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Temperature Associated Growth of White Shrimp in Louisiana

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INTRODUCTION

The growth of laboratory-reared postlarval white shrimp is temperature-dependent (Zein-Eldin and Griffith 1969); the same association between growth rate and temperature of older shrimp may be expected. This association must be quantified in order to estimate potential yield, a critical aspect in management of the fishery. An actual dependence of growth on temperature cannot be proven from observational studies of wild shrimp, but a correlation between the two can be documented.

This report presents a preliminary analysis of growth data obtained from a white shrimp mark-recapture experiment carried out in 1977 by the National Marine Fisheries Service and the Louisiana Department of Wildlife and Fisheries. The association between growth and water temperature is studied and modeled for white shrimp in their natural environment.

DATA

The data used in this study include growth information on white shrimp and water temperature measurements. I used growth data from white shrimp mark-recapture experiments carried out in Louisiana during 1977. Shrimp were marked with numbered plastic ribbons and released at inshore and offshore locations near the site of initial capture. Inshore releases were made in Caillou Lake during four periods: July 18-21, August 1-10, September 12-26 and October 11-20. Offshore releases were made between the mouth of the Mississippi River and the Louisiana-Texas border during three periods: September 18-26, October 27-30 and December 2-4.

The 3522 white shrimp used in this study were returned by fishermen between July 1977 and February 1978. No shrimp which had over-wintered

were returned. Approximately 92% of the recaptured shrimp were from inshore releases and 8% were from offshore releases. For each animal, the recorded growth information included the date and tail length at release and recapture. Throughout this paper, "length" refers strictly to tail length (mm) measured from the anterior margin of the first abdominal segment to the posterior margin of the telson.

Some shrimp showed "negative growth". However, data from 29 shrimp released and recaptured the same day showed calculated growths between -6 mm and 11 mm. Since these shrimp should not have appreciably changed in size, this indicates the presence of measurement errors in the recorded lengths. Only measurement errors resulting in negative growth can generally be detected, while those resulting in positive growth can not. Thus, animals showing a decrease in size were retained for the analysis to avoid a systematic bias in the estimation of growth equations.

I employed hourly surface temperature readings taken at Caillou Lake, Louisiana, during 1977 by the Louisiana Department of Wildlife and Fisheries. There was no data from August 30 to September 6, but as this was during a period of little temperature variation, the average of temperatures for August 29 and September 7 was used. There were no measurements available for January and February of 1978, so the 1977 temperatures for these months were used. Since there were only 10 shrimp at large in 1978, the possible resulting error is likely of little consequence. Sufficient offshore temperatures were not available; thus, the inshore readings were applied to all recaptured shrimp.

METHODS

A. The models.

To investigate the possibility of linear growth, I compared the least squares fit of three asymptotic models (Richards, von Bertalanffy and logistic) to that of the linear growth model (Appendix). Of these three asymptotic equations, the Richards must necessarily produce the best least squares fit (i.e., the smallest residual sum of squares); for certain values of one parameter, the Richards equation is identical to the von Bertalanffy or the logistic equation. On the basis of its "best fit", the Richards equation was chosen for use in this study. Marquardt's algorithm (Conway, Glass and Wilcox 1970) was used to fit all asymptotic equations.

B. Independent variables.

For each growth model, one of two time-dependent variables was used with release length to predict recapture length. One was the traditional "time at large" in terms of months. The other incorporated the Caillou Lake temperature measurements. For every day of 1977, the average of the hourly temperature readings was found:

$$D_i' = \left(\sum_{k=1}^{24} {}^{o}C_{ki}\right)/24$$

where D_i' is the average for the day i of the year, and ${}^{o}C_{ki}$ is the reading in degrees Celsius at the kth hour of the day.

D_i' was then redefined for each day as:

$$D_i = D_i' - 17.0 \qquad \text{for } D_i' > 17.0$$

$$D_i = 0.0 \qquad \text{for } D_i' \leq 17.0$$

The base of 17.0°C. was used for reasons discussed below.

