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A Mass-balance Model for Evaluating Food Web Structure and Community-scale Indicators in the Central Basin of Puget Sound

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Table of Contents

List of Figures	v
List of Tables	vii
Executive Summary	ix
Acknowledgments.....	xi
Abbreviations and Acronyms	xiii
Introduction and Objectives.....	1
Methods	4
Model Domain: The Puget Sound Central Basin	4
Ecopath with Ecosim.....	5
Functional Groups	7
Data Assimilation and Parameter Development.....	7
Model Balancing	10
Model Assessment.....	11
Results.....	15
General Characteristics and Mass Balancing of the Ecopath Model.....	15
Biomass, Functional Diversity, and Evenness Patterns.....	25
Throughput and Transfer Efficiency	25
Mortality.....	27
Dynamic Model Responses	33
Discussion.....	44
Objectives 1 and 2: Model Development and Assessment.....	44
Objective 3: Identifying Data Gaps.....	46
Conclusions	49
References.....	51
Appendix A: Species and Functional Group Descriptions	79
Primary Producers	79
Zooplankton and Pelagic Invertebrates	85
Benthic Invertebrates.....	93
Pelagic Fishes	113

Salmon.....	118
Gadiforms.....	130
Other Demersal Roundfish.....	135
Flatfish.....	142
Chondrichthyans.....	145
Seabirds.....	149
Marine Mammals.....	159
Bacterial and Detrital Pools.....	162
Appendix B: Omitted Groups.....	165
Primary Producers.....	165
Invertebrates.....	165
Fishes.....	167
Seabirds.....	168
Marine Mammals.....	169
Appendix C: Frequently Used Estimation Methods.....	171
Biomass Estimation for Bottom Fish.....	171
Biomass Estimation for Seabirds.....	172
<i>P/B</i> Estimation for Benthic Invertebrates.....	172
<i>P/B</i> Estimation for Fish.....	173
<i>Q/B</i> Estimation for Fish.....	173
Use of Q_{10} for Temperature-dependent Rate Estimation.....	174
Bottom Fish Diet Estimation.....	175
<i>Q/B</i> Estimation for Seabirds and Marine Mammals.....	175
Commercial Harvest Estimates.....	176
Appendix D: Representing Life History.....	179

List of Figures

Figure 1. Map of central Puget Sound, the spatial domain for the Ecopath with Ecosim model.....	4
Figure 2. Food web diagram for the PSCB Ecopath model.....	16
Figure 3. Biomass of coarsely pooled categories of functional groups in the PSCB Ecopath model.....	26
Figure 4. Plot of Shannon diversity index against functional evenness for coarsely pooled categories of functional groups in the PSCB Ecopath model	27
Figure 5. Relationship between the rankings of functional group biomass and functional group throughput in the PSCB Ecopath model	30
Figure 6. Transfer efficiency as a function of trophic level for consumer groups in the PSCB Ecopath model	31
Figure 7. Allocation of mortality to fishing, predation, or other sources.....	32
Figure 8. Screen captures from 50-year Ecosim simulation of PSCB food web responding to stochastic variability in phytoplankton biomass	34
Figure 9. Screen capture from 50-year Ecosim simulation of PSCB food web responding to a sharp reduction in raptor biomass.....	38
Figure 10. Ecosim outputs representing trophic cascade dynamics caused by a decline in raptor biomass	39
Figure 11. Screen captures from 50-year Ecosim simulations of the PSCB food web subjected to either baseline fishing mortality or a closure of all fisheries in year 1	41
Figure 12. Relationship between F_{MSY} and P/B for targeted functional groups in the PSCB Ecosim model	43

List of Tables

Table 1. Bathymetry of the PSCB.....	5
Table 2. Functional groups in the model with major representatives	8
Table 3. Ecopath parameters for the functional groups in the PSCB model.....	17
Table 4. Ecopath diet matrix for consumers in the PSCB model.....	19
Table 5. Landings by gear type of targeted groups.....	24
Table 6. Biomass, throughput, and transfer efficiency of functional groups	28
Table 7. Trophic relationships in the Ecopath model where a predator accounts for at least 25% of the total predation mortality experienced by a prey group	33
Table 8. Results of pairwise MAR analyses of relationships between phytoplankton and each functional group at lags of 1–5 years.....	35
Table 9. Groups that changed by at least 10% following the raptor decline in year 20 of the raptor simulation.....	40
Table 10. Groups that changed by at least 10% following a closure of all fisheries in year 1	41
Table 11. Productivity, fishing rates, and MSY for targeted groups	42
Table A-1. Seasonal production rates of nanoplankton and net plankton in oceanic estuaries.	80
Table A-2. Key representatives of the rockfish functional group in the PSCB EwE model.....	136
Table A-3. Key families and representatives in the demersal fish functional group in the PSCB EwE model.....	141
Table A-4. Key representatives of the flatfish functional groups in the PSCB EwE model.....	142
Table A-5. Key representatives of the marine bird functional groups in the PSCB EwE model.....	150

Executive Summary

Scientists, policy makers, and stakeholders in coastal regions are increasingly calling for ecosystem-based approaches to managing marine resources and services. Such approaches, generally referred to as ecosystem-based management (EBM) of marine systems, recognize the importance of linkages between (and trade-offs among) species, processes, and stakeholder uses. Puget Sound is a system in which EBM methods are especially applicable, because it supports a diverse assemblage of species and a growing human population that derives a range of services from natural resources and processes. These services span far beyond fisheries. Recognizing the need for EBM in Puget Sound, the State of Washington established a consortium—the Puget Sound Partnership (PSP)—in 2007 to identify goals and actions pursuant to ecosystem restoration and sustainability, particularly with respect to species, habitat, water quality, water quantity, and human health and well-being.

Ecosystem models have emerged as important tools in support of EBM. They provide frameworks for synthesizing information and evaluating the efficacy of alternative management actions. Here we describe the development of an ecosystem model of the contemporary food web in the Puget Sound Central Basin. This model, developed using Ecopath with Ecosim software, is ultimately intended to support PSP goals by identifying meaningful indicators that can be used to monitor the efficacy of management actions, quantify risk, and stimulate alternate ecosystem management scenarios. In this document, however, our objective was to describe the development of the model; we catalog the assimilation of available data that went into model construction, describe basic model outputs and scenario-based simulations used to assess model performance, and identify data gaps that could constrain further model development and the quality of model outputs.

The model consists of 65 functional groups, including primary producers, invertebrates, vertebrates, and detrital groups from nearshore, offshore, pelagic, and demersal habitats; it also includes several fisheries. Using a range of sources, we developed parameter estimates for biomass, production, consumption, fishery losses, and diet. These parameters were input into the initial (Ecopath) model framework and were modified iteratively in order to achieve mass balance. The mass-balance model provided general, descriptive information on biomass allocation, functional group diversity, energy flow, and mortality. A series of scenarios were then run, examining model responses to temporal changes in key functional groups (phytoplankton and raptors) and to changes in fishing mortality.

Our model depicts a system dominated, in terms of biomass, by demersal species, although high energy throughput in the pelagic community compensates for its lower biomass. Biomass is highly aggregated, with seven functional groups (phytoplankton, copepods, soft infauna, infaunal bivalves, geoducks [*Panopea abrupta*], small crustaceans, and ratfish [*Hydrolagus colliiei*]) comprising nearly 68% of living biomass. Bottom-up dynamics strongly influence trophic flows, although there are examples of top-down control; for example, bald

eagles (*Haliaeetus leucocephalus*) appear capable of eliciting trophic cascades. Current levels of fishing mortality appear to be sustainable and below the maximum sustainable yield level, due in part to declines in commercial catches in recent decades; however, because recreational catches are not well accounted for in our model, some fishing mortality levels are likely underestimates.

Many important data gaps became obvious over the course of model development. However, these gaps do not preclude use of this model in EBM-related applications; rather, they help model users to define the limits within which model output is applicable. Major gaps at this point include: the lack of basin-scale, scientifically robust estimates of biomass for a majority of functional groups; evidence of interaction strengths among different food web components; diet information across a representative range of seasons, sizes, depths, and habitats; and empirical estimates of recreational fishing mortality.

We will continue to develop and apply this model to ask questions about the value of different functional groups as indicators, and also to address community-scale ecological or management questions that can be complemented with fieldwork, experimental research, and engagement with managers and stakeholders. Moreover, we will undertake further modeling efforts that account for spatial patchiness, biophysical coupling, and a wider range of ecological and societal processes critical to the functioning of the Puget Sound ecosystem.

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Abbreviations and Acronyms

<i>BA</i>	biomass accumulation
BRT	biological review team
CSIRO	Commonwealth Scientific and Industrial Research Organization (Australia)
DPS	distinct population segment
EBM	ecosystem-based management
<i>EE</i>	ecotrophic efficiency
EwE	Ecopath with Ecosim
<i>F</i>	fishing mortality rate
HAB	harmful algal bloom
<i>M</i>	mortality
MAR	multivariate autoregressive
M_0	other mortality
MSY	maximum sustainable yield
NWFSC	Northwest Fisheries Science Center
NWIFC	Northwest Indian Fisheries Commission
PacFIN	Pacific Fisheries Information Network
PFMC	Pacific Fishery Management Council
<i>P/B</i>	production:biomass ratio
<i>P/Q</i>	production:consumption ratio
PSCB	Puget Sound Central Basin
PSP	Puget Sound Partnership
<i>Q/B</i>	consumption:biomass ratio
S/a	subadult
TL	trophic level
WDE	Washington Department of Ecology
WDFW	Washington Department of Fish and Wildlife
WDNR	Washington Department of Natural Resources
YOY	young of the year

Introduction and Objectives

As a discipline, marine ecosystem-based management (EBM) has mostly emphasized fisheries applications. An ISI Web of Knowledge search¹ of the primary literature from 1998 to 2007 found 100 citations with the terms “marine,” “ecosystem-based,” and “management.” If the terms “fishery” or “fisheries” were excluded, the total dropped to 26. However, as marine EBM evolves, scientists, agencies, organizations, and institutions are pursuing integrative approaches, focusing not just on fisheries but also on issues including habitat, species diversity, water quality, recreation and tourism, coastal commerce, human health, and sustainable energy development. In densely populated, highly impacted coastal ecosystems, fisheries and other sectors are inextricably linked. Ignoring those linkages may only increase uncertainty, risk, and conflict associated with single-sector decision making (Halpern et al. 2008). Truly integrated EBM offers the promise of greater understanding of ecosystems that support diverse sectors and ecosystem services, provided that tractable conceptual, empirical, theoretical, and institutional frameworks for integration are available.

Puget Sound is a classic case of an imperiled marine ecosystem in which multiple sectors and stakeholder groups have strong and often opposing interests (Ruckelshaus and McClure 2007). This large estuarine system supports iconic species of ecological, economic, and cultural significance, including Pacific salmon (*Oncorhynchus* spp.), killer whales (aka orcas, *Orcinus orca*), bald eagles (*Haliaeetus leucocephalus*), and Dungeness crab (*Cancer magister*). These and hundreds of other dynamically interacting species inhabit the sound’s diverse habitats, which include sandy beaches, eelgrass beds, river deltas, high-relief rocky reefs, narrow straits with intense tidal currents, and deep (>150 m) soft-sediment zones. Nearby mountain ranges and forests further contribute to the region’s considerable natural beauty.

