> 7.5	-----	-----	-----
II	59	15.0	7.0	12.1	-----	-----
III	162	17.4	6.9	11.6	15.5	-----
IV	5	20.1	6.0	12.2	16.0	18.8
Grand average calculated length	-----	-----	7.0	11.8	15.5	18.8
Increment of average	-----	-----	7.0	4.8	3.7	3.3
Grand average increment of length	-----	-----	7.0	4.8	3.8	2.8
Sum of average increments	-----	-----	7.0	11.8	15.6	18.4

few age groups were well represented (Peshtigo, 1948, and the three 1950-51 samples) the discrepancies in calculated length appear to be randomly distributed. The two samples that had fair to good representation of several age groups within the range II-VI (Lake Michigan, 1948; Cedar River, 1949) gave some indication of a progressive decline of calculated lengths with age of the younger fish and then an increase among the older fish.

The lack of a progressive change of growth with increase in age leads to closely similar results in the estimation of general growth by grand average calculated length and by the summation of grand average increments of length (see bottom portions of tables 8-14). The summation of increments does have the decided advantage, however, of smoothing out these irregularities brought about in the data for the later years of life by the successive dropping out of poorly represented age groups. Growth curves based on the annual increments were chosen, therefore, for the comparison of growth of whitefish in the different collections (table 15).

TABLE 15.—*Calculated total length of whitefish from Lake Michigan and central Green Bay*

[Based on successive addition of grand average increments]

Location and year of capture	Calculated length at end of year of life								
	1	2	3	4	5	6	7	8	9
1948									
Lake Michigan	<i>In.</i> 5.6	<i>In.</i> 9.8	<i>In.</i> 13.8	<i>In.</i> 17.2	<i>In.</i> 19.6	<i>In.</i> 21.2	<i>In.</i> 22.3	<i>In.</i> 23.3	<i>In.</i> 24.1
Peshtigo	6.2	11.2	15.0	17.7	-----	-----	-----	-----	-----
1949									
Cedar River	6.0	11.1	15.4	18.6	20.5	21.9	22.8	23.8	24.5
1951									
Cedar River	6.8	12.1	16.9	20.1	22.5	-----	-----	-----	-----
Gills Rock	7.0	12.2	16.7	20.1	-----	-----	-----	-----	-----
1952									
Washington Island	7.3	12.4	16.6	19.5	-----	-----	-----	-----	-----
Minneapolis Shoals	7.0	11.8	15.6	18.4	-----	-----	-----	-----	-----

The general growth data for the seven collections from six localities show considerable differences among calculated lengths for each year of life. The Lake Michigan whitefish stands clearly apart from all others, however, by reason of its poorer growth in the first 3 years of life. In all comparisons during the first 3 years of life the Lake Michigan fish are smaller; the minimum difference was 0.4 inch (1949 Cedar River fish at the end of the first year of life) and the maximum difference was 3.1 inches (1951 Cedar River fish at the end of the third year of life). Improved growth of the Lake Michigan fish in later years reduced the differences from the Green Bay fish to unimportance, but the form of the growth curve in the two areas was decidedly different. The growth of fish from Gills Rock, collected only a few miles from Europe Bay in Lake Michigan proper (fig. 1), differed from growth in Lake Michigan in about the same manner as did the growth of whitefish from other Green Bay localities.

The records for central Green Bay collections leave little doubt of the existence of real differences in the growth of whitefish of the various samples, but do not warrant any general conclusion on the presence of stocks with permanent and significant differences of growth. The substantial differences in growth (15.4 and 16.9 inches at the end of 3 years, and 18.6 and 20.1 inches at the end of 4 years) of fish in the two collections from Cedar River are much the same as the difference (15.0 and 16.6 inches at 3 years and 17.7 and 19.5 inches

at 4 years) of fish from Peshtigo and Washington Island, or the difference (15.6 and 16.9 inches at 3 years and 18.4 and 20.1 inches at 4 years) of fish from Minneapolis Shoals and Cedar River, 1951.

Although the effects of such factors as random variability, gear selection, and segregation by size should not be discounted entirely, a major cause of variation in estimates of growth has been found by many investigators to be annual fluctuations of growth rate in combination with sample differences of year-class composition. The samples of the present study as a group are poorly suited for studies of fluctuations in growth—lack of collections in consecutive years from any locality, small numbers of well-represented age groups in the majority of samples. Two, however (Lake Michigan, 1948; Cedar River, 1949), do lend themselves to the type of analysis described by Hile (1941) and subsequently employed by numerous investigators.

Growth fluctuated from roughly 16 percent above to 13 percent below average (total range, 29 percent) in Lake Michigan and from 4 percent above to 3 percent below (total range, 7 percent) for Cedar River within the 6-year period 1943-48 (table 16). Fluctuations of this magnitude, especially those in Lake Michigan, can affect estimates of growth materially. Even wider year-to-year changes in growth of Lake Erie whitefish were reported by Van Oosten and Hile, 1947, who recorded a change from 15 percent above to the 1924-30 average in 1927 to 25 percent below in 1930.

A feature of the data on fluctuations of growth is the close agreement between Lake Michigan and Cedar River collections. Without exception the direction of the annual change was the same in the two localities and the annual percentage deviations were also all on the same side of the mean. So close was the agreement that the coefficient of correlation (r) between the two series was 0.824, a value that is significant at the probability level $0.05 > p > 0.02$. Evidence is strong therefore that the factors that brought about changes in growth rate in the two areas were closely similar or had similar fluctuations.

If the differences among growth curves for the whitefish in the various samples from Green Bay were attributable primarily to fluctuations in growth rate, the calculated lengths of members of the same year class from different localities should

agree very closely. The selected comparisons of table 17 do not lead to a clear conclusion. The three year classes collected at both Peshtigo and Cedar River (1943, 1944, and 1945) give evidence of a difference in the style of growth at the two localities. The calculated lengths for Peshtigo whitefish were greater than those of whitefish from Cedar River in 7 of 9 comparisons (exceptions 5.8 and 5.9 inches at the end of the first year for the 1945 year class; and 14.8 and 15.3 inches at 3 years for the 1944 year class) over the first 3 years of life, but the Peshtigo fish had the shorter calculated lengths in all of six comparisons beyond the third year.

TABLE 16.—Annual fluctuations in the growth of whitefish in two samples expressed as percentage deviations from the 1943-48 mean

[Estimates based on annual increments of length of age groups II-V of the 1948 collection from Lake Michigan and age groups III-VI of the 1949 collection from Cedar River; analysis followed procedure described by Hile (1941)]

Year	Percentage deviation from mean	
	Lake Michigan	Cedar River
1943.....	-7.8	-1.0
1944.....	6.7	.7
1945.....	-1.4	-3.0
1946.....	15.7	4.2
1947.....	.1	1.8
1948.....	-13.5	-2.6

TABLE 17.—Comparisons of growth of whitefish of the same year class collected at different localities in central Green Bay

[Data from tables 9-14]

Year class and locality	Year of capture	Age group	Number of fish	Calculated length at end of year of life					
				1	2	3	4	5	6
<i>1943</i>				<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>
Peshtigo.....	1948	V	29	6.4	11.7	15.2	17.7	19.3	20.5
Cedar River....	1949	VI	114	5.8	11.0	15.1	18.3	20.2	21.6
<i>1944</i>									
Peshtigo.....	1948	IV	37	6.1	10.8	14.8	17.6	19.0	-----
Cedar River....	1949	V	3	5.9	10.7	15.3	17.9	19.1	-----
<i>1945</i>									
Peshtigo.....	1948	III	9	5.8	11.5	15.6	18.0	-----	-----
Cedar River....	1949	IV	15	5.9	10.7	15.3	18.3	-----	-----
<i>1948</i>									
Cedar River....	1951	III	70	6.8	12.3	17.1	-----	-----	-----
Gills Rock.....	1951	III	78	6.9	12.3	16.9	-----	-----	-----
Washington Island.	1952	IV	21	6.5	12.0	16.2	19.1	-----	-----
Minneapolis Shoals.	1952	IV	5	6.0	12.2	16.0	18.8	-----	-----
<i>1949</i>									
Gills Rock.....	1951	II	41	7.1	12.4	-----	-----	-----	-----
Washington Island.	1952	III	89	7.4	12.5	16.6	-----	-----	-----
Minneapolis Shoals.	1952	III	162	6.9	11.6	15.5	-----	-----	-----

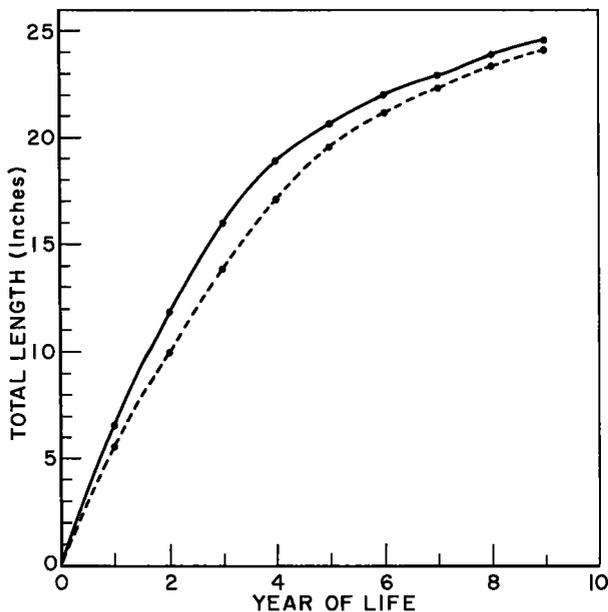


FIGURE 4.—Calculated length of whitefish from Lake Michigan (broken line) and central Green Bay (solid line).

The calculated lengths of members of the 1948 year class from Cedar River and Gills Rock agreed very well; the lengths were shorter at Washington Island than at the former localities and still shorter at Minneapolis Shoals (exception in second year of life).

Whitefish of the 1949 year class had slightly lower calculated lengths at Gills Rock than at Washington Island, a situation directly opposite that shown by the 1948 year class. No explanation can be offered for this disagreement between

the data for two year classes from the same collections.

The data for whitefish from Minneapolis Shoals were consistent in that calculated lengths for both the 1948 and 1949 year classes ran lower than at other locations.

The general conclusion seems warranted that some real growth differences may exist among whitefish in different localities within central Green Bay. These differences probably are not large and most likely can be exceeded by year-to-year differences at a single locality. It appears valid, therefore, to combine the data for all Green Bay samples to describe the general character of growth in the area (table 18).

The calculated lengths of table 18, like those of the component samples, lack a trend toward systematic change with age, except for a slight tendency for the calculated lengths for the first 3 or 4 years of life first to decrease and then to increase with the age of the fish on which calculations were based. The agreement between estimates of general growth from grand average calculated lengths and from the summation of the grand average increments was good. The latter estimate was selected for the comparison of the growth of whitefish in Lake Michigan and central Green Bay (table 19; fig. 4).

The outstanding difference between the growth of whitefish in Lake Michigan and central Green Bay was the slower growth of the Lake Michigan fish for the earlier years of life and their more rapid growth in the later years. The situation is seen most clearly in the annual increments.

TABLE 18.—Calculated total length of whitefish from central Green Bay waters

[All collections combined]

Age group ¹	Number of fish	Calculated length at end of year of life								
		1	2	3	4	5	6	7	8	9
		Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches
I.....	2	7.3								
II.....	100	7.1	12.3							
III.....	442	6.9	12.0	16.2						
IV.....	90	6.2	11.1	15.4	18.2					
V.....	33	6.4	11.7	15.2	17.9	19.1				
VI.....	114	5.8	11.0	15.1	18.3	20.2	21.6			
VII.....	2	8.3	12.9	17.5	20.1	21.7	22.8	23.8		
VIII.....	2	7.8	13.8	17.4	20.3	21.6	22.7	23.1	24.5	
IX.....	2	7.7	10.5	15.9	18.9	20.6	21.9	23.1	23.8	24.5
Grand average calculated length.....		6.6	11.8	15.8	18.2	20.0	21.7	23.3	24.1	24.5
Increment of average.....		6.6	5.2	4.0	2.4	1.8	1.7	1.6	.8	.4
Grand average increment of length.....		6.6	5.2	4.2	2.9	1.7	1.4	.9	1.0	.7
Sum of average increments.....		6.6	11.8	16.0	18.9	20.6	22.0	22.9	23.9	24.6

¹ Age groups of late-autumn samples have been combined with the next higher age groups of spring and summer samples.

TABLE 19.—*Calculated total length of whitefish from Lake Michigan and central Green Bay*

[Data from tables 8 and 18; based on successive addition of grand average increments]

Year of life	Lake Michigan		Green Bay		Difference of length	Ratio of increments
	Length	Increment	Length	Increment		
	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	
1.....	5.6	5.6	6.6	6.6	1.0	1.1
2.....	9.8	4.2	11.8	5.2	2.0	1.2
3.....	13.8	4.0	16.0	4.2	2.2	1.05
4.....	17.2	3.4	18.9	2.9	1.7	.8
5.....	19.6	2.4	20.6	1.7	1.0	.7
6.....	21.2	1.6	22.0	1.4	.8	.8
7.....	22.3	1.1	22.9	.9	.6	.8
8.....	23.3	1.0	23.9	1.0	.6	1.0
9.....	24.1	.8	24.6	.7	.5	.8

The increments for Lake Michigan whitefish were the shorter by 1.0 inch in both the first and second years of life and by 0.2 inch in the third. Subsequently the increments for Lake Michigan fish were greater than those for Green Bay fish with the single exception of the equal values of 1.0 inch for the eighth year. The ratio of the annual increment for Green Bay fish to that of Lake Michigan fish exceeded 1.0 the first 3 years and was 0.7–1.0 the next 6 years. This shift in the relation of the increments causes the growth curves to diverge to a maximum of 2.2 inches at the end of 3 years of life and then to converge until the Green Bay fish were the longer by only 0.5 inch at the end of 9 years.

Whitefish of both stocks attained the minimum legal length of 17 inches in the fourth growing season. Green Bay whitefish reached that length fairly early in the fourth year but those from Lake Michigan were not 17 inches long until near the close of the growing season.

CALCULATED GROWTH IN WEIGHT

The difference between linear growth in Lake Michigan and central Green Bay whitefish and differences in the length-weight relation are reflected in differences in general growth in weight (table 20; fig. 5).

Although the calculated weights were nearly the same at the end of the first year (0.9 ounce, Lake Michigan; 1.0 ounce, Green Bay), the Green Bay fish were the heavier by 3.7 ounces at the end of the second year. This advantage increased rapidly to 12.0 ounces at the end of 4 years, declined to 8.7 ounces at the end of 7, and then rose to the maximum of 12.2 ounces at the end of 9 years.

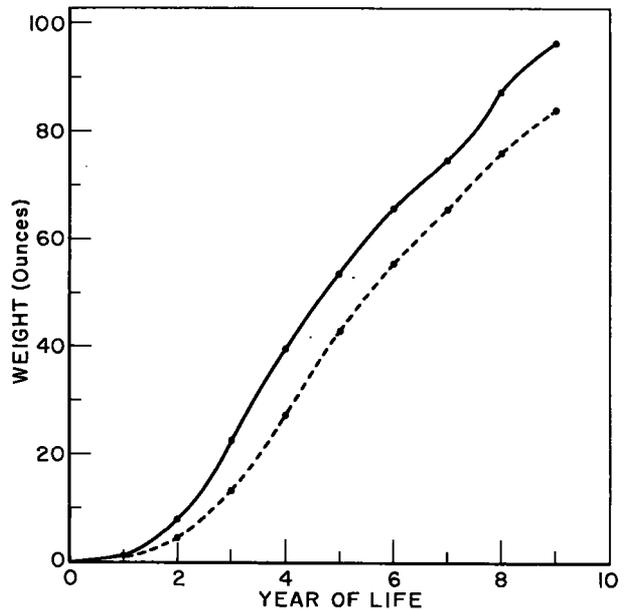


FIGURE 5.—*Calculated growth in weight of whitefish from Lake Michigan (broken line) and central Green Bay (solid line).*

TABLE 20.—*Calculated weight at the end of each year of life of whitefish from Lake Michigan and central Green Bay*

[Weights were computed from the calculated lengths of table 19 by means of the general length-weight equations]

Year of life	Lake Michigan		Green Bay		Difference of weight	Ratio of increments
	Weight	Increment	Weight	Increment		
	<i>Ounces</i>	<i>Ounces</i>	<i>Ounces</i>	<i>Ounces</i>	<i>Ounces</i>	
1.....	0.9	0.9	1.0	1.0	0.1	1.1
2.....	4.2	3.3	7.9	6.9	3.7	2.1
3.....	13.1	8.9	22.4	14.5	9.3	1.6
4.....	27.4	14.3	39.4	17.0	12.0	1.2
5.....	42.6	15.2	53.7	14.3	11.1	.9
6.....	55.4	12.8	65.9	12.2	10.5	.95
7.....	65.7	10.3	74.4	8.5	8.7	.8
8.....	76.1	10.4	87.3	12.9	11.2	1.2
9.....	84.0	7.9	96.2	8.9	12.2	1.1

The ratio of increments of weight showed the Green Bay fish to have greater annual growth in weight the first 4 years of life (low of 1.1 the first year and a high of 2.1 the second); the trend was reversed the next 3 years, when the Lake Michigan fish displayed greater annual increases. Increases for the Green Bay fish were again the greater in years 8 and 9. This relation differs from that of linear growth because once the Lake Michigan fish had the greater annual increments their increments continued to be the larger, with a single exception, for years 4 through 9.

The annual increments of weight of the Lake Michigan whitefish increased from 0.9 ounce at the

end of the first year to a maximum of 15.2 ounces in the fifth and thereafter declined (except for the eighth) to 7.9 ounces in the ninth year. The increments of central Green Bay fish increased from the first-year value of 1.0 ounce to the fourth-year maximum of 17.0 ounces. The downward trend was then irregular; the lowest value was 8.5 ounces at the seventh year of life.

Without exception the Green Bay fish attained the weights of 1, 2, 3, 4, and 5 pounds in a year earlier than did the Lake Michigan fish (examples, 1 pound during third year in Green Bay and fourth in Lake Michigan; 3 pounds in fifth year in Green Bay and sixth in Lake Michigan; 5 pounds in eighth year in Green Bay and ninth in Lake Michigan).

The 2-pound size limit in effect in the State of Michigan waters of Green Bay at the time of sampling was reached by the Green Bay fish during the fourth year of life.

COMPARISON WITH GROWTH IN OTHER LAKE MICHIGAN WATERS

This section has been limited to the growth of whitefish in Lake Michigan since a full review and comparison of growth in the various Great Lakes waters was recently published by Dryer (1963). The data of table 21 are limited to the first 4 years of life, the period covered in the only previous publication on the growth of whitefish in Lake Michigan (Roelofs, 1958). Among the four areas for which growth data are now available, the South Fox Island fish had by far the poorest growth (only 13.2 inches at the end of 4 years). The central Green Bay fish grew the fastest; they were at least 1.0 inch longer than the others at any of the 4 years of life. Growth was similar in the Lake Michigan and Big Bay de Noc (northern Green Bay) areas. The calculated lengths were equal at 5.6 inches at the end of the first year and at 13.8 inches at the end of the third. The Lake Michigan fish were the longer at the end of 2 years (9.8 as compared to 9.4 inches) but the Bay de Noc fish were the larger (17.9 as compared to 17.2 inches) at 4 years.

The South Fox Island whitefish and the central Green Bay fish are different from each other and from both the Lake Michigan and Big Bay de Noc fish. The data offer no evidence, however, as to whether the growth rates of Lake Michigan and Big Bay de Noc fish are significantly different.

TABLE 21.—Growth in total length of whitefish in different parts of Lake Michigan

Area and source of data	Calculated length at end of year of life			
	1	2	3	4
Present study:				
Lake Michigan.....	Inches 5.6	Inches 9.8	Inches 13.8	Inches 17.2
Central Green Bay.....	6.6	11.8	16.0	18.9
Roelofs (1958):				
Big Bay de Noc.....	5.6	9.4	13.8	17.9
South Fox Island.....	4.3	7.0	9.9	13.2

SEX RATIO

The sex ratio ranged so widely from sample to sample (36 to 84 percent males—see bottom part of table 22) that it is extremely difficult to judge the possible effects of local and seasonal differences, or gear selectivity.

Data on sex ratio often vary erratically when samples are collected near or during the spawning season. The strong preponderance of males in the October 1948 collections from Lake Michigan (77 percent) and Peshtigo (84 percent) might be attributed to prespawning segregation, but the equally great abundance of males (80 percent) in the June 1951 sample from Gills Rock makes this explanation much less attractive. The two collections made in late spring and early summer at Cedar River (45 and 48 percent males) agreed well. Agreement was good also between the July and September samples from Minneapolis Shoals (combined in table 22); the percentage of males was 59 in July and 60 in September. These two pairs of samples from the same locality, then, offer some evidence of local stability, within certain months at least. The only sample in which males were extremely scarce was taken in February 1952 at Washington Island.

Evidence is lacking for any effect of gear on the sex-ratio data. The two gill net samples had the highest (84 percent, Peshtigo) and the lowest (36 percent, Washington Island) percentages of males. The variation was wide also among the remaining samples, all from pound nets; here the percentage of males ranged from 45 (Cedar River) to 80 (Gills Rock).