For each shrimp, the variable T was defined as the sum of the D_i for each day it was at large, except the first and last days. For those days, only $D_i/2$ was added in because it was assumed that the shrimp was at large only one-half of the first and last days. T was the temperature/time variable (henceforward called the "temperature variable") then used in the four growth equations (Appendix).

The base of 17 °C. corresponds to a threshold of temperature below which growth essentially ceases, as determined from the mark-recapture data. Laboratory studies on post-larval white shrimp (Zein-Eldin and Griffith 1969) indicate that their growth is nearly stopped at temperatures below 15 °C. A lower threshold for growth was first set at 0 °C., then 15°C. and then varied between 13 °C. and 18 °C. at 1-degree intervals in fitting the Richards model (using T) to the entire data set. The base temperature of 17 °C. produced a minimal sum of squares in the fit of the Richards model. A similar technique at high temperatures showed no upper threshold. The differences in sums of squares resulting from the various choices of threshold temperature could not be tested for statistical significance; however, all choices between 13 °C. and 18 °C. resulted in about 7% smaller residual sums of squares than when 0 °C. was used.

The base temperature of 17 °C. is best for this data set, this definition of a temperature variable and this model. Because the estimate is data and model-dependent, this threshold value is not intended to be interpreted as an accurate population parameter estimate but is for use only in this study. I believe that more extensive temperature information should be used to estimate the population value.

C. Converting mark-recapture models to size-at-temperature models

The mark-recapture data determine the shape of the growth models. In order to plot the equations and the data in two dimensions (Figures 1-3), it is necessary to convert the mark-recapture models to size-at-temperature models (Appendix). Usually it is assumed that, for a particular growth model, the animals had grown according to that model since birth. I chose, however, to assume only that the animals grew according to any of these models after they equalled the size of the smallest release in the data (i.e., 37 mm). The variable T* (Appendix) is defined as total T measured from the time when a shrimp was 37 mm in tail length; this is the temperature variable then used in the size-at-temperature models. Thus the parameter S_o is set at 37 mm, the length when T* is zero; the parameter B is determined using this S_o. With these definitions of T* and S_o, the curves are not extrapolated beyond the range of the data.

The mark-recapture data has been plotted (Figures 2-3) in two dimensions by calculating the value of T* corresponding to a given release length using the chosen size-at-temperature equation. This initial T* is then added to the T observed while the animal was at large, resulting in the T* corresponding to the recapture length.

D. Measuring the effectiveness of the regression.

For every mark-recapture equation, when the growth parameter k is qual to zero, the equation reduces to

$$L_{2i} = L_{1i} + \varepsilon_i$$

where L_{2i} is the length at recapture for the ith animal, L_{1i} is the length at release, and ε_i is random error. Thus the use of R^2, the square of the multiple correlation coefficient in linear least squares, is not appropriate

for these equations. I have defined a similar measure of the effectiveness of the regression as:

$$P = \frac{SSL - SSE}{SSL}$$

where

$$SSL = \sum_{i=1}^{N} (L_{2i} - L_{1i})^2$$

and SSE is the residual sum of squares from fitting a growth equation. SSL is the amount of variation between L_{2i} and L_{1i}, and corresponds to the "total sum of squares". Then the statistic P is the percent of this total variation which is explained by either of the independent variables time at large or T in the growth model. It is a measure of the contribution of that variable to the prediction of recapture size.

The values of the statistic P have been calculated after fitting the growth models in order to evaluate and compare the various equations.

RESULTS

A. Comparisons among growth models.

The residual sums of squares from the regressions (Table 1) and a "total sum of squares" (SSL) of 546,348 were used to determine the values of the statistic P as defined above. The percent of variation between L_2 and L_1 explained by any of the models is between 70.8% and 81.2% (Table 1), indicating that all of the growth models are reasonably good predictors of length.

The linear models clearly explain less variation than do the Richards models and predict large recapture lengths much less closely. Though the differences among the percents of variation explained cannot be tested for

statistical significance, these results support the choice of an asymptotic growth curve.