On the other hand, Puget Sound provides services to and faces stresses from many human sectors. The watershed is home to a growing human population of approximately 4 million people (PSP 2008), mostly in and around the major cities of Everett, Seattle, Tacoma, and Olympia. The ports of Seattle and Tacoma accounted for approximately 16% of the total volume shipped through commercial ports on the U.S. West Coast in 2007 (American Association of Port Authorities, online at <http://www.aapa-ports.org>). Fish and invertebrate populations support commercial, tribal, and recreational fisheries, and some fisheries have been closed due to declines in stock sizes (e.g., Gustafson et al. 2000). Impoundments throughout the watershed support hydropower, irrigation, and water provisioning for industrial and consumptive purposes (Ruckelshaus and McClure 2007). The hydrology of the system is further affected by land use changes that alter sediment porosity, vegetation, and transpiration. In many areas, runoff has been transformed from a slow, disseminated process to a fast, point-source process that carries large loads of sediment, nutrients, and pollutants. While these changes and activities affect many

¹ Online at <http://apps.isiknowledge.com>, search conducted 3 December 2009.

of the region's hallmark species, they are also linked to a way of life and a level of affluence that many people consider desirable (Ruckelshaus and McClure 2007, PSP 2008).

To better preserve the species and functioning of the Puget Sound ecosystem while also promoting sustainable use of its goods and services, the State of Washington established the Puget Sound Partnership (PSP) in 2007. PSP is a consortium of individuals, citizens groups, businesses, government agencies, tribes, and scientists that has identified a number of goals related to ecosystem restoration and sustainability (PSP 2008). These goals focus on achieving desirable, measurable progress for the species, habitat, water quality, water quantity, and human health and well-being in the region. The PSP Action Agenda (PSP 2008) further states that these goals should be achievable by the year 2020. The ecological and societal complexity inherent to Puget Sound presents a fundamental challenge to management agencies and policy makers mandated with meeting PSP goals. Moreover, it challenges scientists to develop tools that managers and policy makers can use to examine the effectiveness of management alternatives and the trade-offs associated with them.

Ecosystem-scale simulation modeling has proven to be an extremely valuable tool for synthesizing large amounts of diverse information for the sake of understanding marine ecosystem dynamics in the context of EBM (Fulton et al. 2005, Plagányi 2007, Townsend et al. 2008). Ecosystem models can provide conceptual frameworks in which to examine many of the salient questions and objectives put forth in the PSP Action Agenda (PSP 2008). They may range from relatively simple methods that focus in detail on a subset of important ecosystem components (such as single-species models with environmental drivers or “minimum realistic models” with a few interacting species) to full ecosystem models that incorporate entire communities and abiotic features (Plagányi 2007). Within these frameworks, modelers can compile the best available information pertinent to a particular issue, and develop thought experiments that quickly and inexpensively test questions or make predictions about ecological relationships and the effects of human activities on ecosystem components. Models also help quantify important variables that are difficult to measure (e.g., energy flow through a food web), and may reveal unanticipated interactions or knowledge gaps (Townsend et al. 2008). In short, models are essential tools that complement monitoring, empirical study, and experimentation in support of managing and restoring marine resources.

Scientists at NOAA's Northwest Fisheries Science Center (NWFSC), in partnership with other agencies and institutions, are developing several ecosystem-scale models of the Puget Sound marine ecosystem, with some direct links to freshwater and terrestrial processes. This report documents the development of one such model, a food web model of the Central Basin of Puget Sound using Ecopath with Ecosim (EwE) software created by scientists at the University of British Columbia (Christensen et al. 2005).

The EwE model of the Puget Sound Central Basin (PSCB) was developed for reasons consistent with goals outlined in the PSP Action Agenda (PSP 2008) and the NOAA Sound Science report (Ruckelshaus and McClure 2007). Our major objectives for this document were to:

1. Assimilate available data on species abundance, vital rates, diets, and habitat associations into a trophodynamic model framework.

2. Assess model performance through a series of contrasting scenario-driven simulations.
3. Identify significant data gaps that could potentially constrain model development or increase uncertainty in the outputs.

Objectives 1 and 2 involve incorporating available information into a model that can serve as a caricature of a system. Such models can be used in a variety of applications, including simulation-based estimates of ecosystem responses to management actions (Townsend et al. 2008). Modeling exercises of this sort can also improve understanding of the structure and functioning of a food web, which is important given the diversity and complexity of Puget Sound's living resources (Ruckelshaus and McClure 2007). It is for this reason that we present output from several dynamic scenarios that realistically perturb the system at multiple trophic levels (i.e., variability in primary production, long-term changes in abundance of a top predator, and a fishery closure). Testing the model in these diverse ways is intended to provide a sense of how well our simulated system behaves in comparison to the real world system.

Objective 3 is a corollary to Objective 1 and Objective 2. It is addressed implicitly in the Methods and Results sections and the Appendices, and is discussed explicitly in the Discussion section in the sense of lessons learned at this point of model development. The broader long-term objectives for this project (including evaluating the usefulness of different metrics as ecosystem indicators, analyzing the risk of different functional groups with respect to potential threats, and simulating alternate ecosystem management scenarios) are not discussed in detail in this document. However, the efficacy of this model as a management tool depends on how well Objectives 1, 2, and 3 are addressed within this document and as the model continues to evolve.

Methods

Model Domain: The Puget Sound Central Basin

Puget Sound is a complex fjord-like ecosystem that is part of the larger Salish Sea (the inland marine waters of Washington and British Columbia, Figure 1). Its basins drain a total area of 35,500 km². Each basin has unique geography, land coverage, hydrology, oceanography, and species composition (Ruckelshaus and McClure 2007). We focused on the PSCB because it is where most of the human population resides and where considerable anthropogenic alterations have occurred; thus, it is an area where many management activities will be directed in order to

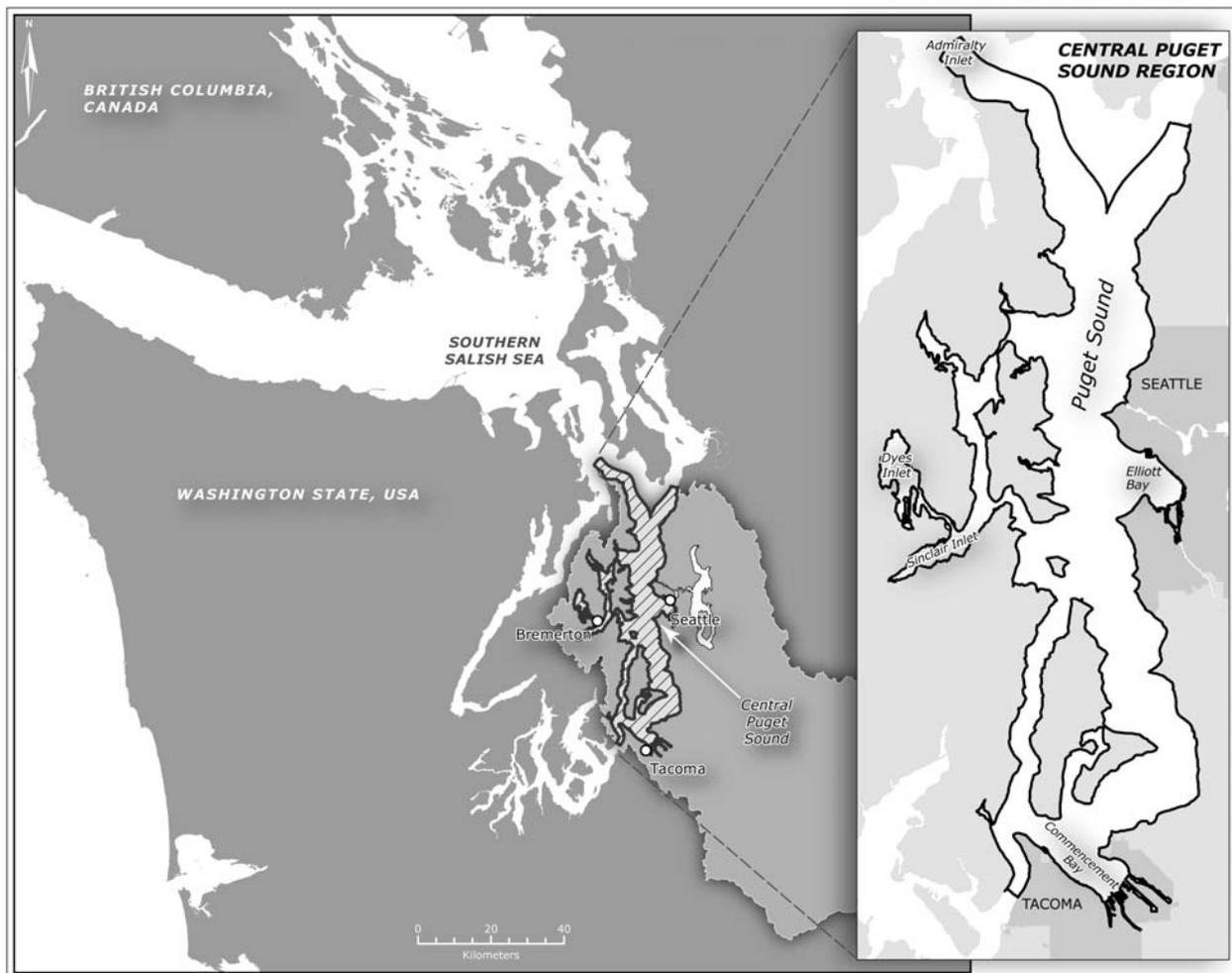


Figure 1. Map of central Puget Sound, the spatial domain for the EwE model, and the rest of the southern Salish Sea, as well as catchment areas (lightly shaded) that feed directly into central Puget Sound. Inset shows Puget Sound in more detail.

achieve PSP goals. Moreover, EwE software is not spatially explicit; it treats the model domain as a single biogeographic box with no clear differentiation of spatial gradients or patchiness (Aydin et al. 2002). That framework seems best suited for modeling a single basin of Puget Sound, not for modeling multiple basins simultaneously.

PSCB domain boundaries (Figure 1) correspond to the combined north central and south central action areas as delineated and described by the PSP (2008). The PSCB model domain encompasses all marine habitats ranging from Tacoma Narrows in the south to just south of Whidbey Island in the north, and includes such large bays as Elliott Bay, Commencement Bay, Sinclair Inlet, and Dyes Inlet. It does not include Admiralty Inlet. General features of this system have been well summarized elsewhere (e.g., Strickland 1983, Gustafson et al. 2000, PSP 2008). In brief, the system spans from intertidal habitats dominated by sand, gravel, and occasional eelgrass or algal habitats to offshore pelagic zones and muddy-bottomed and sandy-bottomed habitats with depths of more than 250 m. Bathymetrically, approximately one-third of the total area of the system is less than 40 m deep; below 60 m, the bottom gradient drops relatively steeply until 160 m, slows until about 210 m, then drops off again (Table 1). The water column is typically well mixed during the cooler, windy winters and stratified during warmer summers when freshwater runoff overlies deep, cool, saltier water. Tide energy is high, and tidal height differences can be on the order of 6 m.

Ecopath with Ecosim

To address our objectives, we used the EwE software (Christensen et al. 2005), which has been applied to dozens of freshwater and marine ecosystems worldwide in recent decades. EwE is a trophodynamic model in which different species or guilds are represented as biomass pools. The size of pools is regulated by gains (consumption, production, and immigration) and losses (mortality and emigration). Pools are linked to one another by predation or in some cases by reproduction and maturation. Fisheries extract biomass of targeted groups and bycatch groups. The principles of mass balance and energy conservation govern all processes. EwE enables the

Table 1. Bathymetry of the PSCB, broken down by 10 m depth increments and proportion of the total area that falls within that increment.

Depth (m)	Proportion of total area	Depth (m)	Proportion of total area
0–10	0.137	131–140	0.017
11–20	0.081	141–150	0.019
21–30	0.061	151–160	0.029
31–40	0.050	161–170	0.053
41–50	0.049	171–180	0.068
51–60	0.049	181–190	0.064
61–70	0.031	191–200	0.052
71–80	0.028	201–210	0.032
81–90	0.027	211–220	0.020
91–100	0.029	221–230	0.017
101–110	0.027	231–240	0.013
111–120	0.024	241–250	0.004
121–130	0.017	250+	0.005

user to simulate ecological or management scenarios, such as how the system and its components respond to changes in primary production, habitat availability, or fishing intensity (e.g., Field et al. 2006, Ainsworth et al. 2008b).