It seems to be impossible also to speak of a trend in sex ratio with increase of age. A trend toward decrease in the percentage of males with increased age is clearly apparent in the Lake Michigan data but is lacking in the data for Cedar River, 1949—the other sample that covered a fair range of age groups. No clear trend can be established for the remaining samples.

TABLE 22.—Sex composition of whitefish from Lake Michigan and central Green Bay

Age and item	Lake Michigan October 1948	Peshigo October 1948	Cedar River May 1949	Cedar River June 1951	Gills Rock June 1951	Washington Island February 1952	Minneapolis Shoals July and September 1952
I group:							
Percentage males	100				100		100
Number of fish	(4)				(1)		(1)
II group:							
Percentage males	100		33		100		51
Number of fish	(40)		(3)		(41)		(59)
III group:							
Percentage males	100	100	50	48	70	33	63
Number of fish	(27)	(9)	(34)	(70)	(78)	(89)	(162)
IV group:							
Percentage males	80	87	40	43	60	48	20
Number of fish	(20)	(37)	(15)	(7)	(5)	(21)	(5)
V group:							
Percentage males	61	76	67	0			
Number of fish	(106)	(29)	(3)	(1)			
VI group:							
Percentage males	33		46				
Number of fish	(3)		(114)				
VII group:							
Percentage males			50				
Number of fish			(2)				
VIII group:							
Percentage males	100		0				
Number of fish	(1)		(2)				
IX group:							
Percentage males			100				
Number of fish			(1)				
Ages combined:							
Percentage males	77	84	45	48	80	36	60
Number of fish	(201)	(75)	(174)	(79)	(125)	(110)	(227)

The only conclusion warranted by the data of table 22 is that segregation by sex can be pronounced at times other than near the spawning period and/or that local differences in the sex ratio are extremely large.

AGE AND SIZE AT MATURITY

Usable data on both sex and maturity were available only for the Minneapolis Shoals collections of July and September 1952.

The single I-group male and all females of age group II were immature (table 23). Some males (16.7 percent) were mature as age group II and most males (87.3 percent) and a majority of the females (61.0 percent) were mature as age group III. The five IV-group whitefish (one male and four females; no older fish in the sample) all were mature.

All whitefish shorter than 14.5 inches were immature and all longer than 18.4 inches were mature. The first mature males appeared at 14.5–14.9 inches. The percentage of mature males reached 71.5 at 16.0–16.4 inches and was 100 percent above 18 inches (table 24). The first mature female appeared at 16.5–16.9 inches (2 inches longer than for the males); 68.7-percent maturity was reached at 17.0–17.4 inches and 100

percent above 18.4 inches (0.5 inch longer than for males). More than half of all fish of each sex were mature at all lengths, greater than the 17-inch size limit.

TABLE 23.—Relation of age to maturity of whitefish taken at Minneapolis Shoals in July and September 1952

[The single I-group male was immature; the 5 IV-group fish (1 male; 4 females) were all mature]

Sex and state of gonads	Age group	
	II	III
Male:		
Mature	5	60
Immature	25	13
Percentage mature	16.7	87.3
Female:		
Mature	0	36
Immature	29	23
Percentage mature	0.0	61.0

TABLE 24.—Relation of total length (inches) to maturity of whitefish taken at Minneapolis Shoals in July and September 1952

[All fish shorter than 14.5 inches were immature, and all longer than 18.4 inches were mature]

Length	Males		Females	
	Number of fish	Percentage mature	Number of fish	Percentage mature
14.5–14.9	6	16.7	4	0.0
15.0–15.4	11	9.0	8	.0
15.5–15.9	6	16.7	5	.0
16.0–16.4	7	71.5	7	.0
16.5–16.9	15	93.3	6	16.7
17.0–17.4	39	79.5	16	68.7
17.5–17.9	20	90.0	21	71.5
18.0–18.4	18	100.0	9	77.7

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LITERATURE CITED

- BALDWIN, NORMAN S., AND ROBERT W. SAALFELD.
1962. Commercial fish production in the Great Lakes 1867–1960. Great Lakes Fishery Commission, Technical Report No. 3, 166 pp.
- DEASON, HILARY J., AND RALPH HILE.
1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Transactions of the American Fisheries Society, vol. 74, for the year 1944, pp. 88–141.

- DRYER, WILLIAM R.
1963. Age and growth of the whitefish in Lake Superior. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 63, No. 1, pp. 77-95.
- EDSALL, THOMAS A.
1960. Age and growth of the whitefish, *Coregonus clupeaformis*, of Munising Bay, Lake Superior. Transactions of the American Fisheries Society, vol. 89, No. 4, pp. 323-332.
- HART, JOHN LAWSON.
1931. The growth of the whitefish, *Coregonus clupeaformis* (Mitchill). Contributions to Canadian Biology and Fisheries, N.S., vol. 6, No. 20, pp. 427-444.
- HILE, RALPH
1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Transactions of the Wisconsin Academy of Science, Arts, and Letters, vol. 33, pp. 189-337.
1950. Green Bay walleyes—a report on the scientific investigation of the marked increase in abundance of walleyes in Green Bay. The Fisherman, vol. 18, No. 3, pp. 5-6. (Grand Haven, Mich.)
- HILE, RALPH, AND HOWARD J. BUETTNER.
1959. Fluctuations in the commercial fisheries of Saginaw Bay 1885-1956. U.S. Fish and Wildlife Service, Research Report No. 51, 38 pp.
- HILE, RALPH, GEORGE F. LUNGER, AND HOWARD J. BUETTNER.
1953. Fluctuations in the fisheries of State of Michigan waters of Green Bay. U.S. Fish and Wildlife Service, Fishery Bulletin 75, vol. 54, pp. 1-34.
- MOFFETT, JAMES W.
1952. The study and interpretation of fish scales. The Science Counselor, vol. 15, No. 2, pp. 40-42.
- MORAWA, F.W.F.
1960. Jahreszeitliche Veränderungen der chemischen und gewichtsmässigen Zusammensetzung von *Coregonus fera* Jurine des Genfer Sees. Annales de la Station Centrale d'Hydrobiologie Appliquée, tome 8, pp. 281-306.
- PYCHA, RICHARD L.
1961. Recent changes in the walleye fishery of northern Green Bay and history of the 1943 year class. Transactions of the American Fisheries Society, vol. 90, No. 4, pp. 475-488.
- ROELOFS, EUGENE W.
1958. Age and growth of whitefish, *Coregonus clupeaformis* (Mitchill), in Big Bay de Noc and northern Lake Michigan. Transactions of the American Fisheries Society, vol. 87, for the year 1957, pp. 190-199.
- SMITH, STANFORD H.
1954. Method of producing impressions of fish scales without using heat. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 16, No. 2, pp. 75-78.
- VAN OOSTEN, JOHN.
1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. Zoologica, Scientific Contributions of the New York Zoological Society, vol. 2, No. 17, pp. 380-412.
1939. The age, growth, sexual maturity, and sex ratio of the common whitefish, *Coregonus clupeaformis* (Mitchill), of Lake Huron. Papers of the Michigan Academy of Science, Arts, and Letters, vol. 24, for the year 1938, part 2, pp. 195-221.
- VAN OOSTEN, JOHN, AND RALPH HILE.
1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Transactions of the American Fisheries Society, vol. 77, for the year 1947, pp. 178-249.

FEEDING AND GROWTH OF JUVENILE SOFT-SHELL CLAMS, *MYA ARENARIA*

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ABSTRACT

Laboratory experiments and observations on the growth of juvenile clams, *Mya arenaria*, of known age were conducted to aid in developing artificial rearing procedures. Laboratory clams held in running natural sea water without supplemental food, or in standing water with supplemental food, grew as well or better than those in nearby clam flats. The only suitable foods for artificial feeding were species of unicellular algae. Population density affected growth chiefly through competition for food. Growth increased with

temperature when food was adequate, although the winter decline in growth rate apparently was related to decreased food supply as well as to low temperature.

When clams were fed artificially, the concentration of food in the water was critical: concentrations of over 30,000 cells per ml. water led to inefficient utilization by the clams. Need for additional information on water pumping rates, duration of feeding activity, efficiency of food utilization, and the abundance and kinds of clam food in natural sea water is discussed.

Estimating the age of an organism is essential in studying its growth rate and calculating the potential yield of a population. The age of the soft-shell clam, *Mya arenaria*, is generally estimated by counting winter checks or annuli on the shells; however, this method may result in error because the first and possibly the second annulus is apt to be obscured or worn away. Judgement of the first year's growth often is based on experience gained from field observation of juvenile clams at different times of the year. These observations are apt to be misleading, for one seldom knows exactly when the small clams were spawned or whether they represent one or several spawnings, perhaps months apart. Small clams observed in midsummer could be either slow-growing individuals spawned the previous year or fast-growing individuals spawned in the current year. Furthermore, sampling procedures ordinarily used in field studies may introduce a bias leading to inaccurate estimates of size distribution.

Unless the clam-bearing sediments are subjected to long and painstaking separation in the laboratory, the smallest individuals generally are missed. The customary practice of sieving the sediments in the field becomes impracticable with mesh small enough to retain the early postlarval juveniles.

Observations on the growth of clams of known age should provide a more accurate means of interpreting field data. In addition, a knowledge of early clam growth is valuable in planning artificial culture techniques. The artificial culture of shellfish, particularly the hatching and rearing of juveniles as "seed," has achieved worldwide interest in recent years. Although much of the current interest concerns species other than *Mya*, the artificial propagation of this clam frequently has been proposed as a management tool. Because economical artificial rearing demands rapid growth rates, the conditions favoring such growth and the factors limiting it should be understood.

The experiments described in the following pages were undertaken to determine whether juvenile

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clams could be reared under artificial conditions. Although primarily intended as guidelines for the development of rearing techniques, the results provided basic biological information about the early growth of clams. The purpose of this paper is to present (1) a standard of growth for clams of known age under laboratory conditions; (2) an evaluation of this standard (the degree to which it is representative of natural growth in various clam producing areas); and (3) information about environmental influence on growth.

METHODS

The growth experiments described in this paper utilized clams of known age, having been spawned and reared in the laboratory. Clams used in any one experiment were from the same brood (i.e., all spawned at the same time, but not necessarily from the same parents). Some of the clams were held in natural running sea water, while others were subjected to experimental treatments in both running and standing sea water. When standing sea water was used, periodic changes of the water and artificial feeding were necessary. These conditions provided better control of some environmental factors, such as food supply, than did the use of running water.

Except where temperature was itself the variable under investigation, all experiments were conducted at prevailing seasonal temperatures; that of the sea water in the supply lines (fig. 1, A) or of the ambient air in the laboratory. Laboratory air temperatures, which determined the temperature of most standing water experiments, ranged from 18° to 22° C. in summer and from 14° to 17° C. in winter. Water temperatures were varied by immersing standing-water containers in a water bath. Running water was heated or cooled by passing the incoming water through a heat exchanger. In early experiments, these heat exchangers were polyethylene cylinders equipped with electric immersion heaters or a refrigerator coil controlled by thermostats. For Experiment 7, a specially engineered control system provided desired flow rates and temperatures.

Growth, the criterion used to evaluate the effects of experimental treatment, was determined by measuring the shell length before and after treatment. Clams over 2 mm. long were measured with vernier calipers, those less than 2 mm.,

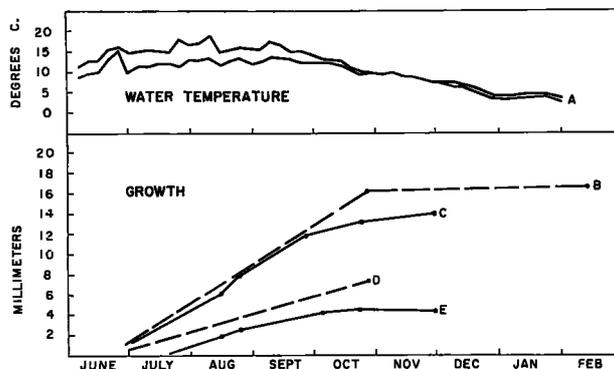


FIGURE 1.—Growth of laboratory reared clams in running sea water. Dash lines indicate lack of intervening measurements.

- A. Five-day averages of maximum and minimum supply line water temperatures.
- B. Growth of May 28 brood at a population density of less than one clam per 5 cm.².
- C. Same as (B), except disturbed periodically for measurement.
- D. Growth of May 28 brood at a population density of more than one clam per cm.².
- E. Growth of June 20 brood at a population density of more than one clam per cm.².

with an ocular micrometer. In Experiment 2, the number of clams was large and the individuals were small and difficult to measure; therefore, some of the initial and terminal mean sizes were estimated from samples rather than from measurements of all individuals. These estimates and the mean growth derived from them were subject to sampling error. However, the estimated mean sizes plus or minus two standard errors were found reliable at a confidence level of 95 percent or better. For growth means (the difference between initial and terminal mean sizes) with this degree of reliability the following confidence limits were assigned: the lower limit was the difference between the terminal mean size less two standard errors and the initial mean size plus two standard errors; the upper limit was the difference between the terminal mean size plus two standard errors and the initial mean size less two standard errors. When only the initial mean size was estimated from a sample and the terminal mean size was determined by measuring every individual, the 95 percent confidence interval was reduced by about one-half. When all the clams were measured, before and after the treatment period, sampling error was not involved.

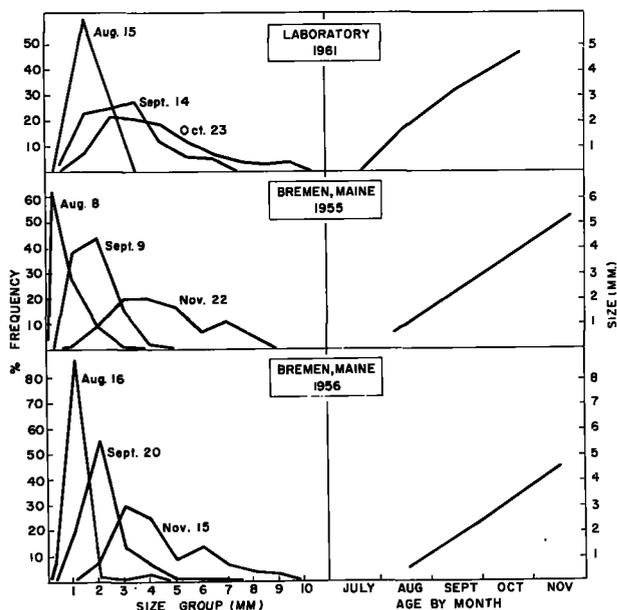


FIGURE 2.—Size-frequency distributions and mean lengths of laboratory and natural clam populations at monthly intervals.

Except when held in running water, clams were fed suspensions of unicellular algae of known volume and measured for cell concentration with a haemocytometer. When dry-weight values of the food supply were desired, 10 volumetric samples of the food suspension were filtered, washed, dried, and weighed, and the mean weight converted to dry weight per million cells.

RESULTS

Concurrently with the experiments described below, the broods providing the experimental clams were held in containers of running sea water and were not disturbed except for occasional measurements. The population density under these conditions was relatively high—in excess of one clam per cm^2 ; therefore, a portion of one brood was removed and held at a much lower density (about one clam per 5 cm^2) for comparative observation. The growth of these clams, reflecting the most elementary sort of laboratory culture, served as a guide for evaluating growth under more artificial conditions. Dense populations grew more slowly than populations from the same brood held at reduced density. Growth was slightly better when the clams were not disturbed than when they were removed periodically for measure-

ments. The optimum growth rate achieved averaged about 3.8 mm. per month. The growth rate in the high density populations averaged about 1.8 mm. per month. Growth in all groups became slower during the fall, and virtually ceased in the winter. The comparative growth rates are shown in figure 1. The size-frequency distributions of a dense population (that shown in figure 1, E) at each measurement period are shown in figure 2, top left.

EXPERIMENT 1

Effect on Growth of Competition Between Fast and Slow Growing Individuals

The size frequency distribution of young clams of the same age changes as the clams grow, reflecting an increase in range and skewness. The large individuals grow faster than the smaller ones. Not only does the growth increment per unit time increase with size, but this increment as a fraction of the total length also increases. The non-linearity of the early growth rate skews the distribution curve to the right. Although this is a recognized attribute of early growth in many organisms, it seemed possible that the phenomenon also was influenced by interaction among the clams. Thus, if the food gathering ability of the individuals increased with size, fast growing clams might grow even faster at the expense of the others. To test this experimentally, two sizes of clams were distributed in 200-ml. glass finger bowls of filtered sea water:

- (1) Bowls 1 and 2 with 50 "small" (about 1.2 mm.) clams each.
- (2) Bowls 3 and 4 with 5 "large" (about 2.6 mm.) clams each.
- (3) Bowls 5 and 6 with 4 "large" and 10 "small" clams each.

The individual and mean sizes of the "large" and "small" clams in each bowl were recorded. The relative numbers of "large" and "small" clams assigned to each bowl were determined on the basis of the cube of their length: one "large" clam was assumed equivalent to 10 small ones. Thus, the total food requirement for each bowl was considered equal. The mean daily ration was 35.9×10^6 algal cells (*Dicrateria* sp. and *Monochrysis lutheri*) per bowl. After 27 days, the clams were measured and the mean growth of both "large" and "small" clams determined (table 1).

The similarity in growth between "small" clams with and without competition from the larger, and also between the "large" clams with and without the competition of the smaller, indicates that interaction between clams of different sizes does not have a more appreciable effect on the growth rate than competition between clams of similar sizes.

TABLE 1.—Growth of juvenile clams in populations of uniform and of mixed sizes

Experimental group	Initial size	Terminal size	Growth
	Millimeters	Millimeters	Millimeters
"Large" clams only.....	2.5	6.7	4.2
"Large" clams only.....	2.6	6.7	4.1
"Small" clams only.....	1.1	3.1	2.0
"Small" clams only.....	1.2	3.0	1.8
"Large" clams in mixed populations.....	2.7	6.7	4.0
"Large" clams in mixed populations.....	2.8	6.4	3.6
"Small" clams in mixed populations.....	1.2	3.3	2.1
"Small" clams in mixed populations.....	1.2	3.1	1.9

EXPERIMENT 2

Effect of Population Density on Growth

Although the effects of reducing population density are apparent (fig. 1), a more precise test was desirable, particularly to ascertain whether the effects were associated with density in some way other than in competition for food. The mean size of the clams in the December 1 brood was estimated from a sample of 127 individuals on February 9. From this brood, 1,480 individuals were distributed among 16 glass bowls, each containing 200 ml. of filtered sea water, so that one series of four bowls contained 200 clams each; a second series, 100 clams each; a third series, 50 clams each; and a fourth series, 20 clams each. To facilitate feeding and handling, the physical positions of the bowls were not randomized, but arranged in a square of four rows of 4 bowls at each population density. The clams composing the population of each bowl were selected at random. The initial mean size of the clams in all but the last 4 bowls was assumed to be that of the brood mean plus or minus two standard errors. The initial mean size of the clams in the last 4 bowls was determined by measuring all individuals. Food (*Dicrateria* sp.) was supplied twice daily in measured quantities, so that one bowl in each series received twice that of the second bowl, 4 times that of the third bowl and 8 times that of the fourth. Thus a range of feeding rates (food available per clam) was obtained. This range in-

cluded several duplications of feeding rates resulting from different combinations of food supply and numbers of individuals to share it. Twenty-four days later, the clams were again measured. From the four high-density bowls, randomly selected samples of 100 individuals were measured; from the other bowls, all of the clams were measured (table 2 and fig. 3).

TABLE 2.—Effects of competition on the growth and size distribution of juvenile clams

Bowl number	Clams used	Food		Mean size		Growth	
		Cells supplied	Cells per clam	Initial	Terminal	Absolute	Relative
	Number	Millions	Millions	Millimeters	Millimeters	Millimeters	Millimeters
1.....	200	992	4.96	1.62	2.08	0.46	0.09
2.....	200	496	2.48	1.62	2.09	.47	.19
3.....	200	248	1.24	1.62	1.93	.31	.25
4.....	200	124	.62	1.62	1.99	.37	.59
5.....	100	992	9.92	1.62	2.26	.64	.06
6.....	100	496	4.96	1.62	2.02	.40	.08
7.....	100	248	2.48	1.62	1.92	.30	.12
8.....	100	124	1.24	1.62	1.87	.25	.20
9.....	50	992	19.84	1.62	2.48	.86	.04
10.....	50	496	9.92	1.62	2.35	.73	.07
11.....	50	248	4.96	1.62	2.08	.46	.09
12.....	50	124	2.48	1.62	1.90	.28	.11
13.....	20	992	49.6	1.53	2.60	1.08	.02
14.....	20	496	24.8	1.65	2.41	.76	.03
15.....	20	248	12.4	1.41	2.16	.75	.06
16.....	20	124	6.2	1.47	1.66	.19	.03

As expected, growth was inversely proportional to population density and directly proportional to the amount of food supplied, although this relationship did not appear significant at the highest population density. These results could be related to competition for food alone, or to competition for food plus other density dependent effects. In almost every instance, however, where the amount of food per clam was similar and the population density was different, growth showed no consistent or significant relationship to the density. This can be seen by tracing the positions of corresponding geometrical symbols across figure 3. Here only the three highest population densities are considered, since among these are several cases of duplication or triplication of feeding rates. Feeding rates of 1.24×10^6 cells per clam occurred in bowls 3 and 8; rates of 2.48×10^6 cells per clam occurred in bowls 2, 7, and 12; rates of 4.96×10^6 cells per clam in bowls 1, 6, and 11; and rates of 9.92×10^6 cells per clam in bowls 5 and 10. These feeding rates are indicated in the graph by crosses, squares, circles and triangles, respectively. In no case is there a consistent or significant slope to the lines determined by corresponding symbols.