	Independent variable			
	time at large		T (temperature)	
	Residual sum of squares	Percent of variation explained	Residual sum of squares	Percent of variation explained
Richards	126673	76.8	102587	81.2
logistic	126753	76.8	102600	81.2
von Bertalanffy	129024	76.4	103334	81.1
linear	159263	70.8	114503	79.0

Table 1. Residual sums of squares for growth models fitted to white shrimp data, and the percent of total variation between L_2 and L_1 explained by the independent variable (time at large or T).

The four temperature-dependent growth equations are better predictors of recapture length for these data than are their counterparts which do not incorporate temperature. Using the temperature variable T rather than time at large in the growth equations explains an additional 4.4% of the variation between L_2 and L_1 for the Richards equation, to as much as 8.2% more for the linear equation (Table 1). The three temperature-dependent asymptotic equations are not greatly different from one another, explaining approximately the same amount of variation. When converted to size-temperature equations (by setting T=0 at L_2=37 mm), they vary in their prediction of recapture size by less than 2 mm in the region where 98% of the data fall, 40 to 100 mm in recapture length (Figure 1). Although the Richards quation (Figure 2) is chosen as best in this study, any of the asymptotic

quations based on T could be used.

B. Parameter estimates

Although the three temperature-dependent asymptotic curves are very close to each other (Figure 1), the estimates of the asymptote (S_∞) vary somewhat (Table 2). The same is true for the time-dependent models. I feel that this is because of a lack of data for large shrimp. Indeed, in this data set, fewer than 2% of the recaptured shrimp are greater than 100 mm; none are greater than 115 mm, although many of the tagged shrimp were greater than 115 mm at release. Thus I feel that the data are not sufficient to accurately determine the asymptote. Because of the high correlation among all the parameters of the growth equations, the other parameter estimates also may not be biologically meaningful. The growth equations should be viewed here only as empirical functions to predict recapture size in order to study the association between temperature and growth.

Model		Parameter				
		S_∞	k	m	S_o	B
temperature-dependent	Richards	107.	-.0019	1.77	37.	
	logistic	105.	.0016			1.84
	von Bertalanffy	131.	.0006			.72
	linear		.0347		37.	
time-dependent	Richards	101.	-.439	2.49	37.	
	logistic	102.	-.576			1.76
	von Bertalanffy	115.	.266			.68
	linear		10.99		37.	

Table 2. Estimates of the parameters of growth equations for white shrimp.

C. An example

Temperature-correlated growth and the better prediction of recapture length by the temperature-dependent model can be clearly seen by examining some of the data. There were 167 animals between 44 and 112 mm at release and at large from 29 to 39 days; these were separated by month of release (July, August, and September). Of these, 156 were then separated into 10-mm length categories (40-49 cm, ..., 70-79 mm). The average increase in tail length for each subset and for the entire group was calculated for each release month. The average length increase shows a marked decreasing trend over months for all size classes and for the entire group (Figure 4(a) and Table 3). If time at large were an adequate predictor (with release length) of recapture length, then the average increase should stay nearly constant across months within each size class because all the animals were at large for about 30 days. The patterns of the average increase across months are very similar to those of the average values of T, the temperature variable, associated with each group (Figure 4(b) and Table 3).

The superiority of the temperature-dependent Richards model can be seen by using the two models to predict recapture length for the average release size in each size-by-month group. The average time at large (approximately 30 days) is used in the time-dependent model, and in the temperature-dependent model the average value of T is used. A comparison of the errors of prediction (Figure 4(c) and Table 3) shows the temperature-dependent model to be consistently more accurate than the time-dependent model for these data (with two minor exceptions).

Length class	Release month	Sample size	Average value of T	Average release length	Average increase in length	Predicted increase using T	Predicted increase using time
all	July	91	424.4	62.1	16.8	15.5	12.8
	Aug	32	376.9	63.5	14.3	13.7	12.5
	Sept	44	257.1	59.5	8.1	10.1	13.2
40-49mm	July	7	425.6	45.9	19.3	17.6	14.0
	Sept	12	279.6	46.6	11.3	11.7	14.0
50-59mm	July	21	426.5	54.6	20.1	16.9	13.7
	Aug	12	374.0	54.9	21.1	14.9	13.7
	Sept	12	259.2	52.8	8.2	10.7	13.8
60-69mm	July	44	423.2	63.6	15.7	15.1	12.5
	Aug	11	380.2	64.1	12.4	13.7	12.4
	Sept	11	259.4	63.8	6.5	9.7	12.5
70-79mm	July	17	422.8	72.2	14.7	13.0	10.6
	Aug	4	380.8	74.0	10.3	11.5	10.0
	Sept	5	232.6	75.2	6.4	7.2	9.8

Table 3. Sample size, average value of T, average release length, average increase in length, and predicted increase in length using two models for white shrimp at large 29 to 31 days, by release length class and release month.