The software consists of two main modules: Ecopath, a static (though not necessarily steady-state) mass-balanced model of the perceived “initial” or reference state of a food web, and Ecosim, a dynamic model in which biomass pools and vital rates change through time in response to perturbations. In Ecopath, key parameters and data are input for each functional group in order to describe the reference state. Inputs include biomass per unit area, rates of production and consumption, diet proportions, and fishery losses. In Ecosim, perturbations in the reference state are simulated, and additional parameters can be changed in order to influence the strength of trophic interactions (e.g., to vary the extent of top-down or bottom-up control), to characterize stock-recruitment relationships, or to integrate temporal patterns of fishing or climate variability.

Ecopath is comprised of a series of linear equations that describe flows of mass into and out of discrete biomass pools, representing functional groups. Each linear equation has the form

$$B_i \times (P/B)_i \times EE_i - \sum_{j=1}^n B_j \times (Q/B)_j \times DC_{ji} - Y_i - E_i - BA_i = 0 \quad (1)$$

where, for species or functional group i , B is biomass, P/B is the production:biomass ratio (which is approximately equal to total mortality, Christensen et al. 2005), EE is ecotrophic efficiency, Y is fishery yield, E is net emigration, and BA is biomass accumulation. EE is the proportion of mortality that is attributable to other model compartments (predators and fisheries), and must be less than one under the assumption of mass balance. The summation term in Equation 1 signifies predatory losses to all predators j , B is the biomass of predator j , Q/B is the consumption:biomass ratio of predator j , and DC_{ji} is the proportion of i in the diet of predator j . We assume that all E_i equals 0.

In Ecosim, biomass pools are dynamic, as governed by coupled differential equations that stem from Equation 1 (Christensen et al. 2005). The Ecosim master equation is

$$\frac{dB_i}{dt} = g_i \times \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i) \times B_i \quad (2)$$

where, for each group i , B is biomass, g is growth efficiency, I is the immigration rate, M is other mortality not accounted for by interactions with groups or fisheries within the model, F is the fishing mortality rate, and e is the emigration rate. In our models, I_i and e_i will always equal 0. The summation terms represent the consumption rate of all groups j by group i (C_{ji}) and of group i by all groups j (C_{ij}). The C terms are actually functional response terms that reflect the fact that at any given time, a portion of a prey biomass pool is, in effect, invulnerable to the predator biomass pool by virtue of spatial discontinuities, refuge habitat or behavior, or other means of predator avoidance (Walters et al. 1997, Christensen et al. 2005).

The formulation for C is complex, taking into account prey invulnerability, predator and prey biomasses, predator and prey feeding times, and handling time; details are presented in Christensen et al. (2005, their Equation 49). Adjusting the parameters involved in determining C can affect the predator-prey relationship (e.g., top-down vs. bottom-up vs. intermediate control, the role of other functional groups in mediating the predator-prey relationships between groups j and I , etc.). In addition, some pools have age structure in order to better represent relatively complex life histories. Age-structured biomass pools are dynamically linked by temporally explicit reproduction and maturation processes; an explanation of those processes is given by Christensen et al. (2005).

Functional Groups

One of the first steps in the model development process was identifying the most important functional groups in the community, that is, the groups that would comprise the food webs we wish to represent in the model. The current list of 65 functional groups is presented in Table 2. Functional groups are either individual species or guilds of ecologically similar species, as described in some detail in Appendix A. The makeup of the list of functional groups was developed through a consultation process with experts from a number of agencies and institutions. Species or guilds were included or rejected based on criteria such as:

- their perceived influence over basic ecosystem functions, such as primary production, secondary production, biogenic habitat provision, etc.,
- their standing stock biomass, relative to other species or guilds,
- their importance in the diets of other groups,
- the amount of time they occur in the model's spatial domain each year,
- their ability to integrate ecological processes (e.g., species that move between habitat types and thus link the ecology of those habitats),
- their importance to commercial, tribal, or recreational fisheries,
- their importance to society for nonconsumptive reasons, and
- the availability of data to characterize their ecology, within the scope of EwE.

The functional group selection process was iterative and largely based on expert opinion and consensus. We did not develop quantitative inclusion or rejection thresholds for the above criteria. In some cases, we initially included groups but subsequently removed them. Several omitted groups, along with the justification for their omission, are listed in Appendix B.

Data Assimilation and Parameter Development

We consulted many sources to gather data for the Ecopath equation (Equation 1) for each functional group. Direct data sources included the primary literature, single species stock assessments, agency reports, and documents and unpublished data. Additionally, we conducted a series of short workshops with experts from state and federal agencies to discuss the source data. Indirect sources of data included parameter estimates from related species or from published

Table 2. Functional groups in the model with major representatives. Boldfaced groups have two age classes (e.g., juveniles and adults). See Appendix A for detailed information on each group.

Functional group	Common name	Scientific classification
Harbor seals	Harbor seal	<i>Phoca vitulina</i>
Sea lions	California sea lion	<i>Zalophus californianus</i>
	Steller sea lion	<i>Eumetopias jubatus</i>
Gulls	Various gulls	<i>Larus</i> spp.
Resident diving birds	Various cormorants	<i>Phalacrocorax</i> spp.
	Pigeon guillemot	<i>Cepphus columba</i>
Migratory diving birds	Western grebe	<i>Aechmophorus occidentalis</i>
	Various loons	<i>Gavia</i> spp.
	Common murre	<i>Uria aalga</i>
Nearshore diving birds	Various scoters	<i>Melanitta</i> spp.
	Various goldeneyes	<i>Bucephala</i> spp.
Herbivorous birds	Dabbling ducks	<i>Anas</i> spp.
	Various geese	<i>Branta</i> spp.
Raptors	Bald eagle	<i>Haliaeetus leucocephalus</i>
Wild salmon	Chum salmon	<i>Oncorhynchus keta</i>
	Chinook salmon	<i>O. tshawytscha</i>
	Coho salmon	<i>O. kisutch</i>
Hatchery salmon	Chum salmon	<i>O. keta</i>
	Chinook salmon	<i>O. tshawytscha</i>
	Coho salmon	<i>O. kisutch</i>
Pink salmon	Pink salmon	<i>O. gorbuscha</i>
Pacific herring	Pacific herring	<i>Clupea pallasii</i>
Forage fish	Surf smelt	<i>Hypomesus pretiosus</i>
	Pacific sand lance	<i>Ammodytes hexapterus</i>
Surfperches	Shiner perch	<i>Cymatogaster aggregata</i>
	Striped seaperch	<i>Embiotoca lateralis</i>
Spiny dogfish	Spiny dogfish	<i>Squalus acanthias</i>
Skates	Longnose skate	<i>Raja rhina</i>
	Big skate	<i>R. binoculata</i>
	Whitespotted ratfish	<i>Hydrolagus colliei</i>
Pacific hake	Pacific hake	<i>Merluccius productus</i>
Pacific cod	Pacific cod	<i>Gadus macrocephalus</i>
Walleye pollock	Walleye pollock	<i>Theragra chalcogramma</i>
Lingcod	Lingcod	<i>Ophiodon elongatus</i>
Rockfish	Copper rockfish	<i>Sebastes caurinus</i>
	Quillback rockfish	<i>S. maliger</i>
Piscivorous flatfish	Pacific sanddab	<i>Citharichthys sordidus</i>
Small-mouthed flatfish	English sole	<i>Parophrys vetulus</i>
	Rock sole	<i>Lepidopsetta bilineata</i>
	Various poachers	Family Agonidae
Demersal fish	Various eelpouts	<i>Lycodes</i> spp.
	Various small sculpins	Family Cottidae
Squid	Opalescent (market) squid	<i>Loligo opalescens</i>
Octopus	Red octopus	<i>Octopus rubescens</i>

Table 2 continued. Functional groups in the model with major representatives. Boldfaced groups have two age classes (e.g., juveniles and adults). See Appendix A for detailed group information.

Functional group	Common name	Scientific classification
Octopus (continued)	Giant Pacific octopus	<i>Enteroctopus dofleini</i>
Shrimp	Pandalid shrimp	Family Pandalidae
	Sand shrimp	<i>Crangon</i> spp.
Cancer crabs	Dungeness crab	<i>Cancer magister</i>
Sea stars	Sunflower star	<i>Pycnopodia helianthoides</i>
	Pink sea star	<i>Pisaster brevispinis</i>
Sea urchins	Green sea urchin	<i>Strongylocentrotus droebachiensis</i>
	Red sea urchin	<i>S. franciscanus</i>
Other grazers	Various snails	Class Gastropoda
	Various chitons	Class Polyplacophora
Small crustaceans	Various amphipods	Suborders Gammaridea, Corophiidea
	Various mysids	Family Mysidae
	Various crabs	Infraorders Brachyura, Anomura
Large sea cucumbers	California sea cucumber	<i>Parastichopus californicus</i>
Predatory gastropods	Moon snail	<i>Euspira lewisii</i>
	Hairy triton	<i>Fusitriton oregonensis</i>
Mussels	Blue mussel	<i>Mytilus edulis</i>
Barnacles	Various barnacles	Suborder Balanomorpha
Geoducks	Geoduck	<i>Panopea abrupta</i>
Infaunal bivalves	Various clams	Subclass Heterodonta
Soft infauna	Polychaetes	Class Polychaeta
Deposit feeders	Brittle stars	<i>Amphiodia urtica</i>
	Various sea cucumbers	Class Holothuroidea
Suspension feeders	Various sponges	Phylum Porifera
	Various bryozoans	Phylum Bryozoa
	Sea pen	<i>Ptilosarcus gurneyi</i>
Tunicates	Various sea squirts	Class Ascidiacea
Bacteria	Various bacteria	
Microzooplankton	Various microzooplankton	
Copepods	Various copepods	Order Calanoida
Euphausiids	Pacific krill	<i>Euphausia pacifica</i>
Small gelatinous zooplankton	Various small jellyfish, ctenophores, and other soft plankton	
Jellyfish	Lion's mane jelly	<i>Cyanea capillata</i>
	Moon jelly	<i>Aurelia labiata</i>
	Fried egg jelly	<i>Phacellophora camtschatica</i>
Macrozooplankton	Various planktonic shrimp, amphipods, and larval crustaceans	
Phytoplankton	Various diatoms, dinoflagellates and phytoflagellates	
Benthic microalgae	Various benthic diatoms	
Benthic macroalgae	Various understory algal species	
Overstory kelp	Bull kelp	<i>Nereocystis luetkeanus</i>
Eelgrass	Native eelgrass	<i>Zostera marina</i>
Detritus	Not available	
Plant/algal material	Not available	
Salmon carcasses	Not available	<i>Oncorhynchus</i> spp.

Ecopath models of nearby systems in the North Pacific Ocean. Also, some consumption or production rate parameters were derived from correlations or mechanistic models that have been developed in the literature. Examples include empirically based correlative relationships between the longevity and the P/B ratio of benthic invertebrate species (Robertson 1979) and mechanistic models of bioenergetics that can be used to infer consumption rates of fishes (e.g., Kitchell et al. 1977). Finally, as described above (Ecopath with Ecosim subsection) some unknown parameters were indirectly estimated through the Ecopath mass-balancing procedure.

The time period for the reference model state is intended to be relatively contemporary. We therefore attempted to restrict our data search to the time period from 1990 to present, particularly for information on biomass standing stocks, recent biomass trends, fishery landings, total mortality, and diet compositions. For Q/B ratios that were estimated through temperature-dependent bioenergetics modeling, we used water temperatures from the 1990s to present as well.