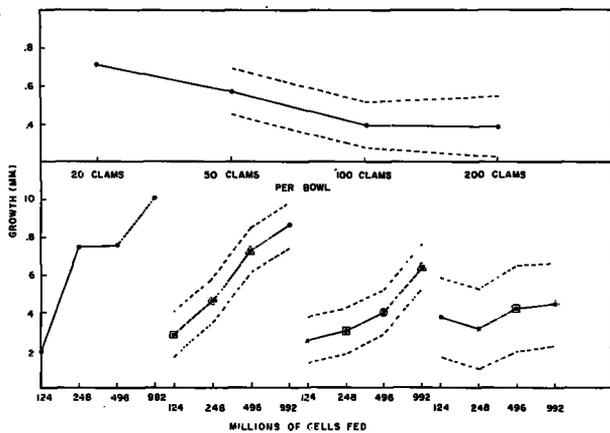


FIGURE 3.—Top: relation between population density and growth. Each point represents the mean growth in all bowls at each population density. Bottom: relation between available food and growth at the four population densities designated above. Corresponding geometrical symbols represent equivalent feeding rates (number of cells available per clam). Dash lines indicate 95 percent confidence limits.

One instructive feature of the data obtained from this experiment is the mean growth plotted against feeding rate (fig. 4). The growth, which increases with feeding rate, does not increase linearly. The growth per unit of food (table 3, last column) is lower at a high feeding rate than at a low feeding rate. This phenomenon suggests inefficient utilization of food at high concentrations. The method of feeding may be partly responsible for this effect. Food was introduced twice daily and, immediately following its introduction, the concentration of cells was highest in the maximally fed bowls. Here the concentration averaged about 145×10^3 cells per ml., substantially higher than clams normally encounter in nature. Had the same amount of food been introduced in smaller quantities at more frequent intervals, the feeding efficiency of the maximally fed clams might have been improved. Some effects of cell concentration on feeding efficiency are described below.

EXPERIMENT 3

Effect of Food Concentration on Feeding Efficiency

Under certain conditions, clams reject masses of particles filtered from the water instead of ingesting them. The presence of these masses (pseudofeces) among the true fecal material in the containers indicates inefficient food utilization.

JUVENILE SOFT-SHELL CLAMS

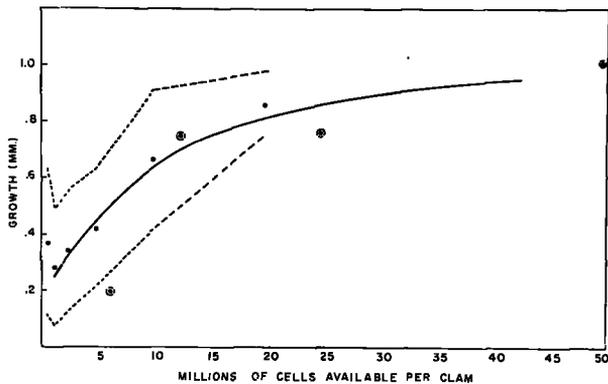


FIGURE 4.—Relationship between growth and feeding rate. Solid points represent estimates based on sampling, for which the 95 percent confidence limits are designated by dash lines. Circled points represent means obtained from measuring entire groups of clams. The curve (solid line) has been fitted by eye.

To determine the effect of food concentration on the amount of pseudofeces produced, food was supplied in different initial concentrations. Four pairs of bowls, each containing five clams (averaging 8.0 mm.) and 200 ml. of filtered sea water were provided with *Dicrateria* cells according to the following schedule:

- (1) First pair fed 90×10^6 cells once in 8 hours.
- (2) Second pair fed 45×10^6 cells twice in 8 hours.
- (3) Third pair fed 18×10^6 cells five times in 8 hours.
- (4) Fourth pair fed 9×10^6 cells 10 times in 8 hours.

All groups, therefore, received the same amount of food, but the initial concentrations of cells in the water were different: 450×10^3 , 225×10^3 , 100×10^3 , and 50×10^3 cells per ml., respectively. After 8 hours the material accumulated in the bowls was examined under the microscope. Much of the food had been rejected as pseudofeces except in those bowls where the concentration immediately after feeding was less than 100×10^3 cells per ml.

EXPERIMENT 4

Effect of Food Concentration on Digestive Efficiency

Food particles ingested and passed through the gut sometimes were not digested, and the presence of intact algal cells in the feces also indicated inefficient food utilization. The effect of cell concentration on this type of inefficiency was

investigated in an experiment similar to the preceding one. Four pairs of bowls, each containing five clams (averaging 16.5 mm. in size) and 1,000 ml. of filtered sea water were provided with *Dicrateria* cells on the following schedule:

- (1) First pair fed 136×10^6 cells once in 8 hours.
- (2) Second pair fed 68×10^6 cells twice in 8 hours.
- (3) Third pair fed 27.2×10^6 cells five times in 8 hours.
- (4) Fourth pair fed 13.6×10^6 cells 10 times in 8 hours.

The initial concentrations therefore were 136×10^3 , 68×10^3 , 27.2×10^3 , and 13.6×10^3 cells per ml., respectively. Examined after 8 hours, the feces in the first and second pairs of bowls contained substantial quantities of undigested cells. In the third pair, fewer undigested cells were present, but only in the fourth pair was the amount negligible. Therefore, at concentrations greater than about 30×10^3 cells per ml., inefficiency of food utilization occurs due to incomplete digestion. Although concentrations of this magnitude are not frequent in the natural environment, they might occur in laboratory clam culture through misguided attempts to force growth. Not only do moderately high concentrations result in poor efficiency, but very high concentrations may inhibit feeding almost entirely (Blake, 1961).

EXPERIMENT 5

Relationship Between Quantity of Food Eaten and Growth

Several attempts were made to relate growth to the quantity (weight) of food eaten. Experimental and control groups of clams were measured and placed in separate bowls, each containing 200 ml. of filtered sea water. The experimental groups were provided with measured quantities of *Dicrateria* cells twice daily, while control groups were fed nothing. After a few weeks the mean growth was determined (table 3). This value was corrected for growth not due to the food supplied, by subtracting the mean growth of the controls. The corrected mean growth was then converted to a monthly basis. The numbers and sizes of the clams, the amount of food provided, and the duration of each experiment are recorded in table 3. In the third group, the 25 experimental clams were divided equally among 5 bowls, rather than held all in one bowl as with the other groups.

The growth rates for 5 mm. clams were 2.7 and 3.0 mm. per month, respectively—rates similar to those observed in running water at low population density. Although the quantities of food supplied were accurately measured, it was not possible to determine how much of this was actually eaten and digested. Since the cell concentration immediately after feeding in these experiments was high (0.2×10^6 – 0.3×10^6 cells per ml.) some inefficiency in utilization probably occurred and the actual consumption of food probably was less than indicated.

In this experiment, as with most of the others, *Dicrateria* sp. was used as food. Experiments to evaluate other algal species showed that a diatom, *Cyclotella nana*, was slightly better, and a flagellate, *Monochrysis lutheri*, was slightly poorer. Still poorer, but not unsatisfactory, foods were *Phaeodactylum tricornutum* and *Olithodiscus* sp. *Chlorella* sp. and *Tetraselmis* sp. promoted very little growth. No growth was obtained by feeding nonliving food materials such as pulverized seaweeds (*Fucus* and *Ulva*), flour, tomato juice, and dehydrated dogfood or mouse food.

TABLE 3.—Growth data for artificially fed clams in experiment 5

	First group		Second group		Third group	
	Experimental	Control	Experimental	Control	Experimental	Control
Number of clams.....	20	20	10	10	25	5
Mean initial length (mm.).....	2.36	2.32	5.02	5.02	5.40	5.40
Mean terminal length (mm.).....	3.90	2.37	6.96	5.11	7.60	5.80
Observed increase (mm.).....	1.54	.05	1.94	.09	2.20	.40
Corrected increase (mm.).....	1.49	-----	1.85	-----	1.80	-----
Millions of cells supplied/day/clam.....	2.49	-----	9.77	-----	8.01	-----
Dry weight of cells supplied (mg./day/clam).....	.03	-----	.11	-----	.21	-----
Duration of experiment (days).....	28	-----	20	-----	18	-----
Growth in mm./month (30 days).....	1.5	-----	2.7	-----	3.0	-----

EXPERIMENT 6

Effect of Temperature on Growth

Observations on juvenile clams in running natural sea water, and otherwise unfed, showed that the growth rate declined in autumn and virtually ceased in winter. Several experiments were conducted to learn the effects of temperature on growth. The first of these were in December and January. Two groups of 60 small clams each were held in running sea water (about 20 l. per

hour), one group at the seasonal temperature of 6° C., and the other at an average temperature of about 19° C. Preliminary trials indicated that as long as the flow rate exceeded the combined pumping rates of the clams, variations in flow rate had no appreciable effect on growth. A third group of 65 individuals was held in standing water, which was cooled in a sea-water bath to an average temperature of 8° C. These clams were fed a daily ration of *Monochrysis lutheri*. After 1 month the fed clams showed a mean growth of 0.7 mm. Those in running water showed negligible growth at either temperature level (table 4).

TABLE 4.—Effect of temperature on the growth of juvenile clams

Season	Mean water temperature	Clams used	Mean size		Duration of experiment	Growth per month
			Initial	Terminal		
	° C.	Number	Milli-meters	Milli-meters	Days	Milli-meters
Summer: In running natural sea water.	6	16	11.28	11.56	22	0.38
	12.5	18	11.31	12.35	22	1.42
	20	18	11.33	12.79	22	1.99
Winter: In running natural sea water. In standing water, artificially fed.	6	60	9.9	9.9	31	—
	19	60	9.6	9.7	31	.1
	8	65	10.7	11.4	32	.7

EXPERIMENT 7

Experiment Conducted the Following September

Three groups of 16 clams were held in running sea water at mean temperatures of 6°, 12°, and 20° C., the flow rates of the water being equal. After 3 weeks, increases in mean size at the temperatures cited were 0.28, 1.04, and 1.46 mm., respectively (table 4).

In summer, growth occurred at all temperatures but was better in warmer water. In winter, little or no growth occurred in either warm or cold natural water, but did occur in cold water when supplementary food was provided. Therefore, reduction of temperature does reduce growth, but with adequate food, some growth can occur in cold water. Furthermore, as little growth was achieved during winter in either warm or cold natural water, the winter decline in growth is probably due to a paucity of food in the water.

DISCUSSION AND CONCLUSIONS

To compare natural and laboratory growth of clams, data obtained in the field are necessary, but for reasons stated earlier, these data are difficult to obtain. Fortunately, some dependable data

were available, taken from samples collected and processed in such a way that unbiased representation of all size groups was assured. These samples were collected during years when the setting period was comparatively short. Bias due to continued recruitment of small, postlarval sizes therefore was minimal. The samples were obtained in the late summer and autumn of 1955 and 1956 from a small cove near Bremen, Maine, a location typical of the Maine coast. In both years, the growth rate and size distribution were similar and not greatly different from those observed subsequently in the laboratory (fig. 2).

A comparison of the three sets of size and growth data reveals that, during the first months, the Bremen clams have slower growth and a narrower range of sizes than the laboratory clams. This may be due to some continued recruitment from the plankton prior to sampling. If so, the first month's growth would be faster than indicated by the data, and the almost linear growth curves for the field samples would be more convex, resembling the laboratory growth more closely.

Growth in other regions could be expected to differ—to be more rapid, for example, in the southern part of the range. Data from Mead and Barnes (1905) seem to demonstrate more rapid growth in southern areas, although their samples probably were biased by the errors previously mentioned, particularly since their sampling was done with "a rather coarse sieve." According to their report, the mean size of clams sampled in upper Narragansett Bay, R.I., increased from 6.1 mm. on July 4 to 23.7 mm. on September 30, an apparent mean growth of about 6 mm. per month. More recent data for southern New England is given by Matthiessen (1960), who measured the growth of marked clams held in trays in a Martha's Vineyard, Mass., salt pond. The smallest of these clams, 15–20 mm. in size, although not specifically aged, were probably the current year's juveniles and were growing at a rate of about 5 mm. per month in September.

The laboratory growth of clams at Boothbay Harbor was markedly better than natural growth when the laboratory clams were held at low population densities. A comparison between the growth of artificially fed clams and either natural growth or laboratory growth in running water is rather difficult, however. The environments, particularly the food supply, are not readily com-

parable. Adequate data, from the literature or from these experiments, are not available to place values on several important parameters necessary for this comparison. The amounts and kinds of food present in sea water, the pumping rates of the clams, the time actually spent in feeding, and the efficiency of food utilization are too imperfectly known. Nevertheless, growth as good or better than that obtaining in Maine coastal water was achieved by artificial feeding at a rate of 0.2 mg. of food daily per 5 mm. clam, and probably could have been achieved with even less food.

The greatest divergence of artificial feeding from natural conditions seemed to be in the rate and method of supplying food rather than the actual quantity or kind supplied. In nature, clams obtain adequate food by filtering large volumes of water containing sparsely dispersed particles. Artificial feeding permits the increase of food concentration, so that the clams may remove much greater quantities at the same filtering rate; however, the intermittent feeding used in the preceding experiments eliminates much of this advantage. In the first place, high initial concentrations are rapidly and wastefully reduced; secondly, residual concentrations between feedings may become too low for adequate nourishment, and energy used in continued water filtering is wasted. More natural conditions and better growth would probably be achieved by frequent or continuous feeding to maintain a more constant food concentration, not exceeding about 30,000 cells per ml.

The detrimental effects of crowding are apparent from the experimental results and are probably related largely to competition for food. Optimum population densities, therefore, would depend on the amount of food available, the water circulation, and the sizes of the clams.

Temperature also has an effect on growth, probably through its effect on water filtering rate. Although growth slows down appreciably in winter, this effect is caused by a decrease in food material in the sea water as well as by a reduction in the water filtration rate. The reduction in growth rate with temperature is not linear. The experimental data show that between 12.5° and 20° C., the rate per month decreases an

average of 0.08 mm. per degree of temperature drop. Between 6° and 12.5°, the rate decreases an average of 0.16 mm. per degree, about twice as much. This decrease extrapolated would indicate cessation of growth at 3.7° C. According to Belding (1930), clams cease feeding entirely at 2.8° C.

These growth rates are based on the availability of food in summer. During the winter, growth ceases at higher temperatures, presumably due to a decrease in the phytoplankton content of the water. When this paucity of natural food was compensated by artificial feeding, the observed growth at a mean temperature of 8° C. was 0.7 mm. per month, almost the same as the expected summer growth calculated at 0.16 mm. per degree above 3.7°.

In conclusion, the results of the laboratory observations supported by the best available field data show that the first summer's growth of young clams in a densely seeded Maine clam flat (and probably in other northern New England areas as well) averages about 5 mm. and seldom exceeds 10 mm. Where the clams are more thinly dispersed or where hydrographic conditions are highly favorable, these values may be greater. In southern New England, warmer summer water temperatures (20°-27° C.) may permit faster growth and a longer growing season.

LITERATURE CITED

- BELDING, DAVID L.
1930. The soft-shelled clam fishery of Massachusetts. Commonwealth of Massachusetts, Department of Conservation, Division of Fish and Game, Marine Fisheries Section, Marine Fisheries Series No. 2, 65 pp.
- BLAKE, JOHN W.
1961. Preliminary measurements of filter feeding activity of the soft-shell clam, *Mya arenaria*, by the use of radioactive algae. Biological Bulletin, vol. 121, No. 2, p. 383.
- MATTHIESSEN, GEORGE C.
1960. Observations on the ecology of the soft clam, *Mya arenaria*, in a salt pond. Limnology and Oceanography, vol. 5, No. 3, pp. 291-300.
- MEAD, A. D., AND E. W. BARNES.
1905. Observations on the soft-shell clam. (Fifth paper.) Thirty-fourth Annual Report of the Commissioners of Inland Fisheries of Rhode Island, pp. 30-68.

COMBINED EFFECTS OF TEMPERATURE AND SALINITY ON DEVELOPMENT OF EGGS AND GROWTH OF LARVAE OF *M. MERCENARIA* AND *C. VIRGINICA*

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ABSTRACT

A study of the effect of temperature on the survival and growth of larvae of the hard clam (*Mercenaria mercenaria*) and American oyster (*Crassostrea virginica*) has shown that the rate of growth of these larvae at different temperatures was critically affected by the type of food organisms available. Both clam and oyster larvae were able to utilize naked algae, such as the chrysophytes *Monochrysis lutheri*, *Isochrysis galbana* and *Dicrateria* sp., and show significant growth at lower temperatures than those at which chlorophytes, such as *Chlorella* sp., which have cell walls, could be utilized. This implies that the enzyme systems required to digest naked flagellates are active at lower temperatures than are the enzyme systems required to digest cell walls.

The cells of *I. galbana* and *M. lutheri* are destroyed by temperatures of 27.5° C.-30.0° C., and growth of larvae receiving these foods at such temperatures was reduced. *Chlorella* sp. can tolerate temperatures of 33.0° C., and the rate of growth of larvae receiving *Chlorella* sp. continued to increase with each 2.5° C. increase in temperature up to 33.0° C.

Salinity also affects the temperature tolerance of clam and oyster larvae. At near optimum salinities the larvae survive and grow over a significantly wider range of temperatures than at salinities near the lower limits of their tolerance. We observed the temperature tolerances of clam and oyster larvae at a series of decreased salinities.

The development of comparatively routine methods for rearing lamellibranch larvae (Loosanoff and Davis, 1950) allowed a number of studies on the effect of various environmental factors on the development of eggs and on the survival and growth of larvae of bivalve mollusks. These studies have, in general, been conducted by varying the one factor under observation, while holding other factors as constant as possible.

Although we have reared the larvae of 20 species of lamellibranchs, at the Bureau of Commercial Fisheries Biological Laboratory in Milford, Conn., we confined experiments on the tolerances of larvae to environmental factors to two species, the American oyster, *Crassostrea virginica*, and the hard clam, *Mercenaria* (= *Venus*) *mercenaria*. We studied the effects, upon the eggs and larvae of

these species, of turbidity, salinity, temperature, the kind and quantity of food, the concentration of eggs and larvae, and a variety of dissolved materials (Loosanoff and Davis, 1963).

Informative as such studies were, the results might not apply absolutely to these organisms in nature where more factors must be considered. We know little about the combined effect of two or more environmental factors on lamellibranchs. Medcof and Needler (1941) attempted to deduce the interaction of temperature and salinity on the condition index of oysters, *C. virginica*, in natural waters, and Costlow, Brookhout, and Monroe (1960, 1962) have obtained laboratory data on the combined effects of temperature and salinity on development of eggs and larvae of the decapod crustaceans *Sesarma cinereum* and *Panopeus herbstii*. Kinne (1963) has reviewed the present

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knowledge of the effects of temperature and salinity on marine and brackish water fish and has emphasized the fact (p. 302) that "monofactorial analysis may lead to conclusions that are ecologically invalid," and "should be replaced wherever possible by bi, tri or polyfactorial approach." We undertook the present study to determine how variations in such factors as food and salinity affected the temperature tolerance of eggs and larvae of the American oyster, *C. virginica*, and the hard clam, *M. mercenaria*.

METHODS

Adult clams and oysters were induced to spawn in the laboratory. Induction was by thermal stimulation and the addition of a water suspension of ripe gametes as previously described (Loosanoff and Davis, 1963). To determine the effects of experimental conditions on development of eggs, 10,000 to 15,000 recently fertilized eggs were placed in each 1-liter beaker. To determine the effects of the same conditions on survival and growth of larvae, three to six 15-liter cultures, each containing approximately 500,000 eggs, were started using our normal sea water (salinity 27.5 parts per thousand (p.p.t.)) at $24.0^{\circ} \pm 1.0^{\circ}$ C. After 48 hours the eggs developed into normal straight-hinge larvae. These larvae were then screened from all containers and resuspended in a single 4-liter container. We measured the number of larvae per unit volume and placed the desired number of larvae (usually 8,000 to 15,000) in each of the 1-liter beakers.

In preliminary experiments to find the effects of different food organisms on survival and growth of larvae at different temperatures, duplicate cultures of 48-hour larvae were set up for each food, or combination of foods, and replicate sets were prepared for each of the six different temperatures tested in a single experiment.

In the experiments to study the combined effects of temperature and salinity on egg development and on survival and growth of larvae, duplicate cultures of eggs were established in each of the six salinities tested and replicate sets were prepared for each of the six different temperatures tested, giving a total of 72 cultures in each experiment.