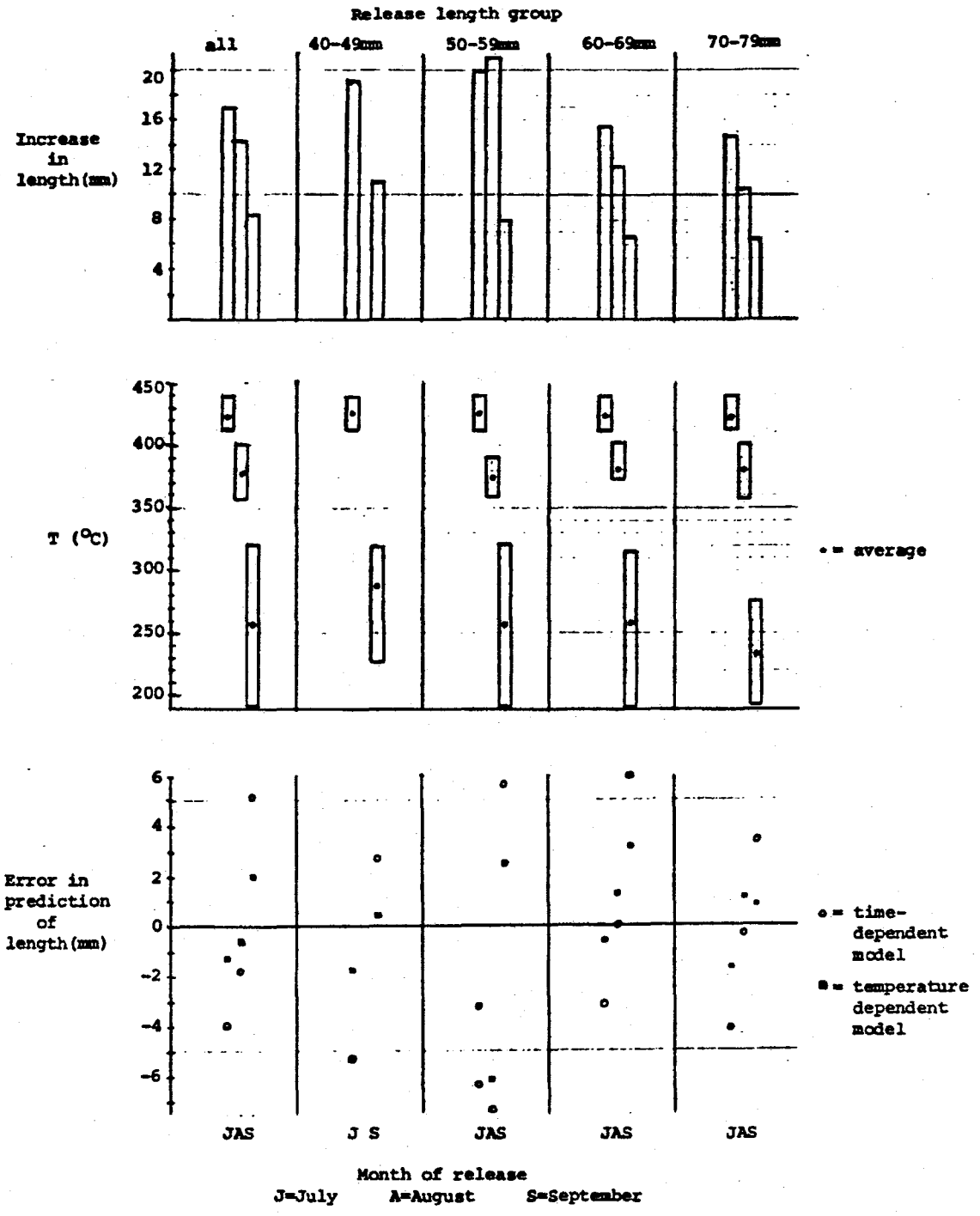

Figure 4. Aspects of the association between temperature and growth for white shrimp at large 29 to 31 days:

(a) average increase in tail length (mm);

(b) average and range of the temperature variable T;

(c) error in prediction of average size for the average release size in each group by 1) the time-dependent Richards model using average time at large, and 2) the temperature-dependent Richards model using the average value of T.

D. The accuracy of the model for large recapture sizes

The temperature-dependent model appears to predict large sizes with less accuracy and precision than small sizes. The plot of the data about the temperature-dependent Richards curve (Figure 2) indicates that the quation may tend to underestimate large recapture sizes. This may be due in part to the lack of data at large sizes. It may also be due to inaccurate values for T being assigned to some shrimp, especially to those spending some time in offshore bottom waters. The plot of the offshore releases about the curve (Figure 3) shows a negative bias in the prediction of recapture size. This could indicate that too low a value of T is being assigned to those shrimp.

Studies of offshore waters (Temple, Harrington and Martin 1977) show that surface and bottom temperatures are approximately equal to depths of 7 meters. However, bottom temperatures at greater depths frequently increase as the surface temperatures decrease. Thus surface temperatures at the inshore location (Caillou Lake) might be quite different from offshore bottom temperatures. This would greatly affect the values of T for those shrimp free in November and December, most of which are large shrimp. When more complete temperature data are available, the model may be updated.

CONCLUSIONS

It is apparent in this study that the models for linear growth do not adequately describe the growth of these shrimp. However, the three asymptotic growth equations which were used do fit the data well, perhaps equally well.

The models which account for water temperature are better predictors of length than are those which do not. The residual sums of squares produced by the temperature-dependent models are consistently smaller than those produced by the time-dependent models. Temperature-dependent asymptotic growth models account for more than 81% of the variation between release size and recapture size for these data. The correlation between growth and water temperature can be readily seen in this data set by comparing the size increases observed during time periods with different water temperatures.

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APPENDIX

The size at age growth equations are:

logistic $S_a = S_\infty / (1+B \cdot e^{-k \cdot a})$, where $B = (S_\infty / S_o) - 1$

von Bertalanffy $S_a = S_\infty (1-B \cdot e^{-k \cdot a})$, where $B = (S_\infty - S_o)/S_\infty$

Richards $S_a = \left[S_\infty^{1-m} - (S_\infty^{1-m} - S_o^{1-m}) e^{-(1-m)k \cdot a} \right]^{1/(1-m)}$

linear $S_a = S_o + k \cdot a$

where a is age, S_a is size at age a, S_∞ is asymptotic size, S_o is size at the chosen origin of age measurement , m is a shape parameter, and k is a parameter related to growth rate. The Richards equation (Richards 1959) is a general form which includes the logistic and von Bertalanffy equations.

With mark-recapture data, absolute age is not known, but the size at release (S_1) , time at large (Δa), and size at recapture (S_2) are known. Following the method of Parrack (1978), the size at age equations can be transformed to mark-recapture equations. The age at recapture can be rewritten as a function of S_1, Δa and the equation parameters, resulting in the mark-recapture growth equations:

logistic $S_2 = S_\infty / (1+((S_\infty - S_1)/S_1) e^{-k \cdot (\Delta a)})$

von Bertalanffy $S_2 = S_\infty - (S_\infty - S_1)e^{-k\cdot(\Delta a)}$

Richards $S_2 = \left[S_\infty^{1-m} - (S_\infty^{1-m} - S_1^{1-m})e^{-(1-m)k(\Delta a)} \right]^{1/(1-m)}$

linear $S_2 = S_1 + k\cdot(\Delta a)$.

When a mark-recapture equation is fitted, all the parameters in the corresponding size-at-age model except S_o or B are determined. Auxiliary information is used to estimate the remaining parameter.