Appendix A has detailed descriptions of the data assimilation and Ecopath parameter development for each functional group, along with citations of the major information sources and discussion of data gaps or limitations. Appendix C and Appendix D describe some of the methods that were most commonly used to develop parameters from the data.

Model Balancing

Equation 1, the Ecopath master equation, contains four core parameters that describe the basic biology of each functional group: biomass, P/B , Q/B , and EE . Typically, all but one of these are input parameters, and the remaining parameter is estimated by the Ecopath mass-balancing algorithm; thus, each group's Equation 1 has one unknown value. In our model, the unknown parameter for a particular group was typically either EE or biomass. Ecopath achieves mass balance by simultaneously solving for the unknowns for all groups i , which is possible because all of the groups are linked directly or indirectly via consumption (Christensen et al. 2005).

Achieving mass balance was a lengthy process. After the initial inputs of Equation 1 parameters, the system was out of balance: the solution for the EE of several groups was greater than 1, indicating mortality rates that were unsustainable and would have depleted the biomass pools. Also, in other cases where the unknown parameter was biomass, P/B , or Q/B , the mass-balance solution appeared unreasonable based on conventional wisdom (e.g., a biomass solution that was unrealistically large, given qualitative observations) or biological principles (e.g., a P/B solution that was very high for a long-lived, slow-growing species). In a similar vein, sometimes EE was the unknown parameter and had a balanced but unreasonable solution. For example, some functional groups from low or intermediate trophic levels had EE solutions that seemed unreasonably low (<0.1), given our perception of their role in the diets of higher consumers.

Achieving mass balance mostly involved iterative adjustments to the input values or revisiting data sources, following model-balancing guidelines provided by Christensen et al. (2005). For example, if the solution for EE_i was greater than 1, we might have increased B_i or $(P/B)_i$ slightly, or we might have decreased the importance of the group in the diet of a predator that was imparting especially heavy predation mortality. To the best of our ability, we made

small adjustments and focused on parameters that had the most uncertainty. Occasionally, we took more drastic steps. In some cases where solutions for EE were consistently greater than one, we elected to input EE and make another parameter (usually biomass) the unknown. We generally did this only for data-poor groups, such as Pacific hake and walleye pollock. Even more drastically, we aggregated some especially problematic groups into other functional groups; for example, Pacific tomcod (*Microgadus proximus*) and plainfin midshipman (*Porichthys notatus*) began as single-species groups, due to their perceived importance in the diets of larger vertebrates, but were later pooled into the demersal fish group to alleviate mass-balancing issues. Descriptions of iterative steps and solutions are provided in Appendix A.

Model Assessment

We assessed model structure, behavior, and performance by examining several indices related to the reference (Ecopath) state and by running a series of simulations in the dynamic (Ecosim) module. These indices and simulations do not constitute formal sensitivity analyses. Rather, they were used by the most experienced EwE user in our group (C. J. Harvey) as an initial means of gauging the feasibility and stability of model estimates and predictions. The dynamic simulations also provide a preliminary glimpse of how the system might respond when some of the most ecologically important functional groups are perturbed.

Indices from the Ecopath Model

In assessing the Ecopath state, we compared biomass estimates among the food web's major constituent groups (e.g., pelagic vs. demersal groups, primary producers vs. invertebrates vs. vertebrates) to get a basic sense of how mass is allocated. We also examined indices of functional group diversity and evenness at broad taxonomic scales (e.g., among primary producers, zooplankton, benthic invertebrates, etc.). We estimated these values using the final mass-balance biomass estimates from Ecopath. We expressed diversity within general functional pools by using a form of the Shannon diversity index:

$$H' = -\sum_{i=1}^s p_i \times \ln(p_i) \quad (3)$$

where diversity (H') is a function of the proportion (p) of each functional group i that makes up the total biomass of the s pools that make up a general functional pool (e.g., primary producers, zooplankton, etc.). As H' increases, species diversity increases. We expressed evenness (E), which indicates how uniformly the biomass of the entire functional pool is allocated across different functional groups i within the pool, with the following expression:

$$E = \frac{H'}{\ln(s)} \quad (4)$$

These indices are relevant because they may be positively related to community stability and resilience (e.g., Stachowicz et al. 2002, Worm et al. 2006, O'Gorman and Emmerson 2009).

Ecopath automatically calculates several indices and rates in the mass-balancing step, and we examined several of these as well. We compiled model-derived estimates of throughput and trophic transfer efficiency to examine energy flow in the system. Throughput is the sum of all flows of mass or energy that enter and exit a food web compartment during a unit of time. In essence, it captures the total production, respiration, and mortality losses of a particular component, and thus describes the ecological footprint of the component better than does biomass (Christensen et al. 2005). A related quantity is transfer efficiency, which is the proportion of mass or energy that passes through a biomass pool and up to higher trophic levels, rather than being lost to respiratory costs or to detritus (Aydin et al. 2002). This metric thus focuses on the portion of a group's throughput that is available to higher consumers.

Ecopath also calculated total mortality of each group and broke it out further into its main components. Mortality is primarily allocated to three sources: predation, take by fisheries and other human activities, and other mortality (M_0) from processes not modeled by EwE (e.g., disease). At a finer scale, Ecopath calculates predation mortality attributed to each predator and fishery mortality attributed to each gear type, so that relative impact can be assessed. The M_0 component includes, among other things, mortality that occurs outside of the PSCB spatial domain. The user can control this in various ways, such as by adjusting the EE input so that migratory groups that spend considerable time outside the domain have relatively low EE .

Simulations to Assess the Ecosim Model: Overview

We assessed Ecosim performance through a series of simulations in which perturbations were introduced and the functional groups responded over time. Simulations were run for 50 years at monthly time steps. Depending on the simulation, we present either the full time series of output, or the output from a specified year. In some cases, we relate outputs to a baseline 50-year simulation in which no perturbation was introduced. The baseline case is slightly different from the Ecopath condition because the Ecopath model is not in true equilibrium: two groups have non-zero BA terms (raptors and tunicates, descriptions in Appendix A), and various juvenile/adult pools are dynamically linked through maturation/reproduction functions (described in Appendix D). By year 50 of the baseline simulation, only 7 out of 65 groups changed by more than 10% from their initial Ecopath biomass values (data not shown).

Bottom-up Control and Stochastic Variation

In the first simulation, we introduced stochastic variation into the food web through phytoplankton. The goal was to evaluate how our characterization of the food web responded to variability in primary production. We introduced variation by using a forcing function to vary annual phytoplankton P/B , according to random draws from a normal distribution with a mean of the initial P/B and a coefficient of variation (CV) of 10%. This resulted in a time series of phytoplankton biomass with an interannual CV of approximately 18%. This simulation demonstrated the responsiveness of the community to variability in a major bottom-up resource.

We tested for significant interactions between the biomass of phytoplankton and the biomass of all other functional groups in the system using multivariate autoregressive (MAR) models at varying time lags. These models take account of intergroup interactions as well as density-dependent effects related to a group's abundance and intrinsic rate of increase (Ives et al.

2003). Time series analyses of marine food webs have found that models incorporating time lags of various lengths between species can effectively describe fish production (Tsitsika et al. 2007, Lindegren et al. 2009). For some longer-lived species, we might expect to observe higher-order time lags in density dependence or interspecific interactions (such as bottom-up effects of prey species on predator abundance), whereas for species with higher turnover rates, the time lags might be shorter. Similarly, we might expect the effects of changes in primary production, such as phytoplankton abundance, to ripple through a food web at multiple time lags. For these reasons, we analyzed time series of functional group biomass using MAR models at time lags from 1 to 5 years.

The formulation of the MAR model is

$$X_t = A + HX_{t-q} + E_t \quad (5)$$

where X_t is a $p \times 1$ vector of (natural log) abundances of p interacting functional groups at year t ; A is a $p \times 1$ vector of constants equal to the intrinsic production rate of each group; H is a $p \times p$ matrix in which elements H_{ij} are interaction coefficients that denote the effect of phytoplankton variability on the per capita production rate of the j th group, with the diagonal elements ($H_{i=j}$) representing density-dependent effects. Because we are only doing pairwise comparisons, all H matrices are 2×2 , and we will consider the elements H_{12} (phytoplankton effects) and H_{22} (density dependence).

Coefficient values generally range from -1 to 1 (H_{12}) and 0 to 1 (H_{22}). H_{12} values closer to $|1|$ indicate stronger interactions, whereas H_{22} values closer to 0 indicate stronger density dependence. Zero values indicate no significant interaction. X_{t-q} is a $p \times 1$ vector of natural log abundances of p interacting groups at year t minus the time lag q (here varied from 1 to 5 years), and E_t is a $p \times 1$ vector of process error at year t , presumed to be stochastic variability not specified in the model, that has a multivariate distribution with mean vector 0 and covariance matrix Σ . For each pair of functional groups, we estimated the vectors A and E and the matrix biomass using conditional least squares, and calculated 95% confidence intervals around each parameter using 2,000 bootstrapped data sets. We assessed the fit of the model by calculating conditional R^2 values for each functional group's estimated time series of biomass. We limited the scope of our analyses to pairs of groups; therefore, the interaction coefficients H_{12} reported here should be interpreted as the maximum potential influence of phytoplankton biomass on the other groups.

Simulations of Top-down Effects

The second simulation tracked the response of the system to a dramatic change in the biomass of a top predator, raptors (bald eagles). We allowed the simulation to evolve normally (i.e., like the baseline scenario) for the first 20 years, then we increased raptor mortality by imposing what amounted to a harvest pressure on them, with an instantaneous annual harvest mortality rate of 0.2 yr^{-1} . This pressure was maintained for the duration of the scenario and caused a dramatic decline in raptor biomass. We did not use the MAR model approach of the previous simulations, but opted instead for a simple examination of the signs and magnitudes of change of other functional groups following the perturbation, in order to demonstrate the responsiveness of the system to this apex predator. In particular, we looked for evidence of

trophic cascade-like dynamics, where a change in a top predator biomass affects biomass dynamics at several lower trophic levels.

In the third simulation, all fisheries were closed in year 1 and kept closed for the duration of the simulation. To assess the effect of the closure, we calculated the ratio of all groups' B_i in year 50 of the no-fishing scenario to B_i in year 50 of the baseline scenario. This simulation demonstrated the response of the system to a top-down, anthropogenic stressor.

Finally, a series of diagnostic scenarios were constructed to examine the equilibrium yield curves of functional groups that are currently targeted or were historically targeted by fisheries, that is, all groups with F greater than 0, along with Pacific hake and walleye pollock. We did not include hatchery salmon, due to the artificial nature of their production that fundamentally alters the relationship between fishing effort and sustainability. In each simulation, F was kept at initial values for all groups except one focal group; that group's F was set at 0 for the first 50-year simulation, then was increased in small increments in successive simulations until we reached an F that drove the group extinct by year 50. We compiled the year-50 landings for all simulations for each group i . The maximum year-50 landing was assumed to be the maximum sustainable yield (MSY) for the group, and the associated F_{MSY} was compared with other sources of mortality (e.g., F_{initial} , total natural mortality) to assess the apparent sustainability of current fisheries. $F_{\text{initial}}/F_{\text{MSY}}$ should be less than one to ensure sustainability in a single-species context, and some authors have further recommended that F should be less than natural mortality (e.g., Gulland 1970, Patterson 1992, Walters and Martell 2004). We also plotted estimated year-50 landings vs. effort for each targeted group and examined the shapes of each group's curve; in general, the curves should be dome-shaped and not have long tails.²

² C. Ainsworth, NWFSC, Seattle, WA. Pers. commun., 4 March 2010.