To learn the effect of the several combinations of salinity and temperature on egg development

48 hours after the eggs were placed in the experimental cultures, the larvae in each culture were collected, on a stainless steel screen of small enough mesh to retain them, and resuspended in a 250-ml. graduated cylinder. After thoroughly mixing them, we withdrew and preserved a 4-ml. quantitative sample. We examined these samples under a compound microscope ($\times 110$) and counted the eggs developing into normal living larvae. To compare the numbers developing normally in successive experiments, we tabulated the results as a percentage of the maximum number developing under any combination of temperature and salinity in that experiment.

In experiments to determine the combined effect of temperature and salinity on survival and growth of larvae, we changed the water in the cultures every second day to eliminate waste products of larval metabolism and reestablish experimental conditions. In most of our work we added supplemental food daily (Davis and Guillard, 1958), but to keep our salinities constant in the experiments involving reduced salinities, we added food only every second day, when the water was changed and the salinities were adjusted.

To determine the percent survival and growth rate of clam larvae, after 10 days at the experimental conditions or when the larvae were 12 days old we took quantitative samples, in a manner similar to that used at 48 hours. The majority of larvae kept at or near optimum conditions had reached setting size by this time, but even those that had metamorphosed were collected on the screen, resuspended, and included in the quantitative samples.

We took samples for comparing growth rates and survival of oyster larvae after 8 days of experimental treatment or when the larvae were 10 days old. Under optimum conditions, some of the larvae were setting between the 10th and 12th days. Since recently metamorphosed oysters cannot be collected on the screen and resuspended, a random quantitative sample cannot be taken once setting starts.

We examined separate preserved samples under a compound microscope, and counted the larvae that survived the experiment. In addition, we measured 50 clam larvae or 100 oyster larvae from each sample, and calculated the increase in mean length during the experiment as a percentage of

the increase in size of larvae in the most rapidly growing culture.

RESULTS

Type of Food and Growth of Larvae at Different Temperatures

Previous experience had indicated that the failure of larvae to grow at 30.0° C. in some experiments might be an indirect effect of the temperature on the marine algae used as foods rather than a direct effect on the larvae themselves. This was supported by Ukeles (1961) who reported that the cells of the chryomonads *Isochrysis galbana* and *Monochrysis lutheri*, the two food organisms used in these early experiments, were destroyed by temperatures above 27.0° C.

Because we were interested in determining the direct effects of temperature and salinity on larvae, we designed preliminary experiments to demonstrate the effect of different foods on growth of larvae at different temperatures. In the first experiment, we kept oyster larvae at temperatures of 10.0°, 15.0°, 20.0°, 25.0°, 30.0°, and 33.0° C. with one culture at each temperature receiving *Dunaliella euchlora*, another *Chlorella* sp. (580),¹ and the third a mixture of *Chlorella* sp. (580), *Dicrateria* sp. (BII),² *I. galbana* and *M. lutheri*. The results are shown in figure 1. At 10.0° and 15.0° C. the larvae did not grow appreciably on any of these three foods. At 20.0° C., however, larvae fed the mixture of algae grew appreciably but those receiving the motile green chlorophyte, *D. euchlora*, showed only slight growth and larvae given only the nonmotile chlorophyte, *Chlorella* sp. (580), which has a distinct cell wall, grew hardly at all.

Above 20.0° C., the growth rate of larvae receiving *Chlorella* sp. (580) increased with each increase in temperature. The growth rate of larvae receiving *D. euchlora*, on the other hand, was similar at 25.0°, 30.0°, and 33.0° C., and the growth rate of larvae receiving the mixed algae increased progressively only up to 30.0° C. At 33.0° C., the growth rate was somewhat slower than at 30.0° C.

A second experiment was run to clarify the upper and lower temperature limits for growth of oyster larvae (fig. 2). Again, larvae fed the

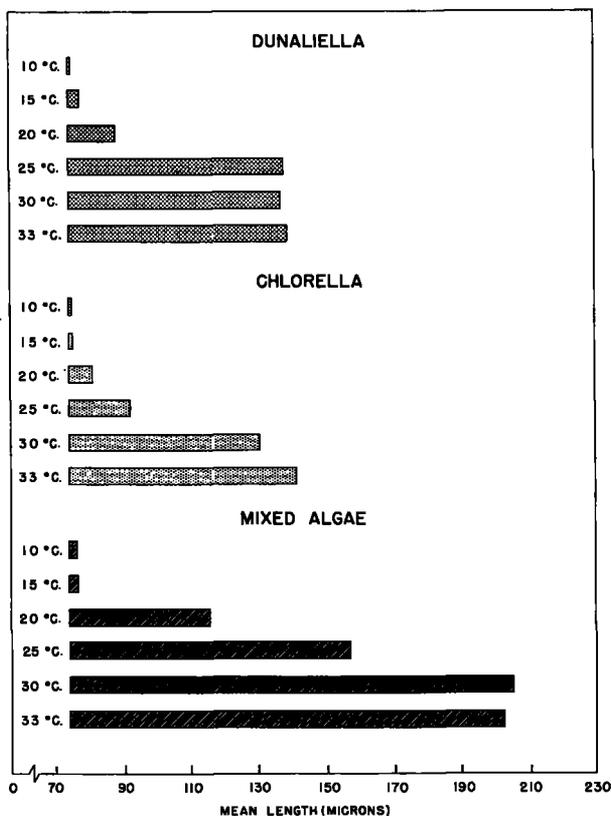


FIGURE 1.—Growth of oyster larvae receiving different foods and reared at different temperatures. Plots are based on mean length of 100 larvae from each temperature at each measuring period.

mixture of algae and kept at 15.0° C. did not grow. Growth of larvae kept at 17.5° C. was minimal, but at 20.0° C. the larvae grew faster, although at 10 days these larvae were still much smaller than those kept at 30.0° or 33.0° C. At 35.0° C., the rate of growth was also much slower than at 30.0° or 33.0° C. and all the larvae died before the end of the experiment.

Since Loosanoff, Miller, and Smith (1951) studied the effect of temperature on the growth rate of clam larvae, we conducted only a single experiment on the effect of different foods on growth of these larvae at different temperatures. Only the *Chlorella* sp. (580) and the mixed algae were tested as foods.

As with oyster larvae, there was a pronounced difference in the ability of clam larvae to utilize the two foods at low temperatures (fig. 3). Although larvae kept at 10.0° C. ingested food, they did not grow and their digestive glands had no

¹ *Chlorella* sp. (Indiana U. collection #580).

² *Dicrateria* sp. (Plymouth collection BII).

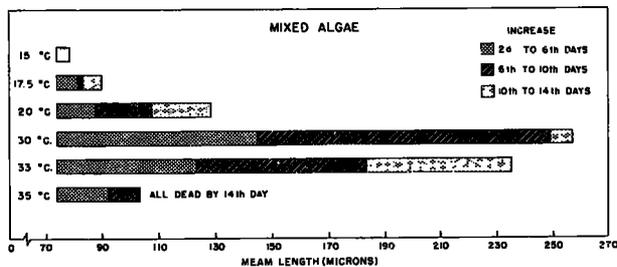


FIGURE 2.—Growth of oyster larvae receiving the mixture of algae as food and reared at high and low temperatures. Plots based on mean length of 100 larvae from each of duplicate cultures at each temperature at each measuring period. Many of the larvae kept at 30.0° and 33.0° C. set between the 10th and 14th days and were not included in the 14-day samples.

coloration, indicating their inability to digest either food. Larvae receiving *Chlorella* sp. (580) and kept at 15.0° C. likewise did not grow and showed no evidence of digesting this food. The digestive glands of larvae kept at 15.0° C. but receiving mixed algae as food did grow, and their digestive glands had normal color, indicating that some of the species of food organisms added were being digested.

All larvae kept at 20.0° C. grew and showed coloration of the digestive gland. Those receiving *Chlorella* sp. (580), however, averaged only 125.45 μ in mean length by the 12th day, while the larvae receiving the mixed algae grew to a mean length of 198.47 μ , i.e., they had reached setting size. At 30.0° C., larvae receiving *Chlorella* sp. (580) were only approaching setting size by the 12th day (mean length 170.0 μ), while those receiving mixed algae already had metamorphosed and averaged 241.45 μ in length.

Effects of Different Salinities on Temperature Tolerance of Eggs and Larvae of Clams

Our methods of determining the percentage of bivalve eggs developing into normal straight-hinge larvae are accurate to about ± 10 percent. Differences of less than 20 percent in the percentages of eggs developing under different conditions, therefore, are of doubtful significance. At our normal salinity, about 27.0 p.p.t., there was no significant difference in the percentage of clam eggs developing normally within the temperature range from 17.5° to 30.0° C. (table 1). At 32.5° and at 15.0° C., however, the percentage was decreased drastically and at 12.5° C. very few normal clam larvae developed.

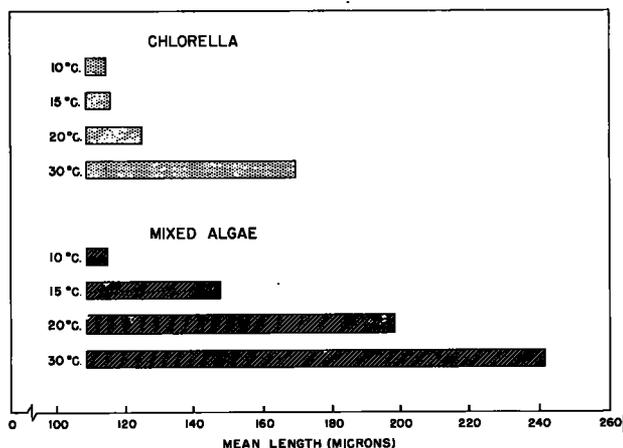


FIGURE 3.—Growth of clam larvae receiving different foods and reared at different temperatures. Plots are based on mean length of 50 larvae from each of duplicate cultures at each temperature. In cultures fed the mixture of algae and grown at 30.0° C. many larvae had already set by the end of the 10-day experimental period but were included in the samples.

At each temperature, fewer eggs developed normally at a salinity of 22.5 p.p.t. than at $27.0 \pm$ p.p.t. Temperatures from 22.5° to 25.0° C. appear to be optimum at the salinity of 22.5 p.p.t. Few of the eggs kept at 32.5° or at 15.0° C. developed normally at this salinity. Moreover, 22.5 p.p.t. was the lowest salinity at which any appreciable number of clam eggs developed.

At 20.0 p.p.t. none of the eggs developed into normal larvae at any temperature except in one experiment where a few normal larvae were found at 20.0° and 25.0° C. It should be emphasized, however, that clam larvae can survive at far lower

TABLE 1.—Percentage of clam eggs developing to the straight-hinge stage at different combinations of temperature and salinity, Milford, Conn.¹

Salinity (P.P.T.)	Temperature (° C.)								
	32.5	30.0	27.5	25.0	22.5	20.0	17.5	15.0	12.5
27.0±	Per- cent 39	Per- cent 81	Per- cent 93	Per- cent 95	Per- cent 92	Per- cent 95	Per- cent 94	Per- cent 24	Per- cent 0
22.5	<1	36	65	79	73	56	52	1	<1
20.0	0	0	0	5	0	<1	0	0	0
17.5	0	0	0	0	0	0	0	0	0
15.0	0	0	0	0	0	0	0	0	0
12.5	0	0	0	0	0	0	0	0	0

¹ Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of eggs developing at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. Only at temperatures and salinities above the broken line was development of eggs comparatively normal.

salinities than the minimum salinity at which clam eggs can develop. From 20.0° to 30.0° C., survival of clam larvae does not decrease significantly until the salinity falls below 17.5 p.p.t. (table 2). Even at 15.0 p.p.t. approximately 50 percent of the larvae kept at temperatures from 17.5° to 25.0° C. survived.

The decrease in survival of clam larvae with a decrease in salinity was most drastic at high temperatures. At 32.5° C., less than 1 percent survived at a salinity of 17.5 p.p.t. At temperatures of 30.0° and 27.5° C., survival dropped from 75 percent at 17.5 p.p.t. to 25 percent or less at 15.0 p.p.t. In contrast, survival of clam larvae, at 12.5° C., although only 56 percent at our normal salinity of 27.0± p.p.t., still averaged 39 percent after 10 days at a salinity of 12.5 p.p.t.

The growth rate of clam larvae was most rapid at 30.0° C. and at a salinity of 27.0± p.p.t. (table 3). In fact 30.0° C. appeared the best temperature for growth of larvae at salinities of both 27.0± and 22.5 p.p.t., although, at all salinities above 17.5 p.p.t., the growth rate was similar at 30.0°, 27.5° and 25.0° C. A temperature of 32.5° C. was obviously above optimum at all salinities.

The temperature range for satisfactory growth of clam larvae narrowed as the salinity decreased. At 27.0± p.p.t. growth was satisfactory, i.e., at least some larvae approached setting size by the 12th day, at all temperatures from 15.0° to 32.5° C. At 17.5 p.p.t., however, satisfactory growth was limited to the temperature range from 20.0° to

TABLE 3.—Percentage increase in mean length of clam larvae kept at different combinations of temperature and salinity for 10 days, Milford, Conn.¹

Salinity (P.P.T.)	Temperature (° C.)									
	32.5	30.0	27.5	25.0	22.5	20.0	17.5	15.0	12.5	
27.0±	65	98	83	93	83	71	53	30	16	
22.5	61	91	85	88	83	68	48	25	12	
20.0	54	85	87	82	80	60	39	17	5	
17.5	15	63	68	66	59	36	21	5	<1	
15.0	0	12	17	31	20	9	3	<1	0	
12.5	0	0	0	2	0	0	0	0	0	

¹ Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The mean increase in length of larvae in the most rapidly growing set of duplicate cultures in each experiment was considered 100 percent for that experiment. The combinations of salinity and temperature above the broken line were the combinations at which the larvae had the most satisfactory growth and shows the similarity of the growth rates at these combinations.

30.0° C.; at 15.0 p.p.t., except at 25.0° C., there was no significant growth of larvae.

When clam larvae kept in various salinities at 12.5° C. were transferred to 24.0° C. water of normal salinity (27.0± p.p.t.), those previously in salinities of 17.5 p.p.t. or higher began to grow normally. Larvae previously kept at 12.5° C. in salinities below 17.5 p.p.t., however, did not recover after the transfer to the higher temperature and salinity and all died within 6 days.

Effects of Different Salinities on Temperature Tolerance of Eggs and Larvae of Oysters

In some experiments oyster eggs developed normally at salinities from 20.0 p.p.t. to 27.0± p.p.t. and temperatures from 17.5° to 32.5° C. In other experiments, however, far fewer normal larvae developed from eggs incubated at the marginal temperatures of 32.5° and 17.5° C. This tendency for poor development at the extremes of the above temperature range became even more pronounced when the eggs were incubated at a salinity of 17.5 p.p.t. (table 4). Of the eggs kept in a salinity of 15.0 p.p.t. only in the cultures kept at 27.5° C. did 30 percent or more of the eggs develop, and at 12.5 p.p.t. only an occasional normal larva developed at any temperature. As shown by Davis (1958), the minimum salinity at which oyster eggs will develop normally is determined in part by the salinity at which the parent oysters were kept prior to spawning.

The survival values for oyster larvae (table 5) indicate that satisfactory survival rates (70 percent

TABLE 2.—Percentage of clam larvae surviving after 10 days, at different combinations of temperature and salinity, Milford, Conn.¹

Salinity (P.P.T.)	Temperature (° C.)									
	32.5	30.0	27.5	25.0	22.5	20.0	17.5	15.0	12.5	
27.0±	77	83	81	75	87	75	71	61	56	
22.5	48	84	87	83	88	76	70	56	46	
20.0	16	72	84	76	77	78	62	50	40	
17.5	<1	76	74	83	85	69	45	50	49	
15.0	0	25	22	57	53	43	58	36	47	
12.5	0	<1	0	12	0	9	12	19	39	

¹ Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of larvae surviving at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. The broken line indicates the ranges of temperature and salinity at which the largest percentage of larvae survived and shows the significant decrease in survival below 17.5 p.p.t.

TABLE 4.—Percentage of oyster eggs developing to the straight-hinge stage at different combinations of temperature and salinity, Milford, Conn.¹

Salinity (P.P.T.)	Temperature (° C.)					
	32.5	30.0	27.5	22.5	20.0	17.5
27.0±	58	86	91	84	83	67
25.0	60	78	88	86	84	80
22.5	58	84	82	88	87	84
20.0	58	77	81	90	86	58
17.5	29	69	89	81	57	10
15.0	1	17	39	24	2	0
12.5	0	0	0	0	0	0
10.0	0	0	0	0	0	0
7.5	0	0	0	0	0	0

¹ Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of eggs developing at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. Only at the combinations above the broken line was development comparatively normal.

or better) were limited to temperatures of 27.5° to 32.5° C. and salinities of 10.0 to 27.5 p.p.t. Survival at 22.5° C. was slightly less. Moreover, almost 50 percent of the larvae survived at all salinities and temperatures tested, except that only 23 percent survived in a salinity of 7.5 p.p.t. at 32.5° C., and 22 percent in a salinity of 27.0± p.p.t. at 17.5° C.

As indicated by the percentage increase in mean length at 10 days (table 6), the growth rate of oyster larvae, at all salinities, shows a very sharp break between 27.5° and 22.5° C. Except at

TABLE 5.—Percentage of oyster larvae surviving after 8 days at different combinations of temperature and salinity, Milford, Conn.¹

Salinity (P.P.T.)	Temperature (° C.)					
	32.5	30.0	27.5	22.5	20.0	17.5
27.0±	75	70	76	56	49	22
25.0	68	64	71	54	43	45
22.5	71	66	68	54	45	42
20.0	75	58	66	60	48	37
17.5	78	71	83	65	37	53
15.0	81	74	81	71	67	42
12.5	86	90	73	67	41	40
10.0	67	79	71	66	49	49
7.5	23	38	48	54	53	38

¹ Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The highest number of larvae surviving at any combination of temperature and salinity in each experiment was considered 100 percent for that experiment. Only at the combinations above the broken line was survival of larvae over 70 percent.

TABLE 6.—Percentage increase in mean length of oyster larvae kept at different combinations of temperature and salinity for 8 days, Milford, Conn.¹

Salinity (P.P.T.)	Temperature (° C.)					
	32.5	30.0	27.5	22.5	20.0	17.5
27.0±	89	92	76	35	19	9
25.0	84	87	74	32	21	11
22.5	88	91	76	32	21	13
20.0	90	94	76	31	22	12
17.5	85	92	77	31	19	10
15.0	79	87	67	28	18	8
12.5	49	69	52	21	11	4
10.0	30	36	36	14	6	1
7.5	2	11	19	6	2	<1

¹ Percentages given are the mean of duplicate cultures in each of two or more replicate experiments. The mean increase in length of larvae in the most rapidly growing set of duplicate cultures in each experiment was considered 100 percent for that experiment. The broken line shows the ranges of temperature and salinity at which the larval growth rate was 70 percent or better.

temperatures above 22.5° C. and salinities above 12.5 p.p.t., a larval growth rate equivalent to 70 percent of the maximum rate was achieved only in a salinity of 12.5 p.p.t. and temperature of 30.0° C. At salinities of 10.0 p.p.t. or lower, the growth rate was less than 50 percent at all temperatures; at temperatures of 22.5° C. or lower the growth rate was less than 50 percent at all salinities.

To determine the time required for larvae to reach metamorphosis at different temperatures, oyster larvae were reared at 20.0°, 22.5°, 25.0°, 27.5°, 30.0° and 32.5° C. and at our normal salinity of 27.0± p.p.t. The experiment continued until all larvae set. The results are shown in table 7.

Because of the slow growth of larvae at low temperatures and low salinities, we did not rear larvae to metamorphosis at all combinations of temperature and salinity.

TABLE 7.—Number of days for oyster larvae to reach metamorphosis at combinations of different temperatures and 27.0± p.p.t. salinity, Milford, Conn.

Temperature ° C.	Days after fertilization to—	
	Beginning of setting	End of setting
30.-32.5	10-12	18-20
27.5	14-16	28-30
25.0	24-26	38-40
22.5	28-30	44-46
20.0	36-40	64-68

DISCUSSION

To determine (1) the minimum temperature at which oyster larvae, grown to setting size at temperatures of $27.0 \pm 1.0^\circ \text{C}$., could set; and (2) the effect of lowered temperatures on intensity of setting, we conducted five experiments. In each 1-liter beaker, we placed approximately 2,000 oyster larvae reared to 80-mesh size ($250\text{--}300 \mu$ in length) at a temperature of $27.0^\circ \pm 1.0^\circ \text{C}$.; two of these cultures were kept at each temperature. Two clean oyster shells in each culture, were examined every second day to determine the occurrence and relative intensity of setting. We counted only those spat occurring on the white inner surface of the test shells. The average numbers of spat per culture recorded are shown in table 8.

In the third experiment, the larvae initially were smaller than in the other experiments, and, although none set at 15.0° or 12.5°C ., some still lived 20 days after transfer to these temperatures. It appeared, from these experiments, that at temperatures of 15.0° and 12.5°C . the only larvae that set were those that were mature and ready to set at the time of transfer to these temperatures. Smaller immature larvae, although living more than 20 days after transfer, apparently were unable to develop to the setting stage.

At temperatures from 25.0° to 17.5°C ., the number of larvae completing metamorphosis declined with each decrease in temperature, and the time required for setting increased. The decrease in intensity of setting with decreasing temperature within this range is probably the result of the cumulative mortality of larvae as a result of the slower growth rate and consequent lengthening of the larval period.