In the present study, a newly-defined variable T related to temperature is used instead of Δa in the mark-recapture equations, resulting in temperature-dependent mark-recapture equations. T*, which is total T measured from a chosen origin, replaces age in the size-at-age equations, resulting in size-at-temperature growth models.

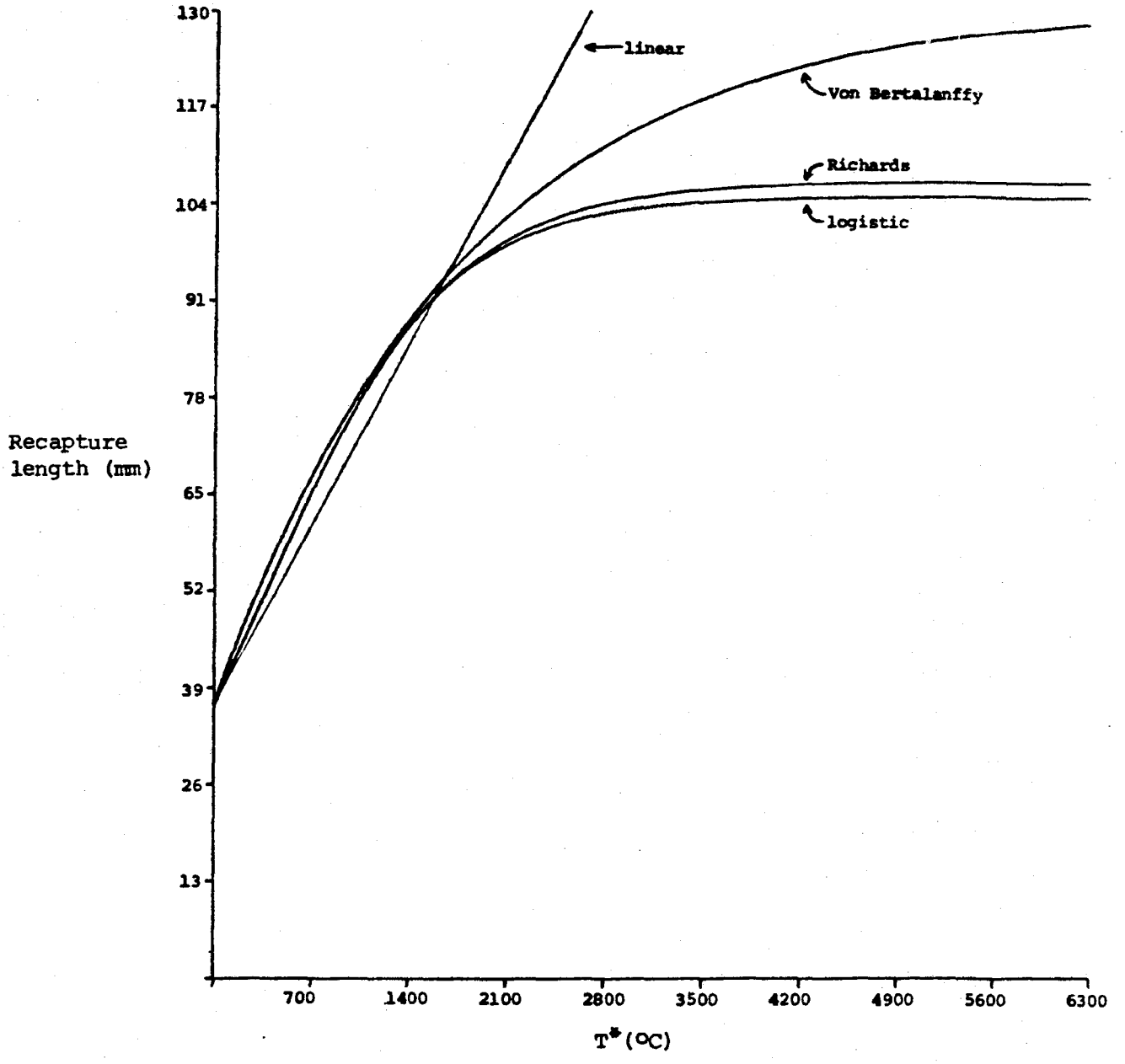

Figure 1. Four temperature-dependent growth equations for white shrimp.