Results

General Characteristics and Mass Balancing of the Ecopath Model

Following the iterative process of adjusting parameters, as described in the Methods section, the PSCB model came into balance. The missing parameter values that Ecopath calculated were generally credible relative to Ecopath models of nearby marine ecosystems (Beattie 2001, Ainsworth et al. 2002, Aydin et al. 2002, Field 2004, Priekshot 2007) and to available empirical data (functional group descriptions, Appendix A). Figure 2 provides a visual representation of the PSCB food web's 65 biomass pools, the trophic relationships that link them together, and the sources of production that fuel the system. The core parameters of the mass-balanced PSCB Ecopath model (including estimated trophic level, TL) are shown in Table 3; further descriptions of the parameters, data sources, and underlying assumptions are provided in Appendix A.

The main indicator of mass balance is that all EE_i are less than one, although some biomass pools have non-zero values for BA , which means that the Ecopath model, though balanced, is not in strict equilibrium. Moreover, all EE_i are greater than zero, indicating at least some level of mortality attributable to another model component, either a predator or a fishery. High EE values indicate a greater degree of linkage between a group and its predators or fisheries, and thus a greater prospect of response to perturbation in dynamic Ecosim scenarios. Low EE values indicate a relative disconnect between functional groups and their predators or fisheries, at least in the reference model state.

Another useful mass-balancing diagnostic is the P/Q ratio (Table 3), which is the P/B ratio divided by the Q/B ratio and is an approximation of growth efficiency. In general, P/Q ratios for consumers were between 0.05 and 0.3, which is reasonable (Christensen et al. 2005); moreover, most groups with low P/Q ratios (<0.05) were longer-lived, slower-growing species, for which P/Q should be low. These groups included seabirds, marine mammals, elasmobranchs, and geoducks.

The finalized Ecopath diet matrix, after all minor adjustments were made for purposes of mass balancing, is shown in Table 4. Sources, general descriptions, and assumptions related to the diet values are presented in detail in the functional group profiles in Appendix A. One prey category of particular note is the Import category. This is a nondynamic pool comprised of all prey resources that are not themselves modeled functional groups. For example, a functional group may migrate out of PSCB for part of the year. During that time, it would be assigned Import for its diet, as it will continue to consume prey resources even though it is outside of the model domain. Or a functional group may remain within PSCB but consume rare prey or exogenous resources; for example, gulls scavenge human garbage, and that component of their diet falls under Import.

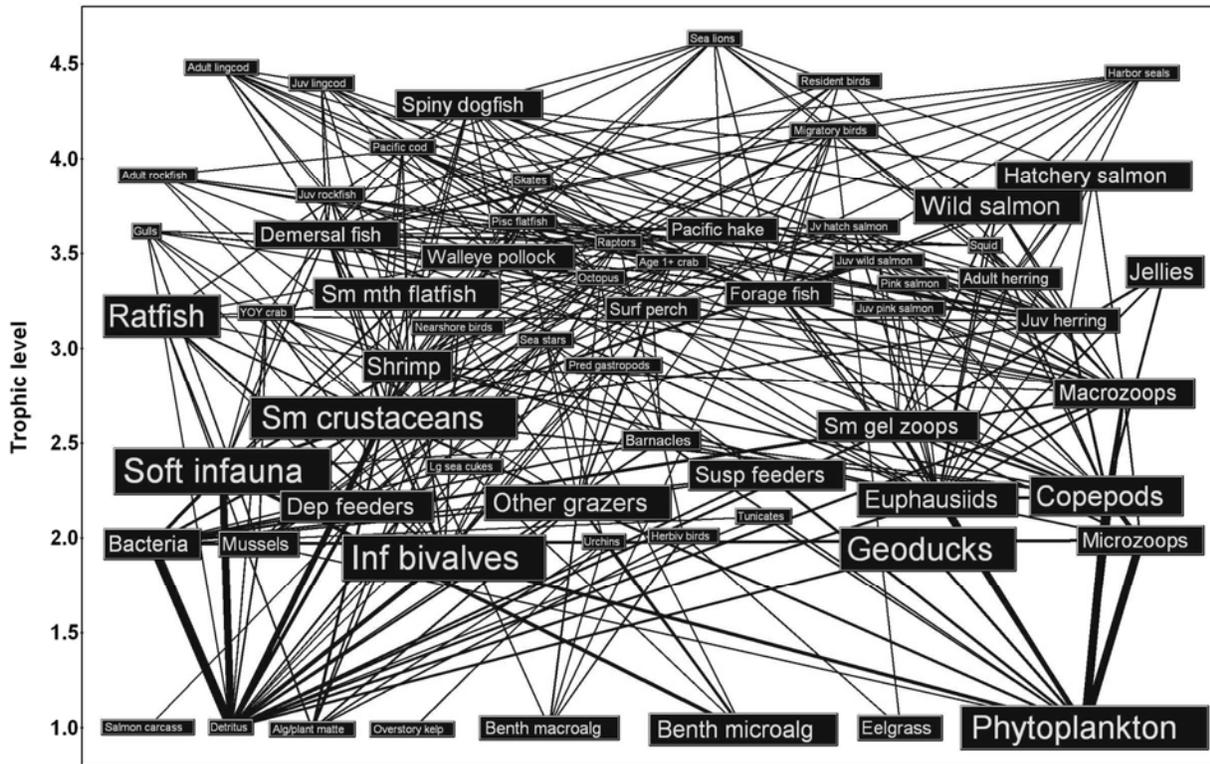


Figure 2. Food web diagram for the PCB Ecopath model, arranged along a vertical axis of trophic level. Sizes of boxes are scaled to the biomass densities of the functional groups. Lines link prey sources to predators; line thickness is scaled to the flow of material from prey to predator.

The diet matrix and mass-balancing step give rise to Ecopath estimates of trophic levels (TL, Table 3) for all functional groups. With primary producers and detrital groups all assigned TL equals 1, the top predator in the system is sea lions (TL = 4.63). (Killer whales are intentionally not included in the models; see Appendix B.) In terms of the cumulative living biomass of the entire community, approximately 82% of the system is at TL less than 3.

The finalized Ecopath fishery landings matrix is shown in Table 5. Estimation methods, data sources, and general descriptions of relevant fisheries and other removals are described in the functional group profiles in Appendix A and the Commercial Harvest Estimates subsection in Appendix C. With a few exceptions, recreational fishery landings are poorly quantified in this model, and should be regarded with caution. Moreover, bycatch mortality and discard across gear type is currently unknown. It is likely that the fishing mortalities in Table 5 are underestimates, although we do not know by how much.

Table 3. Ecopath parameters for the functional groups in the PSCB model. This page, vertebrates only; all remaining functional groups continued on the next page. See the Ecopath with Ecosim subsection of the Methods section for description of parameters. Boldfaced values were calculated by the mass-balancing routine in the Ecopath model.

Group	TL	B (mt km ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE	BA (yr ⁻¹)	P/Q
Harbor seals	4.44	0.0240	0.126	24.594	0.397	0	0.005
Sea lions	4.63	0.0240	0.076	24.350	0.329	0	0.003
Gulls	3.62	0.0622	0.120	172.533	0.600	0	0.001
Resident diving birds	4.42	0.0112	0.164	118.379	0.370	0	0.001
Migratory diving birds	4.15	0.0414	0.195	118.965	0.123	0	0.002
Nearshore diving birds	3.13	0.0846	0.291	205.235	0.076	0	0.001
Herbivorous birds	2.06	0.0550	0.427	329.082	0.080	0	0.001
Raptors	3.56	0.00131	0.314	39.744	0.287	0.09	0.008
Juvenile wild salmon	3.46	0.0951	5.591	30.000	0.200	0	0.186
Subadult wild salmon	3.73	11.918	0.989	7.000	0.200	0	0.141
Juvenile hatchery salmon	3.63	0.0819	6.492	30.000	0.200	0	0.216
Subadult hatchery salmon	3.91	6.0710	1.017	7.000	0.200	0	0.145
Juvenile pink salmon	3.34	0.0085	9.844	32.850	0.200	0	0.300
Subadult pink salmon	3.32	0.0772	1.577	13.429	0.100	0	0.117
Juvenile Pacific herring	3.24	3.4072	3.656	15.984	0.900	0	0.229
Adult Pacific herring	3.28	2.5310	1.600	7.489	0.851	0	0.214
Forage fish	3.30	3.4606	1.500	7.000	0.800	0	0.214
Surfperches	3.20	3.1700	1.300	6.000	0.800	0	0.217
Spiny dogfish	4.28	5.2540	0.103	2.692	0.175	0	0.038
Skates	3.88	0.6800	0.127	3.201	0.084	0	0.040
Ratfish	3.19	36.1000	0.305	1.653	0.105	0	0.185
Pacific hake	3.51	3.4050	0.405	2.602	0.900	0	0.156
Pacific cod	4.07	0.2000	0.260	3.784	0.520	0	0.069
Walleye pollock	3.44	3.7040	0.800	4.000	0.900	0	0.200
Juvenile lingcod	4.38	0.1240	0.389	3.070	0.900	0	0.127
Adult lingcod	4.51	0.3000	0.280	1.932	0.141	0	0.145
Juvenile rockfish	3.81	0.4540	0.360	2.672	0.800	0	0.135
Adult rockfish	3.89	0.3270	0.240	1.437	0.500	0	0.167
Piscivorous flatfish	3.64	1.1550	0.467	6.007	0.686	0	0.078
Small-mouthed flatfish	3.19	7.9620	0.345	5.512	0.654	0	0.063
Demersal fish	3.54	4.5650	1.200	6.000	0.800	0	0.200

Table 3 continued. Ecopath parameters for the functional groups in the PSCB model. This page, all remaining functional groups, including invertebrates, primary producers, and detrital groups. See the Ecopath with Ecosim subsection of the Methods section for description of parameters. Boldfaced values were calculated by the mass-balancing routine in the Ecopath model. NA = not applicable.

Group	TL	B (mt km ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE	BA (yr ⁻¹)	P/Q
Squid	3.50	0.902	3.000	15.000	0.800	0	0.200
Octopus	3.37	1.158	0.860	2.500	0.900	0	0.344
Shrimp	2.94	8.134	2.250	12.000	0.900	0	0.188
YOY <i>Cancer</i> crab	3.17	0.757	2.500	8.197	0.900	0	0.305
Age 1+ <i>Cancer</i> crab	3.45	0.547	1.500	3.084	0.900	0	0.486
Sea stars	3.06	0.346	0.519	2.595	0.125	0	0.200
Sea urchins	2.00	0.453	0.500	10.880	0.500	0	0.046
Other grazers	2.13	11.431	0.753	8.859	0.800	0	0.085
Small crustaceans	2.31	38.195	3.410	25.000	0.900	0	0.136
Large sea cucumbers	2.16	0.0471	0.860	11.300	0.800	0	0.076
Predatory gastropods	2.95	0.979	1.010	6.733	0.700	0	0.150
Mussels	2.01	3.785	0.927	3.090	0.900	0	0.300
Barnacles	2.51	2.310	1.245	6.225	0.800	0	0.200
Geoducks	2.03	52.442	0.036	2.000	0.366	0	0.018
Infaunal bivalves	2.05	70.506	2.059	6.863	0.718	0	0.300
Soft infauna	2.10	67.899	4.400	22.000	0.568	0	0.200
Deposit feeders	2.16	7.512	1.421	25.000	0.344	0	0.057
Suspension feeders	2.10	6.494	2.763	13.815	0.800	0	0.200
Tunicates	2.10	0.157	2.059	10.295	0.099	0.05	0.200
Bacteria	2.00	6.395	150.000	300.000	0.400	0	0.500
Microzooplankton	2.05	5.343	100.000	285.714	0.800	0	0.350
Copepods	2.21	24.419	15.000	75.000	0.800	0	0.200
Euphausiids	2.17	11.152	10.683	44.145	0.800	0	0.242
Sm. gelatinous zooplankton	2.59	6.388	9.000	30.000	0.800	0	0.300
Jellyfish	3.43	8.483	3.000	11.500	0.500	0	0.261
Macrozooplankton	2.77	6.234	7.000	35.000	0.800	0	0.200
Phytoplankton	1.00	51.0	226.300	NA	0.320	0	NA
Benthic microalgae	1.00	4.298	100.000	NA	0.500	0	NA
Benthic macroalgae	1.00	3.182	15.000	NA	0.400	0	NA
Overstory kelp	1.00	0.08	42.955	NA	0.661	0	NA
Eelgrass	1.00	3.558	24.542	NA	0.156	0	NA
Algal/plant material	1.00	1	NA	NA	0.626	0	NA
Salmon carcasses	1.00	1	NA	NA	0.002	0	NA
Detritus	1.00	1	NA	NA	0.393	0	NA

Table 4. Ecopath diet matrix for consumers in the PSCB model. Each column represents the diet proportions of a consumer and sums to 1. Asterisk (*) < 0.001, S/a = subadult.