TABLE 8.—Average numbers of spat at combinations of different temperatures and $27.0 \pm$ p.p.t. salinity, Milford, Conn.¹

Temperature ° C.	Average spat per culture				
	1st ex- periment	2d ex- periment	3d ex- periment	4th ex- periment	5th ex- periment
	Number	Number	Number	Number	Number
25.0	293		723	920	604
22.5	181	723			
20.0	170	519			
17.5		397			
15.0			0	67	
12.5			0	33	1
10.0					0

¹ Oyster larvae used in the individual experiments were grown to setting size at temperatures of $27.0 \pm 1.0^\circ \text{C}$. and a normal salinity of $27.0 \pm$ p.p.t.

The failure of bivalve larvae to grow at low temperatures appears to be the result of their inability to digest available food. Our experiments demonstrated that larvae survived for long periods and ingested food at temperatures below the minimum temperature at which they grow. Moreover, since larvae can utilize some foods at lower temperatures than other foods (figs. 1 and 3), perhaps the enzyme systems needed to digest algae without cell walls, such as the chrysomonads, are active at lower temperatures than are the enzyme systems required to digest algae that have cell walls, such as *Chlorella*. The increase, with increase in temperature, in growth rate of larvae fed any one food probably results from increased activity of the enzyme system at higher temperatures.

From our knowledge of the temperature and salinity tolerances of the food organisms used in these experiments, there is no reason to suspect that the reduced growth rate of larvae at low temperatures and salinities results from an indirect effect on the food organisms. Ukeles (1961), however, showed that at temperatures of 27.0°C . or higher the cells of *I. galbana* and *M. lutheri* are destroyed, while cells of *Chlorella* sp. (580) survive even at 33.0°C .

The growth rate of oyster larvae receiving *Chlorella* continued to increase with each increase in temperature up to 33.0°C ., while larvae fed the mixture of algae showed no increase between 30.0° and 33.0°C . (fig. 1). It seems probable that in the latter case any increase in activity of the enzyme systems of the larvae at 33.0°C . was offset by a reduction in the amount of food available due to the destruction of cells of *I. galbana* and *M. lutheri*. We believe, therefore, that our results at higher temperatures may be partly due to an indirect effect on the larvae through the food chain. Nevertheless, the drastic reduction in rate of growth at 35.0°C . and the heavy mortality of larvae (fig. 2) almost certainly reflect a direct effect of temperature on the larvae themselves.

Both clam and oyster larvae survived in fair numbers and grew appreciably in salinities significantly lower than the minimum salinity at which eggs develop normally. There are, however, striking differences in the tolerances of the

larvae of these two species of lamellibranchs. Virtually none of the clam eggs kept at 12.5° C., the minimum temperature at which clam larvae will grow, developed normally (table 1). In contrast, an approximately normal number of oyster eggs developed at 17.5° C. (table 4), which is the lowest temperature at which oyster larvae show appreciable growth.

The most notable interspecific differences were to the effects of temperature and salinity on growth of larvae. Growth of clam larvae was comparatively little affected by temperature differences within the range from 20.0° to 30.0° C., whereas growth of oyster larvae was markedly affected by every increase in temperature from 17.5° to 30.0° C. The optimum temperature for growth of clam larvae was not well defined but appeared to drop from 30.0° C. at salinities of 22.5 p.p.t. and higher to 27.5° C. at salinities of 17.5 and 20.0 p.p.t. and to 25.0° C. at a salinity of 15.0 p.p.t. Differences in the growth rate of clam larvae at temperatures from 22.5° to 30.0° C. appeared to be almost random, and the optimum growth rate occurred at temperatures other than 30.0° C. at each salinity tested in one or more experiments (table 9).

In contrast, there is a marked stepwise increase in the growth rate of oyster larvae with each increase in temperature up to 30.0° C. (table 6). There is a fairly well defined optimum between 30.0° and 32.5° C. for all salinities except 7.5 p.p.t. where the optimum is 27.5° C. Differences between the growth rate of oyster larvae at 30.0° and at 32.5° C. were usually small with sometimes one and sometimes the other temperature giving the maximum growth rate, indicating that the optimum might well lie between these two temperatures.

Clam and oyster larvae differed also in their growth response to different salinity levels, but whereas oyster larvae were more sensitive than clam larvae to differences in temperature, the latter appeared more sensitive to salinity differences. Growth of clam larvae, at almost all temperatures, decreased stepwise with each decrease in salinity (table 3), and the maximum salinity (27.0± p.p.t.) was the most nearly optimum of the salinities tested. The growth rate of oyster larvae, however, was relatively constant at each temperature within the salinity range from

15.0 to 27.5 p.p.t. and there was no apparent optimum salinity (table 6).

Kinne and Kinne (1962) stated that extreme conditions of temperature, salinity, and oxygen could induce developmental arrest, and that "such arrest may remain reversible if conditions are normalized within hours or a few days; longer periods cause irreversible damage; they are lethal." In our experiments the "developmental arrest" of clam larvae kept at 12.5° C. and at salinities above 17.5 p.p.t. was reversible, but irreversible at salinities of 15.0 p.p.t. or lower.

The data on clam eggs and larvae were remarkably consistent, i.e., there were no major differences between successive experiments in the percentage of eggs developing to the straight-hinge larval stage, in the survival of larvae or in the growth rate of larvae (tables 9 and 10). In experiments with oyster eggs and larvae, however, there were large differences between experiments on the effect of salinity. Moreover, while the data on the salinity tolerances of clam eggs and larvae agreed quite well with Davis (1958), the data on salinity tolerances of eggs and larvae of oysters did not.

In the first experiment with oyster eggs and larvae, for example, the optimum salinity for growth of oyster larvae at all temperatures was either 25.0 or 27.0± p.p.t. (exp. 1, table 11). In experiments 2 and 3, however, the optimum salinity at most temperatures was between 15.0 and 20.0 p.p.t. Because we suspected that better growth at lowered salinities might be a result of diluting toxic external metabolites of algal blooms that sometimes occur in Milford Harbor (Davis and Chanley, 1955), in the fourth experiment we used sea water collected from a considerable distance offshore in Long Island Sound. The egg development data from this experiment (exp. 4, table 12) showed unexpectedly that dilution of dissolved toxins in sea water may indeed be responsible for better results in lowered salinities. None of the eggs kept in the undiluted offshore sea water developed into normal larvae, indicating that our offshore sea water contained a considerable amount of toxins. Although an approximately normal percentage of straight-hinge larvae developed at some temperatures in 20.0 p.p.t., a normal percentage did not occur at all temperatures except in cultures where this sea water had been diluted to a salinity of 17.5 p.p.t. or lower.

In experiments 5 and 7 (tables 11 and 12),

TABLE 9.—Growth of clam larvae at 12 days, at different combinations of salinity and temperature, Milford, Conn.
[Data from individual experiments using clam eggs and larvae]

Salinity (p.p.t.) and temperature (° C)	Mean length of larvae at 12 days					Increase in mean length of larvae (2d to 12th days)				
	Experiment				Average	Experiment				Average
	1	2	3	4		1	2	3	4	
27.5 p.p.t.:										
12.5°			123.8	126.4	125.1			16.0	15.2	15.6
15.0°			141.7	142.4	142.1			31.3	27.7	29.5
17.5°			172.5	168.0	170.3			97.6	47.9	52.7
20.0°	188.9	193.4	188.8	195.2	191.5	63.9	78.4	71.5	69.1	70.7
22.5°	213.9	198.4			206.2	84.3	83.1			82.7
25.0°	213.1	203.6	222.2	234.7	218.4	83.7	85.0	100.0	100.0	83.9
27.5°	211.3	200.0			205.7	82.2	84.6			83.4
30.0°	233.3	216.4	218.2	230.9	224.9	100.0	100.0	96.6	97.0	98.4
32.5°	188.0	181.2			184.6	68.3	67.0			65.1
22.5 p.p.t.:										
12.5°			120.9	121.0	121.0			13.6	11.0	12.3
15.0°			135.7	137.5	136.6			26.1	23.9	25.0
17.5°			164.3	164.3	164.3			50.6	44.9	47.7
20.0°	190.6	192.5	184.9	195.5	188.4	65.5	77.6	68.2	61.5	66.2
22.5°	207.2	201.7			204.5	78.9	96.2			82.5
25.0°	211.6	202.1	212.2	228.7	212.8	82.4	86.6	91.5	91.4	88.0
27.5°	212.3	203.3			207.8	83.0	87.7			85.3
30.0°	216.7	198.9	215.0	238.1	215.9	86.9	83.6	93.9	98.7	90.8
32.5°	177.4	182.0			179.7	54.8	67.8			61.8
20 p.p.t.:										
12.5°			110.7	112.7	111.7			4.9	4.5	4.7
15.0°			124.5	126.8	127.2			16.6	17.0	17.3
17.5°			152.3	154.9	153.6			40.4	37.5	39.0
20.0°	181.3	184.6	172.6	177.3	179.0	58.0	70.2	57.7	55.1	60.2
22.5°	199.5	203.0			201.6	72.6	88.3			80.4
25.0°	206.0	204.3	203.1	210.4	205.9	77.9	88.6	83.7	81.0	82.3
27.5°	217.9	207.8			208.4	87.6	85.4			86.5
30.0°	212.8	207.5	198.2	218.1	209.2	83.4	91.3	79.5	87.0	85.4
32.5°	169.0	173.9			171.4	48.0	60.2			54.1
17.5 p.p.t.:										
12.5°			105.9	106.1	106.0			8	.0	.4
15.0°			111.6	112.9	112.3			5.6	4.6	5.1
17.5°			132.6	131.7	132.2			23.5	19.3	21.4
20.0°	157.2	150.9	145.8	148.0	150.5	38.5	39.0	54.8	32.1	36.1
22.5°	184.4	170.8			177.6	60.5	57.6			59.1
25.0°	193.4	188.5	179.1	182.1	185.8	67.7	73.9	63.2	58.8	65.9
27.5°	188.2	186.6			187.4	63.5	72.1			67.8
30.0°	184.6	187.0	175.7	183.1	182.6	60.6	72.4	60.3	59.6	63.2
32.5°	0	141.3			141.3	0	29.6			14.8
15.0 p.p.t.:										
12.5°			104.2	104.0	104.1			0	.0	.0
15.0°			106.3	106.9	106.6			1.1	.0	.6
17.5°			110.1	110.0	110.1			4.4	2.3	3.4
20.0°	120.9	121.4	116.0	116.5	118.7	9.1	11.0	9.4	7.4	9.2
22.5°	138.2	127.1			132.6	23.1	16.3			19.7
25.0°	153.1	142.9	140.7	139.2	149.2	35.2	31.1	30.5	25.2	30.5
27.5°	152.7	0			152.7	34.8	0			17.4
30.0°	125.9	0	129.3	124.3	126.5	13.2	0	20.7	13.5	11.9
32.5°	0	0			0	0	0			0
12.5 p.p.t.:										
12.5°			104.1	104.9	104.5			0	.0	.0
15.0°			102.7	104.2	103.5			0	.0	.0
17.5°			103.7	101.5	102.6			0	.0	.0
20.0°	0	0	103.5	104.1	103.8	0	0	0	.0	.0
22.5°	0	0			0	0	0	0	.0	.0
25.0°	111.7	0	112.8	103.3	109.3	1.7	0	6.7	.0	2.1
27.5°	0	0			0	0	0			0
30.0°	0	0	102.8	0	102.8	0	0	0	.0	.0
32.5°	0	0			0	0	0			0

¹ All died in one experiment. Average of single experiment in which some survived.

oyster larvae kept at 27.5° and 30.0° C. and salinities of 7.5 and 10.0 p.p.t. showed a much better rate of survival and growth than in experiment 6 of this series or recorded by Davis (1958). It is possible that in experiments 5 and 7 we happened to get genetic crosses that were better adapted to tolerate low salinities than the general population of Long Island Sound oysters. It is conceivable that the variations in growth noted in experiments 1, 2 and 3 also were genetic and that the Long Island Sound oyster population is heterogeneous in tolerance to salinity.

Regardless of the possible effect of toxic pollutants and of genetic factors, the general features of the effect of lowered salinities on temperature tolerance appear clear. By every measure of temperature tolerance, the tolerated range of temperatures narrowed as the salinity decreased. As measured by the percentage of eggs developing normally and as measured by the growth of larvae, this narrowing of the range resulted from more rapid decreases at both extremes of the temperature range than at intermediate temperatures. As measured by the survival of clam larvae, the

TABLE 10.—Development of clam eggs to straight-hinge larval stage and survival of clam larvae at 12 days, at different combinations of salinity and temperature, Milford, Conn.

[Data from individual experiments using clam eggs and larvae]

Salinity (p.p.t.) and temperature (°C)	Eggs developing to straight-hinge larval stage					Larvae surviving to 12th day				
	Experiment				Average	Experiment				Average
	1	2	3	4		1	2	3	4	
27.5 p.p.t.:										
12.5°			0.0	0.0	0.0			31.8	79.6	55.7
15.0°			1.7	56.0	23.6			56.8	65.3	61.0
17.5°			100.0	88.1	94.1			63.6	78.2	70.9
20.0°	99.4	93.4	88.1	98.8	94.9	73.9	85.0	71.2	69.4	74.9
22.5°	92.9	90.1			91.5	74.8	100.0			87.4
25.0°	100.0	93.4	85.6	100.0	94.8	86.6	87.6	62.7	64.6	75.4
27.5°	86.5	100.0			93.3	79.9	83.3			81.4
30.0°	80.0	79.3	80.5	82.7	80.6	89.8	78.2	64.4	100.0	83.1
32.5°	78.1	.0			39.0	61.1	92.3			76.7
22.5 p.p.t.:										
12.5°			.0	1.8	.9			32.2	59.9	46.0
15.0°			1.7	0.6	1.1			34.7	78.2	56.4
17.5°			53.4	50.6	52.0			49.2	89.8	69.5
20.0°	58.7	49.6	62.7	50.6	55.4	91.9	82.5	50.8	78.9	76.0
22.5°	80.0	66.1			73.1	85.5	90.2			87.9
25.0°	80.6	60.3	94.1	79.8	78.7	91.2	88.9	60.2	93.2	83.4
27.5°	70.3	61.2			65.8	89.4	85.5			87.4
30.0°	32.9	6.6	39.8	63.1	35.6	92.6	80.3	76.3	87.1	84.1
32.5°	.0	.8			.4	55.8	39.3			47.6
20. p.p.t.:										
12.5°			.0	.0	.0			14.4	66.0	40.2
15.0°			.0	.0	.0			33.1	66.7	49.9
17.5°			.0	.0	.0			37.3	86.4	61.9
20.0°	.0	.0	.0	1.8	.5	82.0	86.8	51.7	91.8	78.1
22.5°	.0	.0			.0	86.9	66.7			76.8
25.0°	.0	.0	.8	19.6	5.1	99.3	88.5	44.9	72.8	76.4
27.5°	.0	.0			.0	86.9	82.1			84.5
30.0°	.0	.0	.0	.0	.0	89.4	42.7	66.9	89.1	72.0
32.5°	.0	.0			.0	6.0	25.2			15.6
17.5 p.p.t.:										
12.5°			.0	.0	.0			45.8	51.7	48.8
15.0°			.0	.0	.0			39.0	61.2	50.1
17.5°			.0	.0	.0			37.3	61.2	44.6
20.0°	.0	.0	.0	.0	.0	95.8	71.4	33.9	74.1	68.8
22.5°	.0	.0			.0	86.6	82.5			84.5
25.0°	.0	.0	.0	.0	.0	100.0	84.2	67.8	80.3	83.1
27.5°	.0	.0			.0	89.8	57.3			73.5
30.0°	.0	.0	.0	.0	.0	63.3	54.3	100.0	86.4	76.0
32.5°	.0	.0			.0	.0	.9			.5
15.0 p.p.t.:										
12.5°			.0	.0	.0			75.4	18.4	46.9
15.0°			.0	.0	.0			55.1	17.0	36.1
17.5°			.0	.0	.0			78.0	37.4	57.7
20.0°	.0	.0	.0	.0	.0	35.3	17.5	82.2	36.1	42.8
22.5°	.0	.0			.0	76.7	28.6			62.7
25.0°	.0	.0	.0	.0	.0	62.9	22.6	92.4	51.7	57.4
27.5°	.0	.0			.0	43.5	.0			21.8
30.0°	.0	.0	.0	.0	.0	3.9	.0	63.6	32.7	25.1
32.5°	.0	.0			.0	.0	.0			.0
12.5 p.p.t.:										
12.5°			.0	.0	.0			63.6	14.3	38.9
15.0°			.0	.0	.0			30.0	8.8	19.4
17.5°			.0	.0	.0			19.5	3.4	11.5
20.0°	.0	.0	.0	.0	.0	.0	.0	24.6	9.5	8.5
22.5°	.0	.0			.0	.0	.0			.0
25.0°	.0	.0	.0	.0	.0	.7	.0	44.1	3.4	12.1
27.5°	.0	.0			.0	.0	.0			.0
30.0°	.0	.0	.0	.0	.0	.0	.0	1.7	.0	.4
32.5°	.0	.0			.0	.0	.0			.0

narrowing of the range was primarily by marked decreases in percent survival at the higher temperatures. With oyster larvae, in these experiments, apparently at even the lowest salinity tested (7.5 p.p.t.) we were just beginning to get marked effects of salinity on survival. It would appear that here, also, the narrowing of the range would be primarily by heavy mortality at the higher temperatures if the salinity were to be lowered still further.

The difference in the temperature requirements

for satisfactory growth of clam and oyster larvae probably accounts for some of the difference in success of recruitment of these two species of bivalves in many shellfish-producing areas. While many clam larvae, in water at proper salinity, reached setting size by the 12th day at only 15.0° C., oyster larvae in 20.0° C. water required 36 to 40 days to begin setting. Although the actual time required in natural waters would be altered by the type and quantity of food and by other factors, the relative time required probably

TABLE 11.—Growth of oyster larvae at 10 days, at different combinations of salinity and temperature, Milford, Conn.

[Data from individual experiments using oyster eggs and larvae]