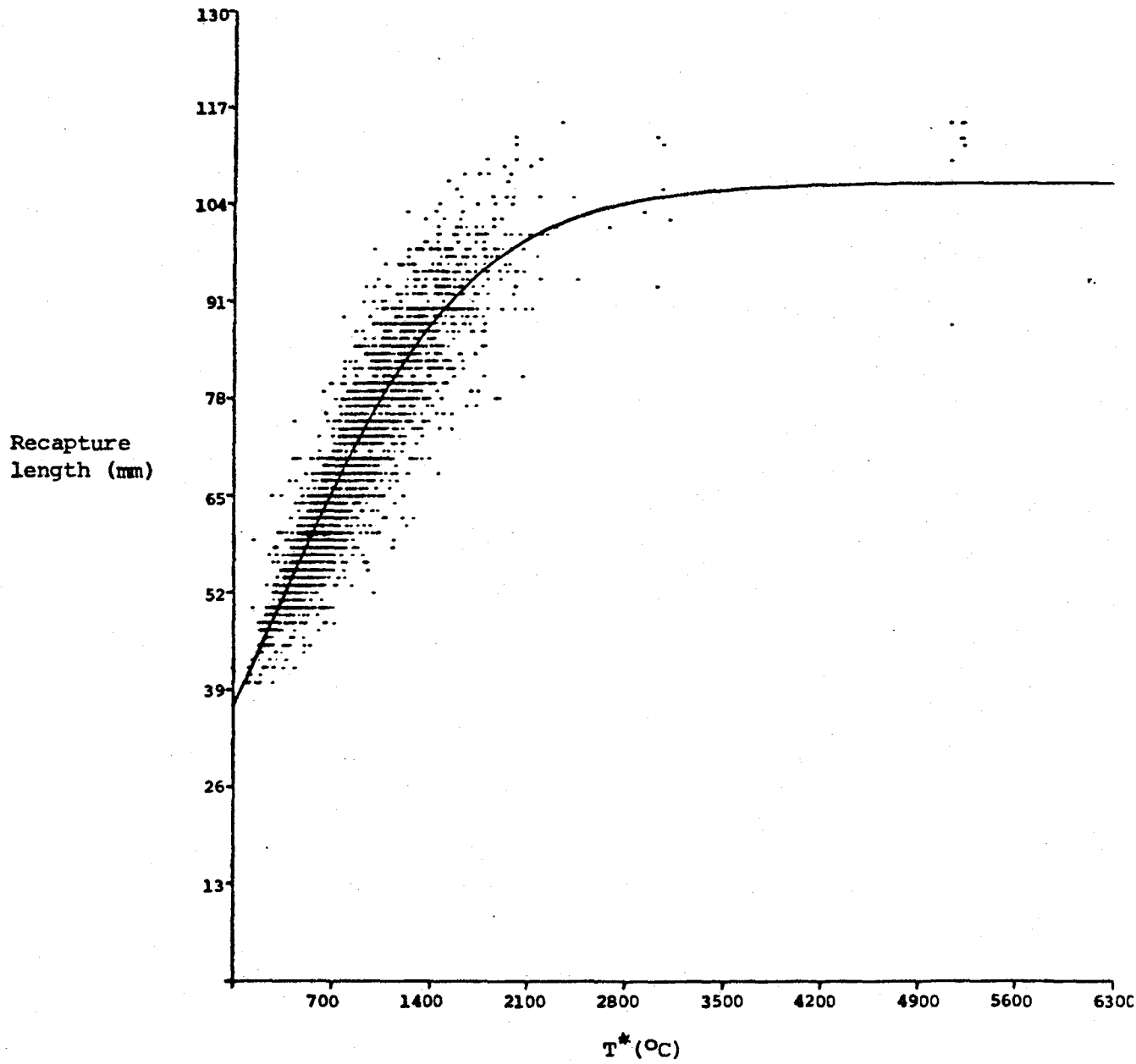

Figure 2. White shrimp data about the temperature-dependent Richards growth equation.