Prey	Predators											
	Harbor seals	Sea lions	Seagulls	Resident diving birds	Migr. diving birds	N'shore diving birds	Herbivorous birds	Raptors	Juvenile wild salmon	S/a wild salmon	Juv. hatchery salmon	S/a hatchery salmon
Harbor seals	—	—	—	—	—	—	—	—	—	—	—	—
Sea lions	—	—	—	—	—	—	—	—	—	—	—	—
Seagulls	—	—	*	—	—	—	—	0.084	—	—	—	—
Resident diving birds	—	—	*	—	—	—	—	0.011	—	—	—	—
Migr. diving birds	—	—	—	—	—	—	—	0.019	—	—	—	—
N'shore diving birds	—	—	—	—	—	—	—	0.036	—	—	—	—
Herbivorous birds	—	—	—	—	—	—	—	0.036	—	—	—	—
Raptors	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile wild salmon	*	—	0.007	0.003	0.006	—	—	—	—	—	—	—
S/a wild salmon	0.052	0.035	—	—	—	—	—	0.003	—	—	—	—
Juv. hatchery salmon	*	—	0.007	0.003	0.006	—	—	—	—	—	—	—
S/a hatchery salmon	0.053	0.035	—	—	—	—	—	0.002	—	—	—	—
Juvenile pink salmon	*	—	*	0.001	0.002	—	—	—	—	—	—	—
S/a pink salmon	0.005	0.005	—	—	—	—	—	0.001	—	—	—	—
Juv. Pacific herring	—	—	0.155	0.034	0.218	0.009	—	—	0.015	0.007	0.032	0.015
Adult Pacific herring	0.425	0.065	—	—	—	—	—	—	—	0.003	—	0.015
Forage fish	0.050	0.010	0.100	0.080	0.121	—	—	—	0.015	0.005	0.032	0.010
Surfperches	0.020	0.005	—	0.065	0.094	—	—	—	0.010	—	0.020	—
Spiny dogfish	0.005	0.075	—	—	—	—	—	0.008	—	—	—	—
Skates	0.010	0.002	—	—	—	—	—	—	—	—	—	—
Ratfish	—	—	—	—	—	—	—	—	—	—	—	—
Pacific hake	0.050	0.150	—	—	0.001	—	—	0.004	—	—	—	—
Pacific cod	*	0.010	—	—	—	—	—	0.004	—	—	—	—
Walleye pollock	0.200	0.025	—	0.001	—	—	—	0.004	—	—	—	—
Juvenile lingcod	—	—	—	—	—	—	—	0.008	—	—	—	—
Adult lingcod	*	0.003	—	—	—	—	—	—	—	—	—	—
Juvenile rockfish	0.025	0.005	—	0.002	—	—	—	0.008	—	—	—	—
Adult rockfish	0.025	0.005	—	—	—	—	—	—	—	—	—	—
Piscivorous flatfish	0.005	0.010	—	0.008	—	—	—	—	—	—	—	—
Sm.-mouthed flatfish	0.005	0.040	—	0.008	—	—	—	0.016	—	—	—	—
Demersal fish	0.050	0.010	0.030	0.430	0.131	—	—	0.010	0.010	—	0.020	—
Squid	0.015	0.010	—	0.001	0.001	—	—	—	—	—	—	—
Octopus	0.005	—	—	—	—	—	—	—	—	—	—	—
Shrimp	—	—	0.001	0.013	0.027	0.023	—	—	0.006	—	0.016	—
YOY Cancer crab	—	—	—	0.001	—	—	—	—	—	—	—	—
Age 1+ Cancer crab	—	—	—	—	—	—	—	—	—	—	—	—
Sea stars	—	—	—	—	—	—	—	—	—	—	—	—
Sea urchins	—	—	—	—	—	—	—	—	—	—	—	—
Other grazers	—	—	0.010	—	0.009	0.063	0.010	—	—	—	—	—
Small crustaceans	—	—	0.053	0.016	0.005	0.116	0.010	0.004	0.260	—	0.195	—
Large sea cucumbers	—	—	—	—	—	—	—	—	—	—	—	—
Predatory gastropods	—	—	0.002	—	—	0.007	—	—	—	—	—	—
Mussels	—	—	0.025	—	—	0.072	—	0.004	—	—	—	—
Barnacles	—	—	0.005	—	—	0.015	—	—	—	—	—	—
Geoducks	—	—	—	—	—	—	—	—	—	—	—	—
Infaunal bivalves	—	—	0.025	—	—	0.286	—	0.016	—	—	—	—
Soft infauna	—	—	—	—	0.009	0.001	—	—	0.010	—	0.010	—
Deposit feeders	—	—	—	—	—	—	—	—	—	—	—	—
Suspension feeders	—	—	—	—	—	—	—	—	—	—	—	—
Tunicates	—	—	—	—	—	—	—	—	—	—	—	—
Bacteria	—	—	—	—	—	—	—	—	—	—	—	—
Microzooplankton	—	—	—	—	—	—	—	—	0.003	—	0.001	—
Copepods	—	—	—	—	—	—	—	—	0.122	—	0.030	—
Euphausiids	—	—	—	0.001	—	—	—	—	0.050	0.010	0.058	0.008
Sm. gelatinous zoopl.	—	—	—	—	—	—	—	—	0.047	0.032	0.006	0.009
Jellyfish	—	—	—	—	—	—	—	—	—	—	—	—
Macrozooplankton	—	—	0.075	—	—	—	—	—	0.122	0.043	0.220	0.043
Phytoplankton	—	—	—	—	—	—	—	—	—	—	—	—
Benthic microalgae	—	—	—	—	—	—	—	—	—	—	—	—
Benthic macroalgae	—	—	—	—	0.017	0.012	0.230	—	—	—	—	—
Overstory kelp	—	—	—	—	—	—	—	—	—	—	—	—
Eelgrass	—	—	—	—	0.017	—	0.100	—	—	—	—	—
Algal/plant material	—	—	0.004	—	—	0.013	0.050	—	—	—	—	—
Salmon carcasses	—	—	—	—	—	—	—	0.095	—	—	—	—
Detritus	—	—	0.100	—	—	—	—	0.040	—	—	—	—
Import	—	0.500	0.400	0.333	0.333	0.383	0.600	0.588	0.330	0.900	0.360	0.900

Table 4 continued horizontally. Ecopath diet matrix for consumers in the PSCB model. Each column represents the diet proportions of a consumer and sums to 1. Asterisk (*) < 0.001, S/a = subadult.

Prey (column list repeated from previous page)	Predators											
	Juvenile pink salmon	S/a pink salmon	Juv. Pacific herring	Adult Pacific herring	Forage fish	Surfperches	Spiny dogfish	Skates	Ratfish	Pacific hake	Pacific cod	Walleye pollock
Harbor seals	—	—	—	—	—	—	—	—	—	—	—	—
Sea lions	—	—	—	—	—	—	—	—	—	—	—	—
Seagulls	—	—	—	—	—	—	—	—	—	—	—	—
Resident diving birds	—	—	—	—	—	—	—	—	—	—	—	—
Migr. diving birds	—	—	—	—	—	—	—	—	—	—	—	—
N'shore diving birds	—	—	—	—	—	—	—	—	—	—	—	—
Herbivorous birds	—	—	—	—	—	—	—	—	—	—	—	—
Raptors	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile wild salmon	—	—	—	—	—	—	—	—	—	—	—	—
S/a wild salmon	—	—	—	—	—	—	0.019	—	—	—	—	—
Juv. hatchery salmon	—	—	—	—	—	—	—	—	—	—	—	—
S/a hatchery salmon	—	—	—	—	—	—	0.018	—	—	—	—	—
Juvenile pink salmon	—	—	—	—	—	—	—	—	—	—	—	—
S/a pink salmon	—	—	—	—	—	—	*	—	—	—	—	—
Juv. Pacific herring	—	0.001	—	0.010	—	—	0.090	0.040	0.025	0.040	—	—
Adult Pacific herring	—	0.001	—	—	—	—	0.100	—	—	0.020	0.200	—
Forage fish	—	0.003	—	0.020	—	—	0.007	0.003	—	0.003	0.050	—
Surfperches	—	—	—	—	—	—	0.001	0.004	0.012	—	—	—
Spiny dogfish	—	—	—	—	—	—	—	—	—	—	—	—
Skates	—	—	—	—	—	—	—	—	—	—	—	—
Ratfish	—	—	—	—	—	—	0.082	—	—	—	—	—
Pacific hake	—	—	—	—	—	—	0.013	—	—	0.045	—	0.030
Pacific cod	—	—	—	—	—	—	—	—	—	—	0.010	—
Walleye pollock	—	—	—	—	—	—	0.088	0.023	0.017	—	0.050	—
Juvenile lingcod	—	—	—	—	—	—	—	—	—	—	—	—
Adult lingcod	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile rockfish	—	—	—	—	—	—	*	—	—	—	—	—
Adult rockfish	—	—	—	—	—	—	*	—	—	—	—	—
Piscivorous flatfish	—	—	—	—	—	—	0.020	—	—	—	—	—
Sm.-mouthed flatfish	—	—	—	—	—	—	0.072	0.010	0.004	—	0.050	—
Demersal fish	—	—	—	—	—	—	0.025	0.017	0.008	—	0.250	0.009
Squid	—	—	—	—	—	—	—	—	—	—	0.005	—
Octopus	—	—	—	—	—	—	0.061	—	—	—	—	—
Shrimp	—	—	—	—	—	0.020	0.030	0.606	0.018	0.145	0.050	0.134
YOY Cancer crab	—	—	—	—	—	—	0.005	0.001	0.014	—	—	—
Age 1+ Cancer crab	—	—	—	—	—	—	0.031	0.008	—	—	0.050	—
Sea stars	—	—	—	—	—	—	—	—	—	—	—	—
Sea urchins	—	—	—	—	—	—	—	—	—	—	—	—
Other grazers	—	—	—	—	—	0.075	—	*	0.010	—	—	—
Small crustaceans	0.030	—	0.050	—	0.150	0.200	0.019	0.083	0.200	0.080	0.150	0.378
Large sea cucumbers	—	—	—	—	—	—	—	—	—	—	—	—
Predatory gastropods	—	—	—	—	—	0.010	—	—	0.001	—	—	—
Mussels	—	—	—	—	—	0.050	—	—	0.002	—	—	—
Barnacles	—	—	—	—	—	0.050	0.003	—	0.002	—	—	—
Geoducks	—	—	—	—	—	—	—	—	—	—	—	—
Infaunal bivalves	—	—	—	—	—	0.325	—	*	0.460	—	0.010	0.001
Soft infauna	—	—	—	—	—	0.010	*	—	0.160	0.016	—	0.001
Deposit feeders	—	—	—	—	—	0.010	—	—	0.025	—	0.050	—
Suspension feeders	—	—	—	—	—	—	—	—	—	—	—	—
Tunicates	—	—	—	—	—	—	—	—	—	—	—	—
Bacteria	—	—	—	—	—	—	—	—	—	—	—	—
Microzooplankton	—	—	—	—	—	—	—	—	—	—	—	—
Copepods	0.250	—	0.800	0.500	0.650	0.250	—	—	*	—	0.025	0.030
Euphausiids	0.130	0.080	0.100	0.370	0.050	—	—	0.016	—	0.504	0.025	0.318
Sm. gelatinous zoopl.	0.130	—	—	—	0.090	—	—	—	—	—	—	—
Jellyfish	—	—	—	—	0.010	—	0.010	—	—	—	—	—
Macrozooplankton	0.060	0.015	0.050	0.100	0.050	—	—	0.189	0.002	0.147	0.025	0.099
Phytoplankton	—	—	—	—	—	—	—	—	—	—	—	—
Benthic microalgae	—	—	—	—	—	—	—	—	—	—	—	—
Benthic macroalgae	—	—	—	—	—	—	—	—	—	—	—	—
Overstory kelp	—	—	—	—	—	—	—	—	—	—	—	—
Eelgrass	—	—	—	—	—	—	0.005	—	—	—	—	—
Algal/plant material	—	—	—	—	—	—	—	—	0.040	—	—	*
Salmon carcasses	—	—	—	—	—	—	—	—	—	—	—	—
Detritus	—	—	—	—	—	—	—	—	—	—	—	—
Import	0.400	0.900	—	—	—	—	0.300	—	—	—	—	—