Salinity (p.p.t.) and temperature (° C)	Mean length of larvae at 10 days								Increase in mean length of larvae (2d to 10th days)							
	Experiment							Average	Experiment							Average
	1	2	3	4	5	6	7		1	2	3	4	5	6	7	
27.5 p.p.t.:	Microns	Microns	Microns	Microns	Microns	Microns	Microns	Microns	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
17.5°	94.70	81.20	82.65	83.07	83.34	87.53	85.42	85.42	22.2	6.7	4.9	4.2	7.0	8.5	8.7	
20.0°	112.76	86.76	86.60	102.85	92.23	106.46	97.93	97.93	41.8	12.7	7.5	14.5	15.4	19.8	18.9	
22.5°	130.94	99.74	102.50	141.21	116.15	130.37	120.15	120.15	63.1	26.7	17.8	34.4	34.7	34.1	35.1	
27.5°	161.05	121.32	135.94	224.38	170.45	208.23	178.59	178.59	97.1	49.9	71.8	77.6	80.4	80.7	76.3	
30.0°	163.59	142.46	223.75	242.26	190.17	240.50	200.35	200.35	100.0	72.7	96.3	86.8	97.0	100.0	92.1	
32.5°	152.73	138.86	229.45	243.77	193.75	220.00	196.33	196.33	87.9	68.8	100.0	87.6	100.0	87.7	88.9	
25.0 p.p.t.:																
17.5°	99.50	79.44	83.98	88.56	87.87	87.87	87.87	87.87	27.1	4.8	5.8	7.0	11.2	11.2		
20.0°	107.83	91.33	89.48	107.25	98.97	98.97	98.97	98.97	37.1	17.6	9.4	19.3	20.9	20.9		
22.5°	120.83	103.97	105.15	141.73	117.92	117.92	117.92	117.92	51.7	31.2	11.1	34.6	32.2	32.2		
27.5°	160.65	130.37	135.88	229.00	173.95	173.95	173.95	173.95	85.8	59.7	71.8	80.0	74.3	74.3		
30.0°	150.98	139.71	224.55	251.44	192.75	192.75	192.75	192.75	91.4	69.8	96.9	91.6	86.6	86.6		
32.5°	156.00	140.98	226.25	239.99	191.87	191.87	191.87	191.87	82.5	71.1	97.7	85.7	84.3	84.3		
22.5 p.p.t.:																
17.5°	97.99	86.96	82.88	91.99	89.96	89.96	89.96	89.96	26.0	12.9	5.1	8.8	13.2	13.2		
20.0°	108.02	93.36	90.20	110.00	100.39	100.39	100.39	100.39	37.3	19.8	10.2	18.2	21.4	21.4		
22.5°	114.84	103.57	101.68	144.03	116.03	116.03	116.03	116.03	45.0	30.8	17.3	35.8	32.2	32.2		
27.5°	157.36	137.85	164.98	238.27	174.62	174.62	174.62	174.62	93.0	67.2	68.3	84.8	75.8	75.8		
30.0°	160.29	156.25	213.18	256.61	194.58	194.58	194.58	194.58	96.3	83.3	89.5	94.3	90.9	90.9		
32.5°	152.63	149.97	226.90	240.40	192.48	192.48	192.48	192.48	87.6	80.8	98.4	85.9	88.2	88.2		
20.0 p.p.t.:																
17.5°	94.47	85.49	85.00	90.09	88.76	88.76	88.76	88.76	22.0	11.3	6.5	7.8	11.9	11.9		
20.0°	107.97	92.59	95.60	110.32	101.62	101.62	101.62	101.62	37.2	19.0	13.3	18.3	22.0	22.0		
22.5°	113.60	98.74	109.23	137.96	114.88	114.88	114.88	114.88	43.6	25.6	22.2	32.7	31.0	31.0		
27.5°	139.83	136.62	191.13	244.42	178.00	178.00	178.00	178.00	73.2	66.4	75.2	88.0	75.7	75.7		
30.0°	153.80	156.25	230.80	267.62	202.12	202.12	202.12	202.12	88.9	87.6	100.0	100.0	94.1	94.1		
32.5°	160.25	160.23	220.85	243.40	193.68	193.68	193.68	193.68	85.0	91.9	94.4	88.0	89.8	89.8		
17.5 p.p.t.:																
17.5°	93.93	85.83	84.55	89.73	79.00	85.81	86.48	86.48	20.8	11.7	6.2	7.6	9.5	9.5		
20.0°	100.38	95.05	97.03	112.56	92.79	102.39	100.03	100.03	28.6	21.6	14.3	19.5	19.4	19.4		
22.5°	108.43	100.95	111.50	136.87	113.59	124.58	116.99	116.99	37.7	28.0	23.6	32.1	30.6	30.6		
27.5°	131.58	147.92	198.18	241.35	166.98	197.12	180.52	180.52	63.9	78.6	79.8	86.4	74.0	76.7		
30.0°	143.45	160.47	223.58	265.29	189.30	224.35	201.73	201.73	77.3	92.1	96.2	98.8	90.3	91.8		
32.5°	144.53	164.52	217.99	231.93	175.10	204.43	189.75	189.75	78.5	93.7	92.6	81.5	84.3	84.8		
15.0 p.p.t.:																
17.5°	89.81	86.26	82.90	85.23	77.96	84.42	84.43	84.43	16.7	12.1	5.1	5.3	6.6	8.1		
20.0°	95.28	97.63	94.75	111.40	89.70	102.36	98.52	98.52	22.9	24.4	12.8	18.9	18.1	18.1		
22.5°	105.08	101.06	109.95	131.32	104.78	126.20	113.07	113.07	34.0	28.1	22.6	29.2	28.4	28.4		
27.5°	120.50	144.20	181.89	243.83	130.59	197.73	169.79	169.79	51.4	74.6	69.2	87.7	67.4	67.4		
30.0°	134.50	166.77	212.80	261.52	160.77	235.62	195.33	195.33	67.2	99.0	89.2	96.8	97.1	86.9		
32.5°	139.08	167.75	209.59	220.44	153.90	192.52	180.55	180.55	72.3	100.0	87.2	75.5	78.8	78.8		
12.5 p.p.t.:																
17.5°					76.20	84.23	80.24	80.24					6.5	3.8		
20.0°					86.05	95.69	90.87	90.87					13.3	11.3		
22.5°					95.85	114.05	104.95	104.95					24.3	21.0		
27.5°					118.47	186.42	152.45	152.45					67.6	52.1		
30.0°					142.31	207.60	174.95	174.95					80.3	68.5		
32.5°					145.37	138.85	142.11	142.11					39.2	49.3		
10.0 p.p.t.:																
17.5°					77.00	74.88	77.99	76.62					2.7	1.4		
20.0°					83.80	80.25	86.51	83.52					7.8	6.1		
22.5°					103.40	86.58	103.54	97.84					18.0	13.5		
27.5°					159.50	103.81	151.70	138.37					46.9	35.6		
30.0°					172.70	106.14	150.69	143.13					46.3	36.3		
32.5°					138.40	109.30	124.42	124.04					30.5	29.7		
7.5 p.p.t.:																
17.5°					78.60	72.26	75.26	73.71					1.1	6		
20.0°					76.40	73.95	79.96	76.77					3.9	2.0		
22.5°					84.50	75.54	91.10	83.71					10.6	5.6		
27.5°					117.40	84.76	123.43	108.53					29.9	19.1		
30.0°					103.00	79.69	103.09	95.26					17.3	10.9		
32.5°					79.40	74.32	79.25	77.66					3.5	1.8		

would be comparable. In Long Island Sound, where the temperature rarely gets above 21.0° C. and where there are strong tides, during such a greatly prolonged free-swimming period most oyster larvae might be lost by dispersal and by natural predation and mortality. The more rapidly maturing clam larvae, however, would suffer much less loss from these causes.

The fact that mature oyster larvae reared at relatively high temperature (27.0° C.) could set when transferred to temperatures as low as

12.5° C. suggests that oyster larvae that had grown to setting size in protected shallow estuaries where the temperature reached 25.0° to 30.0° C. might well be the source of mature larvae that set in the colder waters of Long Island Sound and similar areas.

SUMMARY

1. Both clam and oyster larvae can ingest foods at significantly lower temperatures than the minimum temperatures at which they can digest and

TABLE 12.—Development of oyster eggs to straight-hinge larval stage and survival of oyster larvae at 10 days, at different combinations of salinity and temperature, Milford, Conn.

[Data from individual experiments using oyster eggs and larvae]

Salinity (p.p.t.) and temperature (° C.)	Eggs developing to straight-hinge larval stage								Larvae surviving to 10th day								
	Experiment							Average	Experiment							Average	
	1	2	3	4	5	6	7		1	2	3	4	5	6	7		
27.5 p.p.t.:	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
17.5°	90.8	70.3	79.1	0.0	30.5	38.7	90.9	66.7	23	31	81	35	21	21	38	22	
20.0°	97.5	85.0	100.0	.0	77.3	72.4	66.4	83.1	39	35	86	28	39	66	49	49	
22.5°	100.0	88.4	72.8	.0	88.7	51.5	100.0	83.6	46	20	37	52	47	86	56	56	
27.5°	92.5	93.5	76.2	.0	90.8	100.0	94.1	91.2	64	59	100	63	84	84	76	76	
30.0°	83.0	83.7	75.7	.0	88.7	88.3	97.7	86.2	49	60	79	60	100	79	70	70	
32.5°	82.0	71.6	51.9	.0	20.6	20.9	98.2	57.5	65	54	94	60	86	90	75	75	
25.0 p.p.t.:																	
17.5°	75.5	87.0	78.1	.0				80.2	26	30	87	37				45	
20.0°	87.4	85.5	81.0	.0				83.7	33	31	72	35				43	
22.5°	99.2	91.0	67.0	7.6				85.7	40	35	83	56				54	
27.5°	75.3	91.0	96.6	32.7				87.6	54	81	94	54				71	
30.0°	80.5	75.5	78.6	1.2				78.2	54	64	32	56				64	
32.5°	63.5	50.5	67.0	.0				60.3	52	64	86	71				68	
22.5 p.p.t.:																	
17.5°	67.8	81.5	82.5	5.8				83.9	20	29	83	36				42	
20.0°	95.0	85.0	81.1	55.0				87.0	36	22	78	42				45	
22.5°	99.2	91.0	81.1	71.9				88.4	50	32	77	56				54	
27.5°	93.3	87.6	76.2	.0				82.4	46	88	84	55				68	
30.0°	84.0	96.5	71.8	4.1				84.1	43	72	84	66				66	
32.5°	62.6	50.6	61.6	.0				58.3	61	75	84	64				71	
20.0 p.p.t.:																	
17.5°	41.5	67.0	64.6	9.9				57.7	13	47	71	27				37	
20.0°	94.2	91.8	72.3	81.3				86.1	24	25	88	53				48	
22.5°	95.0	96.5	77.2	84.2				89.6	68	31	73	68				60	
27.5°	82.0	97.0	63.1	100.0				80.7	49	63	83	67				66	
30.0°	80.5	96.0	64.3	42.7				76.9	51	38	79	62				58	
32.5°	51.6	61.4	60.2	10.5				57.7	65	69	97	62				75	
17.5 p.p.t.:																	
17.5°	.0	12.0	7.8	.0	.0	1.2	46.8	9.7	82	73	49	31	46	38	53	53	
20.0°	63.5	55.4	38.3	60.2	20.6	70.6	88.2	56.7	67	19	61	43	33	57	37	37	
22.5°	95.8	73.0	58.2	84.2	79.4	71.2	95.9	80.5	81	24	78	76	60	72	65	65	
27.5°	89.0	100.0	60.2	91.8	100.0	93.3	85.4	88.5	88	65	80	100	81	85	83	83	
30.0°	86.5	77.4	47.1	28.1	69.5	82.2	92.7	69.1	83	64	81	40	68	90	71	71	
32.5°	29.6	25.3	22.8	4.1	6.4	38.0	74.1	28.6	87	88	73	56	85	81	78	78	
15.0 p.p.t.:																	
17.5°	.0	.0	.0	.0	.0	.0	.0	.0	52	57	43	28	29	40	42	42	
20.0°	.8	.0	2.4	.0	.0	.0	7.7	1.6	79	88	80	47	55	50	67	67	
22.5°	28.0	5.3	23.3	18.1	3.5	24.5	63.2	23.7	90	100	73	75	24	65	71		
27.5°	34.8	13.3	31.1	29.8	35.5	55.8	73.6	39.1	100	86	80	45	78	97	81		
30.0°	6.8	.7	8.7	14.6	8.5	28.8	48.2	16.6	81	91	72	37	71	90	74		
32.5°	.0	.0	1.0	1.8	.0	1.2	2.3	.9	81	95	80	70	74	87	81		
12.5 p.p.t.:																	
17.5°					.0	.0	.0	.0					56	23	40	40	
20.0°					.0	.0	.0	.0					33	49	41	41	
22.5°					.0	.0	.0	.0					68	66	67	67	
27.5°					.0	.0	.0	.0					63	83	73	73	
30.0°					.0	.0	.0	.0					79	100	90	90	
32.5°					.0	.0	.0	.0					84	87	86	86	
10.0 p.p.t.:																	
17.5°					.0	.0	.0	.0					49	48	49	49	
20.0°					.0	.0	.0	.0					74	24	49	49	
22.5°					.0	.0	.0	.0					67	65	66	66	
27.5°					.0	.0	.0	.0					61	81	71	71	
30.0°					.0	.0	.0	.0					63	94	79	79	
32.5°					.0	.0	.0	.0					65	68	67	67	
7.5 p.p.t.:																	
17.5°					.0	.0	.0	.0					42	34	38	38	
20.0°					.0	.0	.0	.0					64	41	53	53	
22.5°					.0	.0	.0	.0					57	50	54	54	
27.5°					.0	.0	.0	.0					32	64	48	48	
30.0°					.0	.0	.0	.0					21	54	38	38	
32.5°					.0	.0	.0	.0					39	7	23	23	

¹ Omitted from calculations (see text).

assimilate the food organisms used in these experiments.

2. Both clam and oyster larvae can digest and assimilate naked flagellates, such as *M. lutheri* and *I. galbana*, at lower temperatures than those at which they can utilize algae with cell walls, such as *Chlorella* sp. (580).

3. The minimum temperature for appreciable

growth of clam larvae fed naked flagellates was 12.5° C. and the minimum for growth of oyster larvae was 17.5° C.

4. The optimum salinity for growth of clam larvae was 27.0 p.p.t. (the highest salinity tested) or possibly higher.

5. There was no well-defined optimum temperature for growth of clam larvae at any salinity;

maximum growth occurred at temperatures ranging from 25.0° to 30.0° C. in different experiments at almost all salinities.

6. The optimum temperature for growth of oyster larvae was between 30.0° and 32.5° C. in all experiments for all salinities except 7.5 p.p.t. where the optimum was 27.5° C.

7. There was no well-defined optimum salinity for growth of oyster larvae at any temperature; maximum growth occurred in salinities varying from 15.0 to 27.0 p.p.t. in different experiments at some temperatures and from 20.0 to 27.0 p.p.t. even at 17.5° C., where there was least variation.

8. The effect of reduced salinities on larvae of both clams and oysters was to reduce the range of temperatures tolerated. The temperature range for development of eggs and growth of larvae was shortened from both ends, whereas the range for survival of clam larvae was reduced at least primarily by heavy mortality at high temperatures.

9. The time required for oyster larvae to reach the setting stage, under our laboratory conditions, ranged from 10–12 days at 30.0° to 32.5° C. to 36–40 days at 20.0° C.

10. Oyster larvae reared to setting size at about 27.0° C. and transferred to lower temperatures could set at temperatures as low as 12.5° C., but the percentage of such larvae successfully completing metamorphosis decreased progressively with each decrease in temperature.

LITERATURE CITED

COSTLOW, J. D., C. G. BROOKHOUT, AND R. MONROE.
1960. The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc.) reared in the laboratory. *Biological Bulletin*, vol. 18, No. 2, pp. 183–202.

COSTLOW, J. D., C. G. BROOKHOUT, AND R. MONROE.
1962. Salinity-temperature effects on the larval de-

velopment of the crab, *Panopeus herbstii* Milne-Edwards, reared in the laboratory. *Physiological Zoology*, vol. 35, No. 1, pp. 79–93.

DAVIS, H. C.
1958. Survival and growth of clam and oyster larvae at different salinities. *Biological Bulletin*, vol. 114, No. 3, pp. 296–307.

DAVIS, H. C., AND P. E. CHANLEY.
1955. Effects of some dissolved substances on bivalve larvae. *Proceedings National Shellfisheries Association*, vol. 46, pp. 59–74.

DAVIS, H. C., AND R. R. GUILLARD.
1958. Relative value of ten genera of micro-organisms as food for oyster and clam larvae. U.S. Department of Interior, Fish and Wildlife Service, *Fishery Bulletin* 136, vol. 58, pp. 293–304.

KINNE, O.
1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanography and Marine Biology, An Annual Review*, vol. 1, pp. 301–340.

KINNE, O., AND EVA MARIE KINNE.
1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. *Canadian Journal of Zoology*, vol. 40, pp. 231–253.

LOOSANOFF, V. L., AND H. C. DAVIS.
1950. Conditioning of *V. mercenaria* for spawning in winter and breeding its larvae in the laboratory. *Biological Bulletin*, vol. 98, No. 1, pp. 60–65.

LOOSANOFF, V. L., AND H. C. DAVIS.
1963. Rearing of bivalve mollusks. *Advances in Marine Biology*, Academic Press, vol. 1, pp. 1–136.

LOOSANOFF, V. L., W. S. MILLER, AND P. B. SMITH.
1951. Growth and setting of larvae of *Venus mercenaria* in relation to temperature. *Journal of Marine Research*, vol. 10, No. 1, pp. 59–81.

MEDCOF, J. C., AND A. W. H. NEEDLER.
1941. The influence of temperature and salinity on the condition of oysters (*Ostrea virginica*). *Journal of the Fisheries Research Board of Canada*, vol. 5, No. 3, pp. 253–257.

UKELES, R.
1961. The effect of temperature on the growth and survival of several marine algal species. *Biological Bulletin*, vol. 120, No. 2, pp. 255–264.

A CRITICAL STUDY OF PRIBILOF FUR SEAL POPULATION ESTIMATES

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ABSTRACT

Previously unresolved problems in the population studies of the Pribilof fur seal are reviewed. The tagging estimates of fur seal pups may have been biased by tag mortality and hence the apparent year class fluctuations after 1952 may be unreal. A set of cumulative estimates are given for the number of pups born in each year since 1950. These cumulative estimates depend on the estimate of the ratio of survival of

females to males from birth to age 3. An estimate of this ratio is given. The implications of this study on the population dynamics model of the fur seal are reviewed: in particular while the exact model is less definite, the suggested optimum population level is almost unchanged from that suggested in earlier studies.

Nagasaki (1961) and Chapman (1961) have published models of the population dynamics of the Pribilof fur seal which, while based on different hypotheses, lead to very similar conclusions. These have been summarized in a report of the North Pacific Fur Seal Commission (PFSC).² Both models are based upon estimates of the pup population from tag recoveries.

Such studies of population dynamics are basic to a proper management of the fur seal herds, both to maximize yield and to evaluate the effect of the herd on other living resources of the sea. Moreover the application of methods to this population which has been extensively studied and for which much data are available, are useful; such applications show up the strength and weakness of theoretical procedures and pave the way for a more intelligent application to other valuable marine resources for which studies are in much earlier stages.

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² North Pacific Fur Seal Commission, 1962. North Pacific Fur Seal Commission Report on Investigations from 1958 to 1961. Manuscript report, Washington, D.C. Frequent reference will be made to this report, hereafter called FSCR.

Both authors also noted that there are two basic unresolved questions:

1. Why did the population estimates increase sharply from 1952 to 1956 and drop suddenly from 1956 to 1957?

2. Why do estimates of male survival to age 3 and the estimates of the female population derived from the tagging estimates lead to the conclusion that the survival rate of females from birth to age 3 is much greater than that of males?

The large fluctuations in the pup population as suggested by the estimates do not seem reasonable when the population of breeding females consists of 10 or more age classes. The survival advantage of human females is well known, and there is some evidence of this in other mammalian populations, but the differences are at most a few percent. In an earlier study, however, I suggested that the survival advantage of females over males is 2 to 1 or more.

This study was undertaken with the aim of attempting to determine (1) if the fluctuations in the pup population estimates could be real, and (2) if the differential survival ratio might be much smaller than 2 to 1 or if the differential existed at

all. Actually it is convenient to treat the problems in the opposite order, looking first at all ways of estimating the female population. The apparent differential survival in favor of females could be explained in two ways: (1) Underestimation of the male survival, and (2) overestimation of the number of females based on the tag estimates and the pregnancy rate.

ESTIMATION OF MALE SURVIVAL

The survival of males to age 3 is estimated by adding to the number of returns as counted in the male kill, the estimated escapement of males from the kill. I need not comment on the first of these two factors, except to note that since the survival being calculated is natural survival the kill of a year class at ages other than age 3 has to be adjusted to this age. Thus, in natural conditions, the animals killed at age 2 would have been part of the 3-year-old returns, except for the mortality from age 2 to 3.

The estimation of the escapement (the number of males that survive to age 3 and are not then or later taken in the male kill) is a more complex problem. Such males form what is known as the breeding reserve; if they survive to sociological maturity (roughly age 7), they will become part of the bull herd.

ESTIMATION OF MALE ESCAPEMENT

The method of estimating male escapement was discussed in Kenyon, Scheffer, and Chapman (1954). The males survive the commercial kill either because they arrive at the islands after killing has ended near the end of July or because they are not of the proper sizes at the time of killing. Formerly, animals estimated by eye to be between 41 inches and 45¼ inches were those selected for the kill, and after being killed the animals were quickly measured from the tip of the nose to the base of the tail. This measurement served as a check on the selection but obviously did not prevent errors in selection. In some years the desired lengths have been modified slightly, and more recently measurements have been made of a random sample and according to accepted mammalian procedures, with the selection procedures adjusted accordingly.

In general, any male measuring 40 inches or less in one summer and growing to more than 45 inches

by the following summer might well have been spared. If the male survived to age 6 or 7, it would join the herds of harem or idle bulls. The possibilities of this are seen in the analysis of the data on lengths taken from FSCR tables 82 and 83 on pages 167-172. During the spring and early summer both groups grow at about 3.5 cm. per month. The apparent discrepancy between this figure and the small difference in means of the 3's and 4's (8.71 cm.) is easily explained. The commercial kill selects the larger of the 3-year-olds so that the surviving 4's are the smaller members of the year class. Little is known of growth during the other months of the year; undoubtedly it proceeds at a much slower rate in the less favorable months, but a 5-month growth of 17.5 cm. (almost 7 inches) could change a seal from an undersized animal to an oversized one.

Because of the crude methods used in the past for selecting seals and measuring their lengths, estimation of escapement of the males from the kill has been unsatisfactory. The estimation of escapement due to time of arrival has been based upon a fitting of a normal curve to the kill by "rounds" (a round is a 5-day period in which all hauling grounds of an island are visited). The escapement is estimated from the "tail" of this curve. This estimation has been satisfactory in terms of predicting the kill of 4-year-old males from the escapement of 3-year-olds. Nevertheless, several questions remain unanswered in terms of estimates of the final escapement (i.e., the recruitment to the breeding reserve). For example: is the time of return really normally distributed? Do late returners in one year tend to be late returners in the following year? Are there some animals that do not return to the islands at all at ages 3 or 4, but only return when more fully mature at a later age?

To partially resolve this question, we turn to the

TABLE 1.—Mean lengths of pelagically sampled fur seals in the eastern Pacific, 1958-62¹

Age of seals	March	April	May	June	July
Age 3:					
Mean length (cm.).....	98.7	102.4	106.2	109.0	113.4
Number of seals taken.....	16	49	74	43	26
Age 4:					
Mean length (cm.).....	110.0	110.0	115.3	117.8	121.8
Number of seals taken.....	6	20	26	13	11

¹ Data for 1962 from U.S. samples only. Regression lines fitted to this data yield for 3's: $L=106.0+3.56T$ and for 4's: $L=114.7+3.44T$, where in both cases T is measured in months from mid-May.

data on adult males—the harem and idle bulls. These have been counted annually since 1905 except for the war year 1942. The possible errors in the counts of idle bulls noted in Kenyon et al. (1954) are emphasized. To begin with the pelagic samples obtained in recent years are analyzed for mortality rate estimation. The pertinent data are shown in table 2.