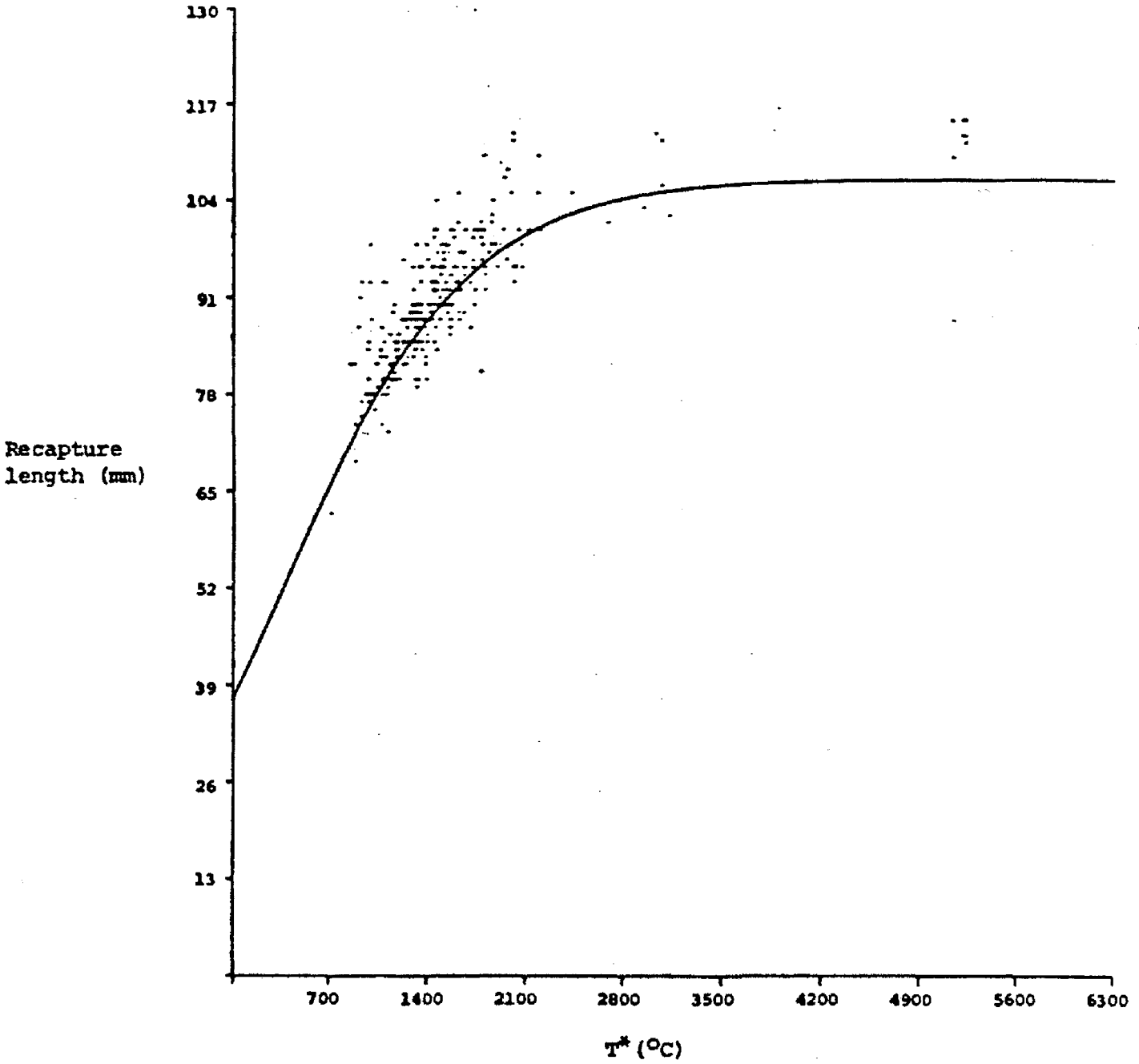

Figure 3. Offshore releases about the temperature-dependent white shrimp Richards growth equation.