Table 4 continued horizontally. Ecopath diet matrix for consumers in the PSCB model. Each column represents the diet proportions of a consumer and sums to 1. Asterisk (*) < 0.001, S/a = subadult.

Prey (column list repeated from previous page)	Predators											
	Juvenile lingcod	Adult lingcod	Juvenile rockfish	Adult rockfish	Piscivorous flatfish	Sm. mouthed flatfish	Demersal fish	Squid	Octopus	Shrimp	YOY Cancer crab	Age 1+ Cancer crab
Harbor seals	—	—	—	—	—	—	—	—	—	—	—	—
Sea lions	—	—	—	—	—	—	—	—	—	—	—	—
Seagulls	—	—	—	—	—	—	—	—	—	—	—	—
Resident diving birds	—	—	—	—	—	—	—	—	—	—	—	—
Migr. diving birds	—	—	—	—	—	—	—	—	—	—	—	—
N'shore diving birds	—	—	—	—	—	—	—	—	—	—	—	—
Herbivorous birds	—	—	—	—	—	—	—	—	—	—	—	—
Raptors	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile wild salmon	*	—	—	—	—	—	—	—	—	—	—	—
S/a wild salmon	—	0.001	—	—	—	—	—	—	—	—	—	—
Juv. hatchery salmon	*	—	—	—	—	—	—	—	—	—	—	—
S/a hatchery salmon	—	0.001	—	—	—	—	—	—	—	—	—	—
Juvenile pink salmon	*	—	—	—	—	—	—	—	—	—	—	—
S/a pink salmon	—	0.001	—	—	—	—	—	—	—	—	—	—
Juv. Pacific herring	0.117	0.044	0.295	0.255	0.060	0.001	0.035	0.100	—	—	0.001	0.001
Adult Pacific herring	0.013	0.005	—	0.050	0.010	—	—	0.030	—	—	—	—
Forage fish	0.295	0.020	0.010	0.010	0.017	*	0.002	0.020	—	—	0.010	0.100
Surfperches	0.022	0.001	0.004	0.005	0.170	0.003	0.018	—	—	—	0.010	0.020
Spiny dogfish	—	0.001	—	—	—	—	—	—	—	—	—	—
Skates	—	—	—	—	—	—	—	—	—	—	—	—
Ratfish	—	—	—	—	—	—	—	—	—	—	—	—
Pacific hake	0.005	*	—	—	0.005	—	0.002	—	—	—	—	—
Pacific cod	—	0.023	—	—	—	—	—	—	—	—	—	—
Walleye pollock	0.068	0.033	—	—	0.010	0.001	0.001	—	—	—	—	—
Juvenile lingcod	0.030	0.047	—	—	—	—	*	—	—	—	—	0.003
Adult lingcod	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile rockfish	0.091	0.128	—	—	—	—	—	—	—	—	—	—
Adult rockfish	0.001	0.007	—	—	—	—	—	—	—	—	—	—
Piscivorous flatfish	0.016	0.032	—	—	—	—	—	—	—	—	—	0.025
Sm.-mouthed flatfish	0.006	0.117	—	0.002	—	—	0.012	—	—	—	—	0.025
Demersal fish	0.185	0.448	0.025	0.035	0.050	—	0.013	—	0.030	—	0.030	0.100
Squid	0.002	*	—	—	0.013	0.004	0.019	0.100	—	—	—	—
Octopus	0.014	0.043	—	—	—	—	—	—	—	—	—	—
Shrimp	0.127	0.035	0.245	0.275	0.084	0.031	0.161	—	0.050	0.020	0.050	0.050
YOY Cancer crab	—	—	—	—	—	*	0.004	—	0.100	—	0.050	0.050
Age 1+ Cancer crab	—	—	0.030	0.060	—	—	—	—	0.020	—	—	0.010
Sea stars	—	—	—	—	—	—	—	—	—	—	—	—
Sea urchins	—	—	—	—	—	—	—	—	—	—	—	—
Other grazers	—	—	—	—	0.011	0.012	0.012	—	0.250	0.010	—	0.025
Small crustaceans	*	*	0.255	0.275	0.215	0.161	0.222	—	0.100	0.200	0.225	0.100
Large sea cucumbers	—	—	—	—	—	—	*	—	—	—	—	—
Predatory gastropods	—	*	—	—	0.001	0.001	0.001	—	0.050	—	—	0.001
Mussels	—	—	—	—	—	—	0.001	—	0.050	—	0.025	0.025
Barnacles	—	—	—	—	0.005	0.002	0.001	—	—	—	0.050	0.010
Geoducks	—	—	—	—	—	—	—	—	—	—	—	—
Infaunal bivalves	—	—	—	—	0.005	0.231	0.025	—	0.350	—	0.400	0.300
Soft infauna	—	—	0.048	0.031	0.080	0.472	0.109	—	—	0.300	0.020	0.010
Deposit feeders	—	—	—	—	0.006	0.011	—	—	—	0.010	—	0.020
Suspension feeders	—	—	—	—	—	—	—	—	—	—	—	0.010
Tunicates	—	—	—	—	—	*	—	—	—	—	—	—
Bacteria	—	—	—	—	—	—	—	—	—	—	—	—
Microzooplankton	—	—	—	—	—	—	—	—	—	—	—	—
Copepods	—	—	0.047	—	0.001	0.002	0.024	0.050	—	0.050	—	—
Euphausiids	0.007	—	0.021	0.002	0.008	0.002	0.112	0.600	—	0.100	—	—
Sm. gelatinous zoopl.	—	—	—	—	—	*	0.001	—	—	—	—	—
Jellyfish	—	—	—	—	—	*	0.001	—	—	—	—	—
Macrozooplankton	—	—	0.020	—	0.170	0.057	0.207	0.050	—	0.060	—	—
Phytoplankton	—	—	—	—	—	—	—	—	—	—	—	—
Benthic microalgae	—	—	—	—	—	—	—	—	—	—	—	—
Benthic macroalgae	—	0.012	—	—	—	0.008	0.013	—	—	—	0.010	*
Overstory kelp	—	—	—	—	—	—	—	—	—	—	—	—
Eelgrass	—	—	—	—	*	*	—	—	—	—	0.009	0.005
Algal/plant material	—	—	—	—	0.079	—	0.004	—	—	—	0.010	0.010
Salmon carcasses	—	—	—	—	—	—	—	—	—	—	—	—
Detritus	—	—	—	—	—	—	—	—	—	0.250	0.100	0.100
Import	—	—	—	—	—	—	—	0.050	—	—	—	—

Table 4 continued horizontally. Ecopath diet matrix for consumers in the PSCB model. Each column represents the diet proportions of a consumer and sums to 1. Asterisk (*) < 0.001, S/a = subadult.

Prey (column list repeated from previous page)	Predators											
	Sea stars	Sea urchins	Other grazers	Small crustaceans	Large sea cucumbers	Predatory gastropods	Mussels	Barnacles	Geoducks	Infaunal bivalves	Soft infauna	Deposit feeders
Harbor seals	—	—	—	—	—	—	—	—	—	—	—	—
Sea lions	—	—	—	—	—	—	—	—	—	—	—	—
Seagulls	—	—	—	—	—	—	—	—	—	—	—	—
Resident diving birds	—	—	—	—	—	—	—	—	—	—	—	—
Migr. diving birds	—	—	—	—	—	—	—	—	—	—	—	—
N'shore diving birds	—	—	—	—	—	—	—	—	—	—	—	—
Herbivorous birds	—	—	—	—	—	—	—	—	—	—	—	—
Raptors	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile wild salmon	—	—	—	—	—	—	—	—	—	—	—	—
S/a wild salmon	—	—	—	—	—	—	—	—	—	—	—	—
Juv. hatchery salmon	—	—	—	—	—	—	—	—	—	—	—	—
S/a hatchery salmon	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile pink salmon	—	—	—	—	—	—	—	—	—	—	—	—
S/a pink salmon	—	—	—	—	—	—	—	—	—	—	—	—
Juv. Pacific herring	—	—	—	—	—	—	—	—	—	—	—	—
Adult Pacific herring	—	—	—	—	—	—	—	—	—	—	—	—
Forage fish	—	—	—	—	—	—	—	—	—	—	—	—
Surfperches	—	—	—	—	—	—	—	—	—	—	—	—
Spiny dogfish	—	—	—	—	—	—	—	—	—	—	—	—
Skates	—	—	—	—	—	—	—	—	—	—	—	—
Ratfish	—	—	—	—	—	—	—	—	—	—	—	—
Pacific hake	—	—	—	—	—	—	—	—	—	—	—	—
Pacific cod	—	—	—	—	—	—	—	—	—	—	—	—
Walleye pollock	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile lingcod	—	—	—	—	—	—	—	—	—	—	—	—
Adult lingcod	—	—	—	—	—	—	—	—	—	—	—	—
Juvenile rockfish	—	—	—	—	—	—	—	—	—	—	—	—
Adult rockfish	—	—	—	—	—	—	—	—	—	—	—	—
Piscivorous flatfish	—	—	—	—	—	—	—	—	—	—	—	—
Sm.-mouthed flatfish	—	—	—	—	—	—	—	—	—	—	—	—
Demersal fish	—	—	—	—	—	—	—	—	—	—	—	—
Squid	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	—	—	—	—	—	—
Shrimp	—	—	—	—	—	—	—	—	—	—	—	—
YOY Cancer crab	—	—	—	—	—	—	—	—	—	—	—	—
Age 1+ Cancer crab	—	—	—	—	—	—	—	—	—	—	—	—
Sea stars	0.025	—	—	—	—	—	—	—	—	—	—	—
Sea urchins	0.050	—	—	—	—	0.010	—	—	—	—	—	—
Other grazers	0.100	—	—	—	0.025	0.100	—	—	—	—	—	—
Small crustaceans	0.020	—	—	0.050	—	—	—	—	—	—	—	—
Large sea cucumbers	0.010	—	—	—	—	—	—	—	—	—	—	—
Predatory gastropods	0.010	—	—	—	—	0.010	—	—	—	—	—	—
Mussels	0.075	—	—	—	—	0.020	—	—	—	—	—	—
Barnacles	0.075	—	—	—	—	0.050	—	—	—	—	—	—
Geoducks	0.001	—	—	—	—	—	—	—	—	—	—	—
Infaunal bivalves	0.350	—	—	0.050	—	0.360	—	—	—	—	—	—
Soft infauna	—	—	—	0.100	—	—	—	0.080	—	—	—	0.050
Deposit feeders	0.100	—	—	—	—	0.050	—	—	—	—	—	—
Suspension feeders	0.100	—	0.030	0.010	0.025	0.250	—	—	—	—	—	—
Tunicates	*	—	—	—	—	0.001	—	—	—	—	—	—
Bacteria	—	—	0.100	0.044	0.100	—	0.005	0.160	0.025	0.050	0.100	0.100
Microzooplankton	—	—	—	0.001	—	—	0.005	0.160	—	—	—	—
Copepods	—	—	—	0.020	—	—	—	0.080	—	—	—	—
Euphausiids	—	—	—	—	—	—	—	—	—	—	—	—
Sm. gelatinous zoopl.	—	—	—	—	—	—	—	—	—	—	—	—
Jellyfish	—	—	—	—	—	—	—	—	—	—	—	—
Macrozooplankton	—	—	—	—	—	—	—	—	—	—	—	—
Phytoplankton	—	—	—	0.050	—	—	0.100	0.320	0.750	0.280	—	—
Benthic microalgae	0.025	0.200	0.450	0.010	0.050	—	—	—	—	—	0.100	0.050
Benthic macroalgae	—	0.200	0.080	0.005	—	—	—	—	—	—	—	—
Overstory kelp	—	0.050	0.020	—	—	—	—	—	—	—	—	—
Eelgrass	—	—	0.020	0.010	—	—	—	—	—	—	—	—
Algal/plant material	—	0.500	0.100	0.050	—	—	—	—	—	—	—	—
Salmon carcasses	—	—	—	—	—	—	—	—	—	—	—	—
Detritus	0.059	0.050	0.200	0.600	0.800	0.149	0.890	0.200	0.225	0.670	0.800	0.800
Import	—	—	—	—	—	—	—	—	—	—	—	—