Assuming a constant mortality rate \hat{a} , the best estimate of this rate is by the Chapman-Robson (1960) formula

$$\hat{a} = 1 - \frac{\bar{x}}{1 + \bar{x} - \frac{1}{n}}$$

where n = total number of animals taken
 \bar{x} = mean age with the ages coded beginning with zero. Here $\hat{a} = 0.36$.

In June and July the breeding animals are on the islands and not as susceptible to pelagic capture; therefore some selection may be involved. For this reason captures in these months have been excluded in the last column of table 2. The estimate of the annual mortality rate based on age composition data from recaptures in months other than June and July is 0.36, identical with the estimate from the whole data. One further check is available on this. In 1960 and 1961 excess bulls were killed on Robben Island by the U.S.S.R. (table 11 of FSCR). Their age classification is shown in table 3.

Since a complete age breakdown is not available, Heincke's estimation procedure is used. This yields:

for 1960 $\hat{a} = 0.37$; for 1961 $\hat{a} = 0.32$;

for the combined data $\hat{a} = 0.34$.

These rates are for a different herd, but their values suggest that the rate given above for the

TABLE 2.—Age distribution of male fur seals taken off Alaska, 1958, 1960, and 1962

Age (in years)	Number taken (all months)	Number taken (excluding June and July)
7	35	22
8	25	23
9	19	11
10	12	7
11	9	7
12	4	2
13	4	3
14	2	2
15		

These data are compiled from FSCR table 30 and from Fiscus, Baines, and Wilke (1964).

TABLE 3.—Age classification of males, age 7 and above, killed on Robben Island, 1960-61

Year	Age (in years)					Total
	7	8	9	10	10+	
1960	463	356	166	94	184	1,263
1961	354	353	227	67	103	1,114
Total	817	709	403	161	287	2,377

Pribilof herd is of the right order of magnitude. As will be shown later this is much higher than the corresponding female rate.

There remains to be estimated the mortality rate of males from ages 3 to 7 and also the number of idle bulls uncounted because they are at sea. On attempt to estimate both of these was based on the historical data. The following equation can be presented:

$$(E_1 + E_2)S = (HM + \Delta H) + k(IM + \Delta I)$$

where E_1 = animals reserved for the breeding stock (a practice in 1923-32)

E_2 = escapement due to size or time of arrival: these animals are also reserved for the breeding stock but no count is made of them.

K = male kill

S = survival rate of males from ages 3 to 7

H = number of harem bulls

M = mortality rate of bulls

ΔH = increase in number of harem bulls

I = number of idle bulls

ΔI = increase in number of idle bulls

k = fraction of idle bulls on land

It is reasonable to assume that E_2 is proportional to $E_1 + K$; hence writing $E_2 = f(E_1 + K)$ the equation is rewritten

$$[E_1 + f(E_1 + K)]S = (HM + \Delta H) + k(IM + \Delta I)$$

This equation holds for any year with the appropriate lag (4 years) between the counts on the left-hand side of the equation and those on the right. While the large variations in annual data preclude my using the equation with such data, I hoped that by averaging over a 5- or 10-year period I might be able to estimate the three unknowns f , S , and k . This presupposes that the fraction escaping the kill remains constant over the several periods involved, that the fraction of idle bulls at sea remains constant, and the seal

counters have had the same definition of an idle bull throughout the period of these data. The method seemed promising because of the large variations in *E* (nearly 10,000 in the 1920's but more recently zero); however, when tried for the periods 1923-27, 1928-37, 1934-38, or for 1923-32, 1933-40, 1946-55, the method gave negative values for *k*. Some of the assumptions made, appear to be invalid.

One other source of information is available—the pelagic catches off Alaska in 1958, 1960, and 1962 (data from same sources as table 2).

TABLE 4.—*Comparison of male and female pelagic captures off Alaska, 1958, 1960, and 1962*

Month	Number of males age 7 and over taken	Number of females age 4 and over taken	Proportion of males to females
June.....	15	677	0.022
July.....	13	504	.026
Total.....	28	1,181	.024

As will be shown later, the herd of females 4 years old or older has in these years averaged about 600,000. Assuming that 80 percent of the females are in the water at any time (based on observations of Bartholomew and Hoel, 1953), this suggests that not more than 12,000 males are in the water. This figure is consistent with the male total (25,000) if these animals spend half their time in the water. More reasonable is the suggestion that harem bulls spend about one quarter of these 2 months at sea, while idle bulls spend half their time on land and half at sea. This suggests that the idle bull count should be increased by about 50 percent to give the correct total. I believe this to be a maximum figure.

Data to estimate the mortality rate from ages 3 to 7 are even more tenuous. A mortality rate of 50 percent in the first year and 20 percent per year thereafter from ages 1 to 3 would be in accord with the observed returns. The mortality rate probably will be lower for these ages than for the mature animals competing for harems, so I use a figure of 0.20 (annual rate) here.

From 1950 to 1959 the bulls recruited through escapement from years of uniform killing averaged about 25,000 (with the idle bull count multiplied by 1.5). The annual mortality of this number at a 0.36 rate is 9,000. The growth of the herd averaged about 1,000 per year so that the recruit-

ment must have been 10,000. To produce this recruitment at age 7 required (if mortality is 0.20 at ages 3 to 7) an escapement of $\frac{10,000}{(0.80)^4}$ or about 25,000.

During 1946-55 the annual male kill averaged 64,350 (25,000 represents a 40-percent escapement). This absolute total and percentage are both much higher than the estimates obtained by methods used formerly. It is clear now from the above analysis that these methods underestimated escapement. Even without allowing for idle bulls at sea and using a mortality rate from ages 3 to 7 of 0.15 the needed escapement for this period was 16,000. This escapement estimate of 25,000, which will be used hereafter as the best figure for the 1946-55 period, applies to both islands. A corresponding estimate for St. Paul only is 80 percent of this, i.e., 20,000.

ESTIMATION OF THE NUMBER OF FEMALES

PREGNANCY RATES

Estimation of the number of females has been based upon the pregnancy rate and the estimated number of pups born. The pregnancy rate is well estimated from pelagic samples for each age class, but to get an average for the whole adult female population, the size of each age class must be known. The age-specific pregnancy rates have been in good agreement from year to year (table 5 and Chapman, 1961, p. 365).

The broad picture for the Pribilof fur seals seems to be that few females give birth at age 4, about 50 percent at age 5, 80 percent at age 6, and 80-90 percent at ages 7 to 10. Thereafter the pregnancy rate declines slowly with age. Before obtaining a best estimate of the pregnancy rate for the whole female herd it is necessary to estimate the age composition.

A serious problem in studying the fur seal has been obtaining representative samples of the whole herd or of major components of it. There is segregation by sex and age at sea and on land. On land the segregation is in part a result of the differential behavior of pregnant females, which tend to come ashore on rookeries, and nonpregnant females, which come ashore on hauling grounds and at the edges of rookeries. This behavior is not without exceptions, and the two kinds inter-

TABLE 5.—Pregnancy rates of northern fur seals¹

Age	North American		Asian	
	1952 sample	1958-61 samples combined	1952 sample	1958-61 samples combined
4.....	0.01 (80)	0.04 (375)	0.37 (288)	0.48 (1133)
5.....	.43 (28)	.45 (408)	.80 (211)	.83 (837)
6.....	.82 (49)	.76 (445)	.89 (120)	.86 (571)
7.....	.72 (39)	.80 (545)	.85 (99)	.89 (340)
8.....	.77 (55)	.85 (609)	.91 (80)	.89 (199)
9.....	.89 (35)	.90 (535)	.88 (58)	.90 (123)
10.....	.74 (31)	.89 (513)	.88 (72)	.89 (72)
10+.....	.75 (187)	.82 (2641)	.84 (124)	.75 (340)

¹ Figures in parentheses represent number of females in the sample. The rates for 1952 are taken from table G, page 82, of Taylor, Fujinaga, and Wilke (1955). The 1958-61 data are given in FSCR table 20, page 94.

mix. In particular, some animals that have given birth are killed with other females on hauling grounds. The pelagic samples show immediately that the youngest age groups are underrepresented. Table 6 shows the combined female catches of the U.S. pelagic research expeditions of 1958-61 off the Pacific Coast of North America. In discussing age-specific pregnancy rates I need to mention mortality rates, since the age composition of the female class is partly reconstructed on the basis of estimated mortality rates. The method of estimating mortality rates (table 6) is given below.

Sampling below age 8 is unrepresentative, but if it is assumed that sampling is representative for age 8 and up, then mortality or survival rates can be estimated from these data. After study, I decided that the most satisfactory fit is obtained with a Gompertz curve, a form used for actuarial studies. The fitted curve is:

$$Y = 6.9143 - (0.5109)(1.1714)^{-x}$$

where Y represents ln (number) and X is age.

The rather low mortality rates during ages 3-10 are in close agreement with those used in

TABLE 6.—Age composition of female seals taken by U.S. research vessels, 1958-61 combined, and estimated mortality rates

Age	Females taken	Mortality rate ¹	Age	Females taken	Mortality rate
Years	Number	Percent	Years	Number	Percent
1.....			14.....	336	0.226
2.....			15.....	293	.265
3.....		0.040	16.....	233	.311
4.....	267	.046	17.....	142	.364
5.....	307	.054	18.....	97	.426
6.....	324	.064	19.....	59	.499
7.....	407	.075	20.....	21	.585
8.....	478	.088	21.....	16	.685
9.....	447	.103	22.....	6	.803
10.....	434	.120	23.....	3	.940
11.....	429	.141	24.....	3	
12.....	387	.165	25.....		
13.....	382	.193	26.....	1	

¹ Percent of each age class dying during the year.

Kenyon et al. (1954, p. 39), based on fewer data and estimated more crudely.

This composite sample (table 6) can also be compared with the 1952 pelagic sample (Taylor et al., 1955, p. 49). Since, in the 1952 sample, ages above 10 were not identified, it is possible only to use a Heincke-type estimate, i.e., the relation of the age 10 group to the 10-year and older animals. For 1952 the average mortality by this method for the 10+ group of females is estimated as 0.142, while from the composite sample (table 6) it is estimated as 0.154. The two estimates are in reasonable agreement.

The rates estimated here are somewhat lower than those given by Chapman (1961, p. 365), based upon the assumption of a constant mortality rate above age 9. More careful scrutiny of the data suggests that mortality increases with age. The average for the female population given in the 1961 paper was 0.14, here it is 0.11. The latter rate is used in the present study but, where pertinent, the implications of the higher rate will be considered.

What are the annual fluctuations in the pregnancy rate? Using the same age distribution and applying the age-specific pregnancy rates obtained in pelagic samples for 1952 (table 5) and for 1958-62 (Fiscus, Baines, and Wilke, 1964, p. 36) the following weighted averages are obtained: 1952, 0.595; 1958, 0.629; 1959, 0.629; 1960, 0.625; 1961, 0.588; and 1962, 0.578. The standard deviation of the six rates is 0.023, which is about 3.8 percent of the average.

A stable herd with these age-specific mortality rates and the age-specific pregnancy rates of the 1958-61 combined samples (table 5) would have an overall pregnancy rate of 0.62. With the somewhat higher mortality rates used by Chapman (1961, p. 366), the estimated pregnancy rate was 0.58. Both rates apply to the female population of ages 3 and older. It is clear that the estimate of 0.6 used for pregnancy rate in Chapman (1961) may be adopted as the most reasonable.

CUMULATIVE ESTIMATES OF THE NUMBER OF FEMALES

The estimates made of mortality and pregnancy rates could be used to estimate the total number of females in any year, if the female recruitments at age 3 for several years past were known. But

all that is known is the male kill by ages for year classes since 1947 and by size groups only for earlier years, together with the escapement estimates derived earlier. From 1940 to 1949 the average male kill was 53,840 per year. The escapement during this period may be estimated at 40 percent of this or 21,536, hence a reasonable estimate of the male survival to age 3 for these years is about 75,000. An estimate of 75,000 may be slightly high for the year classes prior to 1937, but by 1956 such year classes constituted a negligible part of the population or either males or females.

The estimated male natural survival to age 3 (if no 2-year-olds were killed) for the year classes 1947-59 is shown in table 7. This has been calculated using the 40 percent escapement figure for year classes for which killing terminated by July 31. For year classes that experienced an August kill, I have assumed that one third of the August 3-year-male kill and all the August 4-year-male kill represents animals that would have formerly been part of the escapement. Hence, the 40 percent escapement estimate is applied to the balance of the kill from the year class. Raw data for table 7 are found in FSCR table 6.

To estimate the female recruitment I need to know λ (lambda), the ratio of female survival rate to age 3 to the corresponding male survival rate. Because λ is not known, several values are tried, viz, $\lambda=1.0, 1.25, 1.5, 2.0$.

The basic procedure is illustrated with the 1956 estimate of the female population and with $\lambda=1.0$.

The cumulative estimate of the 3-year and older female population in 1956 is:

1953 year class survival to age 3 $\times 1.000 = 62,000$ (1.000)
 +1952 year class survival to age 3 $\times 0.960 =$
 +93,000 (0.960)
 +1951 year class survival to age 3 $\times 0.915 =$
 +83,000 (0.915)
 +1950 year class survival to age 3 $\times 0.866 =$
 +84,000 (0.866)
 +1949 year class survival to age 3 $\times 0.810 =$
 +62,000 (0.810)
 +1948 year class survival to age 3 $\times 0.749 =$
 +70,000 (0.749)
 +1947 year class survival to age 3 $\times 0.683 =$
 +83,000 (0.683)
 +1946 and earlier survival to age 3 $\times 3.013 =$
 +75,000 (3.013)
 Total = 685,000

TABLE 7.—Estimated natural survival of males to age 3, St. Paul Island, 1947-59 year classes

Year class	Total	Year class	Total
1947.....	83,000	1953.....	62,000
1948.....	70,000	1954.....	44,000
1949.....	62,000	1955.....	55,000
1950.....	84,000	1956.....	21,000
1951.....	83,000	1957.....	56,000
1952.....	98,000	1958.....	79,000
		1959.....	60,000

The mortality factors are obtained from those shown in table 6 by successive multiplication.

The foregoing procedure is applied to other years, with other values of λ (table 8). The earliest estimates in the table are biased upward by an overestimate of the contribution of the pre-1940 year classes. There is also some upward bias of the earlier estimates from tagging. In 1960 and subsequently, a more intensive search for tag-lost animals was undertaken, and it was demonstrated that there had been some oversight earlier. (A tag-lost animal is a seal that had been tagged and had lost the tag before recapture; it is identified as an animal that had been tagged by the checkmark that is also placed on the flipper at the time of tagging.) The largest estimate from tagging, however, is of the 1956 year class; the 1960 kill from this class was searched carefully for tags and tag-lost animals.

The last column of table 8 shows 10 different estimates of λ , which are valid only if the tagging estimates are valid.

If the annual mortality rates used here are too low, i.e., if the true rates are similar to the rates

TABLE 8.—Cumulative estimate of 3-year and older female population, St. Paul Island, 1950-62

Year	Postulated differential survival rate of females to males to age 3 (λ)				Best estimate of number of females from tagging estimate of pups ¹	Estimate of λ from tagging estimate of pups
	1.00	1.25	1.50	2.00		
1950.....	683	854	1,024	1,368	No estimate
1951.....	677	846	1,016	1,354	513,000	1.20
1952.....	664	830	996	1,328	² 528,000	1.25
1953.....	674	842	1,011	1,348	1,140,000	1.69
1954.....	682	852	1,023	1,354	1,208,000	1.76
1955.....	699	874	1,045	1,398	1,240,000	1.77
1956.....	685	861	1,034	1,378	1,337,000	1.94
1957.....	635	798	961	1,288	955,000	1.49
1958.....	583	738	892	1,201	967,000	1.62
1959.....	514	648	782	1,050	1,040,000	1.98
1960.....	483	610	736	989	³ 828,000	1.68
1961.....	499	625	750	1,001	(⁴)
1962.....	468	593	719	970	(⁴)
Average.....						1.64

¹ Number of pups as estimated from male tag recoveries in commercial kill divided by best estimate of average pregnancy rate viz 0.6.

² Dead pup count estimated from counts of two areas to be 45,000. Note that a slightly different estimate was used in table 2 of Chapman (1961, p. 359).

³ Estimate based on returns of 3-year males only.

⁴ Estimate not yet available.

given in Chapman (1961), then the present cumulative estimates are too high. This would yield even higher estimates of λ . If the tagging estimates are correct then the differential survival advantage of females at ages 0 to 3 is indeed large. The tagging estimates possess, however, internal inconsistencies, and the possible explanations for these are now considered.

FLUCTUATIONS IN THE APPARENT NUMBER OF PUPS BORN

Another unresolved question is: How could the estimated number of pups born, about 500,000 in 1947-49 and 1952, increase to 584,000 in 1953 in 722,000 in 1954, 744,000 in 1955, and 802,000 in 1956; then drop to 573,000-580,000 in 1957 and 1958? What are the possible explanations of the fluctuation? If there is no bias in the estimates from tagging, there are three explanations: (1) Sampling variations, (2) variations in the pregnancy rate and, (3) variations in the number of adult females.

SAMPLING VARIATIONS

The magnitude of sampling variations is discussed elsewhere (Chapman 1963).³ I showed that the standard deviation of the 1952 or 1956 estimates is less than 20,000, so sampling variation can reasonably explain less than 60,000 of the 300,000 difference. Moreover, there are also the 1953 and 1954 estimates to explain.

VARIATIONS IN THE PREGNANCY RATE

Turning to variations in the pregnancy rate, it is unfortunate that there was no pelagic sample in 1956 nor, in fact, in the years of highest estimates from tagging. However, the samples taken in six different seasons have shown very similar rates, with the variation from highest to lowest of the mean annual rates being only 8.4 percent of the 6-season mean. Furthermore, such variations are inadequate to explain the apparent change in number of pups born, a 60 percent increase from 1952 to 1956. In fact, if the observed 1952 pregnancy rate and the 1952 pup estimate (497,000) were both true, the number of females in 1952 would have been 835,000. If this many females

had 802,000 pups in 1956, the pregnancy rate was 0.96, a rate that is inconsistent with any data available.

VARIATIONS IN THE NUMBER OF ADULT FEMALES

Finally, was there a substantial increase in the number of females between 1952 and 1956? The cumulative estimates suggest, with $\lambda \leq 2$ that the change was 50,000 or less, accounting for a possible increase of about 30,000 pups.

No single cause explains the 1952-56 change; perhaps there was a combination of causes. Consider the 1952 pup estimate +2 standard deviations, i.e., 537,000. With λ pregnancy rate $P=0.595$ this means 903,000 females. Suppose that from 1952 to 1956 there was an increase to 968,000 females. Assume that in 1956 P was 0.653 ($P+2$ standard deviations). This suggests a 1956 pup crop of 69,000. Allowing for the sampling error in the 1956 estimate (2 standard deviations is less than 40,000), the unaccounted discrepancy is still 133,000. That all three factors (nonrepresentative sampling, variation in pregnancy rate, and variation in number of adult females) should act in the same direction in any given year is improbable. Even so, there remains a large unexplained discrepancy in the estimated number of pups born.

BIAS IN ESTIMATES FROM TAGGING

Some of the estimates of pups born from tagging must be biased, and the most likely cause is excess mortality caused by the tag or tagging operation. In general, the years with the poorest survival had highest estimates. An upward biased estimate would result from an increased tendency for tagged pups to die during the fall and winter. The tagging need not bring immediate mortality, though a 1962 experiment indicated that this may occur. Roppel et al. (1963) showed that the mortality on land of tagged pups counted during September was 2.7 times that of untagged pups (33 dead tagged pups expected, 84 dead tagged pups observed), however, such mortality in general appeared to be less than 6 percent of the mortality that occurred prior to the tagging period so that even this differential mortality does not explain the excess mortality postulated to account for the excessive tagging estimates. Consequently, this is a hypothesis rather than a firm fact.

Tagging mortality may be greater in years when

³ Douglas G. Chapman. 1963. Problems in the analysis of tagging experiments with particular reference to Alaska fur seal data. To be published.

survival is poor, but this does not explain why survival has varied so greatly over the past several years. A population at or near its ceiling is expected to fluctuate more widely than one that is actively growing, and, moreover, the range of fluctuation will tend to increase with time through purely random causes. The largest fluctuations in the fur seal herd will be brought about by random fluctuations in survival of the youngest animals, though fluctuations in the pregnancy rate may also contribute some variability.

A possible explanation also may be found in external factors. Abegglen, Roppel, Johnson, and Wilke (1961)⁴ speculated about the relationship between the average temperature for the preceding year and the dead pup counts. They reported the correlation between these variables to be -0.853 , which is significant at the 1 percent level. The correlation between average temperature and total male survival for the year classes 1950-59 is 0.924 , which is also highly significant and even higher numerically than the correlation between dead pup counts and temperature. Data are not yet available for survival from subsequent year classes. The temperatures considered are for the St. Paul Island weather station. It would be more useful to have water temperature for the Bering Sea. Without such data it is only possible to speculate that water temperatures are rather closely related to land temperatures with, however, some lag. A lower water temperature might have a direct effect on the young seals or it might reduce their food supply. Either could result in increased mortality on land during the summer and at sea during the fall and winter. A model I proposed (1961) was based on food at sea as the limiting factor on growth of the pup. Clearly, temperature dependence would be more important if the population were pressing on its food supply than if it were not.

In summary, the tagging estimates show fluctuations that are not explicable in terms of the structure of the herd and known values of other parameters and which therefore suggest some bias is inherent in the estimates. It is, therefore, important to turn to other methods of estimating λ or the female herd size.

⁴ Carl E. Abegglen, Alton Y. Roppel, Ancel M. Johnson, and Ford Wilke. 1961. Fur seal investigations, Pribilof Islands, Alaska, Report of field activities, June-November 1961. Bureau of Commercial Fisheries, Marine Mammal Biological Laboratory, Seattle, Wash.

Another method of population estimation is based upon differential kill of the sexes (Chapman, 1955). This method appears to be ideal for the fur seal where in excess of 70 percent of the males are killed at ages 3 or 4, but only a small proportion of the females is removed. However, the method also requires estimates of the sex ratio before and after the differential kill. While these are available from large pelagic samples in 1958-61, the segregation of the sexes at sea creates difficulties. If the segregation pattern remains constant from year to year, these difficulties might be overcome. The following model was considered:

Let N_1, N_2 be the number of males and females, respectively, at the beginning of any summer season. Define $N = N_1 + N_2$. Assume that a proportion ϕ_i of the N_i are to be found in any area at sea in any season. Then the proportion of males at sea in this area and season will be

$$p' = \frac{\phi_1 N_1}{\phi_1 N_1 + \phi_2 N_2} = \frac{N_1}{N_1 + \phi N_2} \quad (1)$$

where

$$\phi = \frac{\phi_2}{\phi_1}$$

Let R_i be the kill of the N_i in the summer season and s_i the rate of natural survival during the following winter. Then the proportion of males at sea in the same area next spring will be

$$p'' = \frac{N_1 - R_1}{(N_1 - R_1) + \phi s (N_2 - R_2)} \quad (2)$$

where

$$s = \frac{s_2}{s_1}$$

and where all that needs to be assumed is that ϕ , the ratio of ϕ_2 to ϕ_1 , remains constant between years.

If N_1 refers to the number of males at age 3, this can be assumed known, and if information is available as to s , then observations of p', p'' from pelagic data can be used to estimate ϕ and N_2 . In particular, it is reasonable to assume that s equals 1, approximately, since both s_1 and s_2 are close to 1.

Writing $N_2 = \lambda N_1$ and setting $s = 1$ equations (1) (2) may be rewritten

$$\frac{1}{p'} = 1 + \phi\lambda; \frac{1}{p''} = 1 + \phi \left(\frac{\lambda N_1 - R_2}{N_1 - R_1} \right)$$

or

$$\phi = \frac{1 - p'}{\lambda p'}$$

Substituting this last equation in $\frac{1}{p''}$ yields

$$\frac{1 - p''}{p''} = \frac{1}{\lambda} \left(\frac{1 - p'}{p'} \right) \frac{\lambda N_1 - R_2 / \lambda}{N_1 - R}$$

Put

$$\frac{(1 - p'')p'}{p''(1 - p')} = Q$$

Then

$$Q = \frac{N_1 - R_2 / \lambda}{N_1 - R}$$

or

$$(N_1 - R)Q - N_1 = -R_2 / \lambda$$

Changing signs and taking reciprocals produces an equation for λ :

$$\lambda = \frac{R_2}{N_1 - Q(N_1 - R_1)} \quad (3)$$

The following estimates of λ were obtained from the indicated pelagic samples (from which estimates of p' , p'' were obtained). The year in the second column refers to the first year of the paired samples and the year for which the N_1 estimate is determined.

The tagging results and other data suggest that λ should be 1 or greater. The estimates of λ from table 9 are quite unreasonable. This may be due to failure of the basic assumption that the proportion of males to females in any one area and season remains constant from year to year. The estimates of λ by the dichotomy method depend primarily on the size of R_2 . In the standard

application of the dichotomy method, the greater the difference between R_1 and R_2 , the better the estimation of population size; however, with these data this is not so. Perhaps the R_2 values are too small. Also, the small size of the pelagic samples—when only one age-sex class is considered—makes correspondingly great variability in p' , p'' . I attempted to combine data from different years to eliminate or reduce the variability, but the results proved equally unsatisfactory and are not shown here.

POPULATION DYNAMICS OF THE FUR SEAL HERD AND ESTIMATION OF THE NUMBER OF FEMALES

Recent data do not permit resolving the question: What is the value of λ , the ratio of female to male survival from birth to age 3? There are also the data of the early 1920's when counts were made of the number of pups born. Both sets of data are considered below.

We have the obvious fundamental relationship (equation 4):

$$\frac{PS}{2} = (a + g)(1 + g)^2 \quad (4)$$

where

P = proportion of females age 3 and older that are pregnant in any one year

S = survival rate of pups (female) from birth to age 3

a = annual mortality rate (average) of female population

g = annual growth rate of female population

The factor one-half on the left-hand side arises from the assumption that half of the pups born are females, which is consistent with all available information. The factor $(1 + g)^2$ on the right-hand side follows because of the time lapse from

TABLE 9.—Estimate of λ , ratio of differential survival of females to males, by dichotomy method

Area	Year	Age group	p'	p''	R_1	R_2	N_1	λ
Washington	1958	3	0.0	0.06	35,109	11,393	68,000	0.17
Do	1959	3	.33	.25	12,922	2,016	25,000	.29
Do	1960	3	.27	.15	29,381	281	66,000	-.02
Do	1960	4	.25	.07	4,149	562	10,000	-.04
British Columbia	1959	3	.33	.10	12,922	2,016	25,000	-.05
Do	1960	3	.33	.20	29,381	281	66,000	-.01
Do	1961	3	.40	.17	57,871	4,534	96,000	-.14
Do	1961	4	.20	.08	19,836	6,776	31,000	-15.5
California	1958	3	.03	.06	35,109	11,393	68,000	.23
Alaska	1958 (June)	3	.80	.33	35,109	11,393	68,000	-.06
Do	1958 (before June)	3	.85	.28	48,489	18,560	68,000	-.09

¹ 1958 and 1960 pelagic samples are combined so that R_1 , R_2 represent the combined kill of 3s in 1958 and 4s in 1959 for this calculation.

birth to recruitment. It can best be shown by the following diagram:

Year	0	1	2	3
Number of females.....	N	$N(1+g)$	$N(1+g)^2$	$N(1+g)^3$
Increase.....			$N(1+g)^2g$	
Mortality.....			$N(1+g)^2a$	
Number of female pups.....	$\frac{NP}{2}$			
Survivors.....			$\frac{NPS}{2}$	

The recruitment (survivors) must account for growth and mortality losses, whence we have equation (4) above. This equation, of course, is trivial. What is significant is how P , S , and a change as the population changes from a growing one to a stable one.

For later purposes it is convenient to rewrite (4) as (equation 5):

$$\frac{PS'\lambda}{2} = (a+g)(1+g)^2 \quad (5)$$

where S' = survival rate of male pups from birth to age 3 and as before

λ = differential survival of females to males (from birth to age 3)

From data of the early 1920's (Chapman, 1961) the St. Paul kill from the 1920-22 year classes averaged 13,590 (size groups 2, 3, 4). In addition, 22,666 were reserved for the breeding stock in these 3 years (average, 7,555 per year). Adding these two and also adding an estimated 40 percent escapement yields an average male survival of 30,000. Since the average pup count was 150,000 (half male and half female) the estimate of S' is 0.40.

Early pup counts (Kenyon et al., 1954, p. 20) show that the 1916-22 annual rate of increase was 0.08 on St. Paul Island. The St. George rate of increase, however, was 0.07, and the 1920-24 St. Paul annual rate of increase was 0.07. The latter is based on partial counts, but it is likely that the growth rate would begin to decrease about this time, so g is taken to be 0.07. At present the growth of the Asian herds as measured by the pup counts is 8-9 percent annually.

Unfortunately, the values of P and a are not known for 1916-22. It is possible, however, to calculate λ for a range of reasonable values of P and a , assuming that P was no smaller than at

TABLE 10.—Values of λ (differential survival of females to males) corresponding to various possible values of P , pregnancy rate, and a , annual mortality rate (1920's data)

Values of P	Values of a				
	0.11	0.10	0.09	0.08	0.07
0.6.....	1.72	1.62	1.53	1.43	1.34
0.7.....	1.47	1.39	1.31	1.22	1.14
0.8.....	1.29	1.23	1.14	1.07	1.00

present and a no larger. Values for λ are shown in table 10.

Such a table does not provide a close estimate of λ but it does suggest that it was then larger than 1. Concerning the value of P (the pregnancy rate) and a (the annual mortality rate), the following comments are pertinent. If the observed age-specific pregnancy rates from western Pacific samples (1958-61) shown in table 5 are applied to the eastern Pacific age distribution, the resulting pregnancy rate for the whole population would be 0.70. The pregnancy rate of the females on the Asian islands must be slightly higher than this since there is some intermixture of Pribilof seals in these western Pacific samples. To allow for this, average intermixture rates have been calculated from table 43 of FSCR (p. 120). For ages 3 to 6 these averages are 0.18, 0.22, 0.42, and 0.70 (when the dashes are correctly interpreted as zeros). This yields adjusted intermixture rates for those ages of 0.12, 0.60, 1, and 1, respectively.

The equation to determine these adjusted rates is:

$$\pi_p P_p + \pi_A P_A = P_w$$

or

$$P_A = \frac{P_w - \pi_p P_p}{\pi_A}$$

where

π_p = proportion of Pribilof seals in western Pacific samples

π_A = proportion of Asian seals in western Pacific samples

P_p = pregnancy rate of Pribilof seals

P_A = pregnancy rate of Asian seals

P_w = observed pregnancy rate of western Pacific samples

For 4-year-olds the equation becomes

$$(0.04) + (0.78)P_A = 0.48 \text{ or } P_A = 0.60 \quad (22)$$

IMPLICATIONS FOR THE POPULATION DYNAMICS OF THE FUR SEAL HERD

Since the estimates for ages 5 and 6 are impossible, we have used the maximum observed rate, or 0.90, for these ages and for ages 7 and 8 where no intermingling estimates are available. The resulting adjusted pregnancy rates (Asian females) are as follows: Age 3, 0.13; age 4, 0.60; ages 5-9, 0.90; age 10, 0.89; age 10+, 0.75; weighted mean, 0.74.

It seems, therefore, that 0.80 is a reasonable upper limit for the pregnancy rate of the early Pribilof herd.

There is little direct information available as to the annual mortality rate in the early 1920's. The present age distribution of the western Pacific samples suggests higher mortality rates than for the eastern Pacific samples. I do not know whether this is due to nonrepresentative sampling or to a variable intermixture of Pribilof seals. With a growing population the proportion of younger animals would be greater. According to the model given earlier (pages 21 and 22) younger seals have lower mortality rates, so that the average rate for the whole herd would be reduced. The reduction due to this cause would be slight.

Turning to the present data we have $a=0.11$, $g=0$, $P=0.6$ so that equation (5) yields:

$$s'\lambda=0.37$$

Since it is reasonable to suppose s' is less now than in a growing herd $s' \leq 0.40$, whence $\lambda \geq 0.925$. If the 1947-49 and 1952 tagging estimates are accepted (Chapman, 1961, tables 2 and 3) $s'=0.294$ so that $\lambda=1.27$. These agree very closely with the estimates of λ from 1951 and 1952 in table 3. The latter were based on a comparison of cumulative and tagging estimates of the female population. Too much importance must not be attached to this agreement, since essentially the same supporting data are involved.

BEST ESTIMATE OF λ

At the present time there seems to be no best estimate of λ . The data indicate a range of values and suggest that λ is probably slightly greater than 1. A reasonable value for λ from the 1920's data is approximately 1.25, which is also consistent with the 1947-49 and 1952 tagging data. This value is adopted here as best. Higher values of λ are possibly consistent with the available data but seem biologically less reasonable.

The population models of both Nagasaki (1961) and Chapman (1961), utilized the high estimates from tag recoveries of the 1952-56 period. If such estimates are discounted, then the right-hand limb of the parent-progeny relationship (e.g., Chapman, 1961, fig. 1, p. 361) and hence the probable optimum population level is much less well defined.

Nevertheless, the models fitted in my earlier paper may still be fitted either to data from tagging estimates through 1952 or to the cumulative estimates. The results in either case are similar and differ very little from the equations given in the earlier paper. For example, using the cumulative estimates (with $\lambda=1.25$) for the period 1950-59 the average female population was 814,300 which with a pregnancy rate of 0.6 produced an annual pup crop of 489,000. The male survival to age 3 from three-year classes averaged 64,000. Combining this with the 1920's data yields:

$$N_m=0.0293 E^{3/2}-0.00106 E^2 \text{ (Chapman model)}$$

or

$$N_m=0.2306 E-0.000204 E^2 \text{ (parabolic model)}$$

where

$$N_m = \text{male survival to age 3 (in thousands)}$$

E = number of pups born (both sexes, in thousands)

From these equations the maximum sustainable yield (with $\lambda=1.25$, $P=0.6$, and an average mortality rate of the females 3 and older equal to 0.11) is attained when

$$E^x=351 \text{ (Chapman model)}$$

or

$$E^{xx}=366 \text{ (parabolic model)}$$

The estimated male return at these levels would be 64,000 or 57,000 according to the two different models. Of these, about 71 percent or perhaps somewhat more would be available for the commercial harvest. The sustainable female yield according to these equations is 14,000 (Chapman model) or 7,000 (parabolic model).

If the female mortality rates are underestimated, the $E^x E^{2x}$ values given here are slightly high and so are the levels of sustainable kill. On the other hand if the pregnancy rate should increase as the female herd is reduced, the effect would be an opposite one. Such an increase in P may occur only with some time lag.

If we accept the hypothesis that the estimates from tagging since 1953 have been inflated, possibly by tagging-induced mortality, immediate or delayed, and that the best estimate of λ , the ratio of female to male survival from birth to age 3 is about 1.25, then the best estimate of the average 3-year and older female population for 1960-62 is about 609,000. If P , the pregnancy rate, is about 0.6 this implies the average number of pups born in these years was 365,000, very close to the current best estimate of the optimum.

In conclusion, the figures on population sizes, harvests, etc. apply to St. Paul Island. The figures for the Pribilof herd as a whole can be obtained by the usual extrapolation.

In recent years a method of fall sampling has been developed to estimate the number of pups in the year of birth. While this procedure also has biases that are not yet fully resolved, preliminary results indicate strongly that the actual year classes are much less than have been indicated by tagging estimates. Some of the preliminary results are shown in Roppel et al. (1964); additional results of the improved 1963 experiment are to be found in the unpublished annual report of fur seal investigations for 1963.⁵

SUMMARY

1. This study was undertaken to review critically the unresolved questions about Pribilof fur seal population estimates—the apparent large fluctuations in the number of pups born and the apparent differential survival of males and females from birth to age 3.

2. The adult male annual mortality rate is estimated from pelagic samples to be 0.36; the age distribution of the much larger samples from the adult females taken pelagically are fitted by a Gompertz-Makeham curve. The average annual mortality rate for these adult females is estimated to be 0.11.

⁵ Alton Y. Roppel, Ancel M. Johnson, Douglas G. Chapman. 1964. Fur seal investigations, Pribilof Islands, Alaska, 1963. Marine Mammal Biological Laboratory, Seattle, Wash.

3. From counts made in the 1920's, and tagging estimates of 1947-49 and 1952, the best estimate of the ratio of female to male survival from birth to age 3 appears to be about 1.25.

4. This estimate of the differential survival ratio of 1.25 is used in computing a cumulative estimate of the female population 3 years old and older. The best cumulative estimate of the St. Paul Island adult female population is 854 thousand in 1950 fluctuating slightly to 861 thousand in 1956 and decreasing thereafter to 593 thousand in 1962.

5. Possible explanations for the fluctuations in the tagging estimates for post-1952 year classes are reviewed, and it is shown that these are inadequate to explain the magnitude of the changes. The tagging estimates have been biased by tag mortality, and such tag mortality is heaviest in year classes that have poor overall survival. Variations in overall survival may be due to temperature changes that are important at a high population level.

6. An unsuccessful attempt is made to estimate the female herd by a dichotomy method to resolve the contradiction between cumulative and tagging estimates.

7. Equations relating male survival to the original pup population on St. Paul Island are recalculated using the new data and from these the optimum pup population levels determined. These are estimated to be 351-366 thousand pups which corresponds at present pregnancy rates to approximately six hundred thousand adult females.

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APPENDIX

COMPARISON OF U.S.S.R. COUNTS AND TAGGING ESTIMATES

Because it has been possible to count the pups on the Asian islands we hoped that these counts would shed light on the validity of the tagging

estimates there, and by implication, on the Pribilof estimates. Unfortunately, the comparison of counts and estimates on the different areas are contradictory. On Robben Island, where the counting is easy and is believed to be reliable, the counts and estimates (allowing for tag loss of the same order of magnitude as occurs with Pribilof tags) agree (appendix table 1). On the Commander Islands, where counting is difficult and less reliable, the estimates from tagging and the actual counts disagree markedly (appendix table 2).

The estimates from tagging are high because of tag loss, and to a very slight degree because some seals in the kill came from other islands. If the latter factor is ignored, the Robben Island data of appendix table 1 can be used to estimate the tag-lost/tagged ratio. To make N agree with the counted total, s should have been 1,236 for the 1958 year class and 938 for the 1959.

APPENDIX TABLE 1.—Robben Island estimates from tagging¹

Year class	Year of recovery	Males killed (n)	Pups tagged (t)	Tagged males in kill (a)	$N = \frac{(n+1)(t+1)}{s+1}$	Pups counted
1958	1961-62	Number 4,932	Number 7,225	Number 911	Number 38,077	Number 28,813
1959	1962	3,080	9,015	587	47,242	29,598

¹ Data from FSCR.

APPENDIX TABLE 2.—Commander Islands estimates from tagging¹

Year class	Year of recovery	Males killed (n)	Pups tagged (t)	Tagged males in kill (a)	Adjusted ²	$N = \frac{(n+1)(t+1)}{s+1}$	Pups ³ counted
1958	1961-62	Number 4,593	Number 4,887	Number 277	Number 377	Number 59,406	Number 38,100
1959	1962	3,570	7,971	248	397	71,528	41,200

¹ Data from FSCR.

² $s^1 = 1.36 s$ for 1958 year class and $s^1 = 1.60 s$ for 1959 year class.

³ The 1958 count was marked as incomplete. In FSCR an attempt was made to correct for this. Revised figures are here taken from Report on U.S.S.R. Fur Seal Investigations in 1963, V. A. Arseniev, 1963, p. 34. These are based on counts in subsequent years.

Hence we have

Tag-lost/tagged ratio

$$= \frac{1236 - 911}{911} = 0.36 \text{ (1958 year class)}$$

$$= \frac{938 - 587}{587} = 0.60 \text{ (1959 year class)}$$

The estimate for the 1958 year class is very similar to the tag-lost estimates for the Pribilofs; the

larger 1959 value is not higher than the highest observed on the Pribilofs.

These tag-lost estimates have been applied to the Commander Islands recovery data (appendix table 7).

Even allowing for tag loss, the estimates greatly exceed the counts. The estimates may be about 10 percent too high because of the presence of Pribilof animals in the kill. The bulk of the discrepancy is unexplained; whether due to tag mortality or some other cause is unknown. The discrepancy can be used to support the contention that the Pribilof tagging estimates are also in error.

LITERATURE CITED

- BARTHOLOMEW, GEORGE A. JR., AND PAUL G. HOEL.
1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. Journal of Mammalogy, vol. 34, No. 4, pp. 417-436.
- CHAPMAN, DOUGLAS G.
1955. Population estimation based on change of composition caused by a selective removal. Biometrika, vol. 42, parts 3 and 4, pp. 279-290.
1961. Population dynamics of the Alaska fur seal herd. Transactions of the 26th North American Wildlife and Natural Resources Conference, pp. 356-369.
- CHAPMAN, D. G., AND D. S. ROBSON.
1960. The analysis of a catch curve. Biometrics, vol. 16, No. 3, pp. 354-368.
- FISCUS, CLIFFORD H., GARY A. BAINES, AND FORD WILKE.
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 475, 59 pp.
- KENYON, KARL W., VICTOR B. SCHEFFER, AND DOUGLAS G. CHAPMAN.
1954. A population study of the Alaska fur seal herd. U.S. Fish and Wildlife Service, Special Scientific Report—wildlife No. 12, 77 pp.
- NAGASAKI, FUKUZO.
1961. Population study on the fur seal herd. Tokai Regional Fisheries Research Laboratory, Special Publication No. 7, 60 pp.
- ROPPEL, ALTON Y., ANCEL M. JOHNSON, RICHARD D. BAUER, DOUGLAS G. CHAPMAN, AND FORD WILKE.
1963. Fur seal investigations, Pribilof Islands, Alaska, 1962. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 454, 101 pp.
- TAYLOR, F. H. C., M. FUJINAGA, AND FORD WILKE.
1955. Distribution and food habits of the fur seals of the North Pacific Ocean. Report of Cooperative Investigations by Governments of Canada, Japan, and United States of America, February-July 1952. Washington, D.C., Government Printing Office, 86 pp.