Table 4 continued horizontally. Ecopath diet matrix for consumers in the PSCB model. Each column represents the diet proportions of a consumer and sums to 1. Asterisk (*) < 0.001, S/a = subadult.

Prey (column list repeated from previous page)	Predators								
	Suspension feeders	Tunicates	Bacteria	Microzooplankton	Copepods	Euphausiids	Sm. gelatinous zoopl.	Jellyfish	Macrozooplankton
Harbor seals	—	—	—	—	—	—	—	—	—
Sea lions	—	—	—	—	—	—	—	—	—
Gulls	—	—	—	—	—	—	—	—	—
Resident diving birds	—	—	—	—	—	—	—	—	—
Migr. diving birds	—	—	—	—	—	—	—	—	—
N'shore diving birds	—	—	—	—	—	—	—	—	—
Herbivorous birds	—	—	—	—	—	—	—	—	—
Raptors	—	—	—	—	—	—	—	—	—
Juvenile wild salmon	—	—	—	—	—	—	—	—	—
S/a wild salmon	—	—	—	—	—	—	—	—	—
Juv. hatchery salmon	—	—	—	—	—	—	—	—	—
S/a hatchery salmon	—	—	—	—	—	—	—	—	—
Juvenile pink salmon	—	—	—	—	—	—	—	—	—
S/a pink salmon	—	—	—	—	—	—	—	—	—
Juv. Pacific herring	—	—	—	—	—	—	—	—	—
Adult Pacific herring	—	—	—	—	—	—	—	—	—
Forage fish	—	—	—	—	—	—	—	—	—
Surfperches	—	—	—	—	—	—	—	—	—
Spiny dogfish	—	—	—	—	—	—	—	—	—
Skates	—	—	—	—	—	—	—	—	—
Ratfish	—	—	—	—	—	—	—	—	—
Pacific hake	—	—	—	—	—	—	—	—	—
Pacific cod	—	—	—	—	—	—	—	—	—
Walleye pollock	—	—	—	—	—	—	—	—	—
Juvenile lingcod	—	—	—	—	—	—	—	—	—
Adult lingcod	—	—	—	—	—	—	—	—	—
Juvenile rockfish	—	—	—	—	—	—	—	—	—
Adult rockfish	—	—	—	—	—	—	—	—	—
Piscivorous flatfish	—	—	—	—	—	—	—	—	—
Sm.-mouthed flatfish	—	—	—	—	—	—	—	—	—
Demersal fish	—	—	—	—	—	—	—	—	—
Squid	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	—	—	—
Shrimp	—	—	—	—	—	—	—	—	—
YOY Cancer crab	—	—	—	—	—	—	—	—	—
Age 1+ Cancer crab	—	—	—	—	—	—	—	—	—
Sea stars	—	—	—	—	—	—	—	—	—
Sea urchins	—	—	—	—	—	—	—	—	—
Other grazers	—	—	—	—	—	—	—	—	—
Small crustaceans	—	—	—	—	—	—	—	—	—
Large sea cucumbers	—	—	—	—	—	—	—	—	—
Predatory gastropods	—	—	—	—	—	—	—	—	—
Mussels	—	—	—	—	—	—	—	—	—
Barnacles	—	—	—	—	—	—	—	—	—
Geoducks	—	—	—	—	—	—	—	—	—
Infaunal bivalves	—	—	—	—	—	—	—	—	—
Soft infauna	—	—	—	—	—	—	—	—	—
Deposit feeders	—	—	—	—	—	—	—	—	—
Suspension feeders	—	—	—	—	—	—	—	—	—
Tunicates	—	—	—	—	—	—	—	—	—
Bacteria	0.050	0.050	—	0.050	—	0.025	0.100	—	0.100
Microzooplankton	0.050	0.050	—	—	0.200	0.025	0.100	—	0.100
Copepods	—	—	—	—	—	0.100	0.200	0.425	0.300
Euphausiids	—	—	—	—	—	—	0.050	0.200	0.100
Sm. gelatinous zoopl.	—	—	—	—	—	—	0.049	0.245	0.040
Jellyfish	—	—	—	—	—	—	0.001	0.100	0.010
Macrozooplankton	—	—	—	—	—	—	—	0.030	—
Phytoplankton	0.700	0.700	—	0.900	0.800	0.800	0.350	—	0.300
Benthic microalgae	—	—	—	—	—	—	—	—	—
Benthic macroalgae	—	—	—	—	—	—	—	—	—
Overstory kelp	—	—	—	—	—	—	—	—	—
Eelgrass	—	—	—	—	—	—	—	—	—
Algal/plant material	—	—	—	—	—	—	—	—	—
Salmon carcasses	—	—	—	—	—	—	—	—	—
Detritus	0.200	0.200	1.000	0.050	—	0.050	0.150	—	0.050
Import	—	—	—	—	—	—	—	—	—

Table 5. Landings (mt km⁻² yr⁻¹) by gear type of targeted groups. S/a = subadult and asterisk (*) indicates arbitrary placeholder value for a functional group known to experience recreational harvest until more data are available.

Group	Fishery/gear														
	Crab pot	Dip net	Gill net	Jigging	Longline	Dredge	Other net	Shrimp pot	Other gear	Pole	Seine	Set net	Recreational	Diver	Illegal take
Harbor seals			0.0004												0.0008
Sea lions															0.0006
S/a wild salmon		3.6E-08	0.463				0.0002		9.0E-08		1.35	0.162	0.061		
S/a hatchery salmon		9.0E-07	0.186				9.4E-05			6.3E-05	0.164	0.348	0.229		
S/a pink salmon			0.0021				5.0E-06				0.0013	0.0012	0.001		
Juv. Pacific herring		0.0025					0.202				0.0005				
Adult Pacific herring		0.0002					0.02				1.0E-05				
Forage fish			2.4E-07								0.007	5.4E-06	0.0001*		
Surfperches													0.0001*		
Spiny dogfish			0.0007		0.043							0.0032	0.0001*		
Skates					0.0002										
Pacific cod					6.4E-06										
Adult lingcod													0.01*		
Adult rockfish					2.0E-05								0.01*		
Piscivorous flatfish					9.0E-08								0.001*		
Sm.-mouthed flatfish													0.001*		
Squid				6.8E-05									0.0001*		
Octopus					1.5E-05			6.0E-08							
Shrimp								0.0093					0.0001*		
Age 1+ <i>Cancer</i> crab	0.0905												0.015		
Sea urchins														0.0024	
Large sea cucumbers														0.0207	
Mussels													0.0001*		
Geoducks						0.697									
Infaunal bivalves						0.0003			0.0297				0.0001*		
Sum	0.091	0.003	0.652	6.8E-05	0.043	0.697	0.222	0.009	0.03	6.3E-05	1.523	0.514	0.329	0.023	0.001

Biomass, Functional Diversity, and Evenness Patterns

Based on our parameterization, the PSCB Ecopath model reflects a system dominated by species and guilds associated with demersal habitats. In Figure 3, the initial biomass estimates of all nondetriral functional groups are coarsely aggregated by taxonomy, functional role, and habitat use. About 54.5% of all living standing stock biomass are comprised of benthic invertebrates, and 12.9% of living biomass are bony and cartilaginous fishes that spend much of their lives on or near the bottom. Including the relatively small amount of benthic primary producer biomass, bottom-associated functional groups make up about 70% of the living biomass in the PSCB Ecopath model. Species and functional groups that are primarily pelagic in nature comprise 28.7% of the total biomass, with several zooplankton pools making up the largest component. Phytoplankton, the dominant source of total system production, makes up about 10.2% of total standing biomass in the mass-balanced model. Less than 2% of total biomass is comprised of species and guilds that are considered to make extensive use of both pelagic and benthic habitats (e.g., bacteria, pinnipeds, seabirds, squid).

In biomass terms, several individual functional groups stand out as major components of the PSCB food web. In terms of sheer biomass, more than 68% of living biomass are comprised of just 7 functional groups: infaunal bivalves, soft infauna, geoducks, phytoplankton, small crustaceans, ratfish, and copepods (Table 3). A plot of functional diversity (H') vs. functional evenness (E) shows a mildly negative relationship between the two variables (Figure 4). These results are heavily influenced by our biases in how we aggregated species into functional groups, however, particularly among the lower trophic levels. For example, benthic primary producers, small zooplankton, and large zooplankton are each dominated by a few catch-all groups. Phytoplankton and bacteria were excluded from the relationship altogether because their E values could not be calculated (each of these groups had one representative and thus had a zero in the denominator of Equation 4). Diversity was greatest in the benthic invertebrate pool, although this pool ranked somewhat low in terms of evenness, largely because its biomass was dominated by four functional groups (infaunal bivalves, soft infauna, geoducks, and small crustaceans). Fish groups and seabirds also ranked high in diversity, reflecting our familiarity with their ecology and our bias to realistically represent their contribution to ecosystem services.

Throughput and Transfer Efficiency

At a community scale, throughput was dominated by phytoplankton and detritus, which together comprised 67.1% of total system throughput (Table 6). That in itself is an underestimate because Ecopath does not calculate the respiratory losses of primary producers and thus discounted the total throughput through phytoplankton. Of the total throughput accounted for by Ecopath (i.e., all but primary producer respiration), about 98.6% moved through nonvertebrate pools (i.e., primary producers, invertebrates, and detritus); this high proportion is typical of Ecopath models (C. J. Harvey, personal observation).

What is perhaps more interesting is the manner in which different functional groups rank in terms of throughput and biomass. We ranked all functional groups from greatest to least in terms of throughput and biomass (except detritus, algal/plant material, and salmon carcasses, for which biomass estimates were not available, Appendix A) and conducted linear regression of

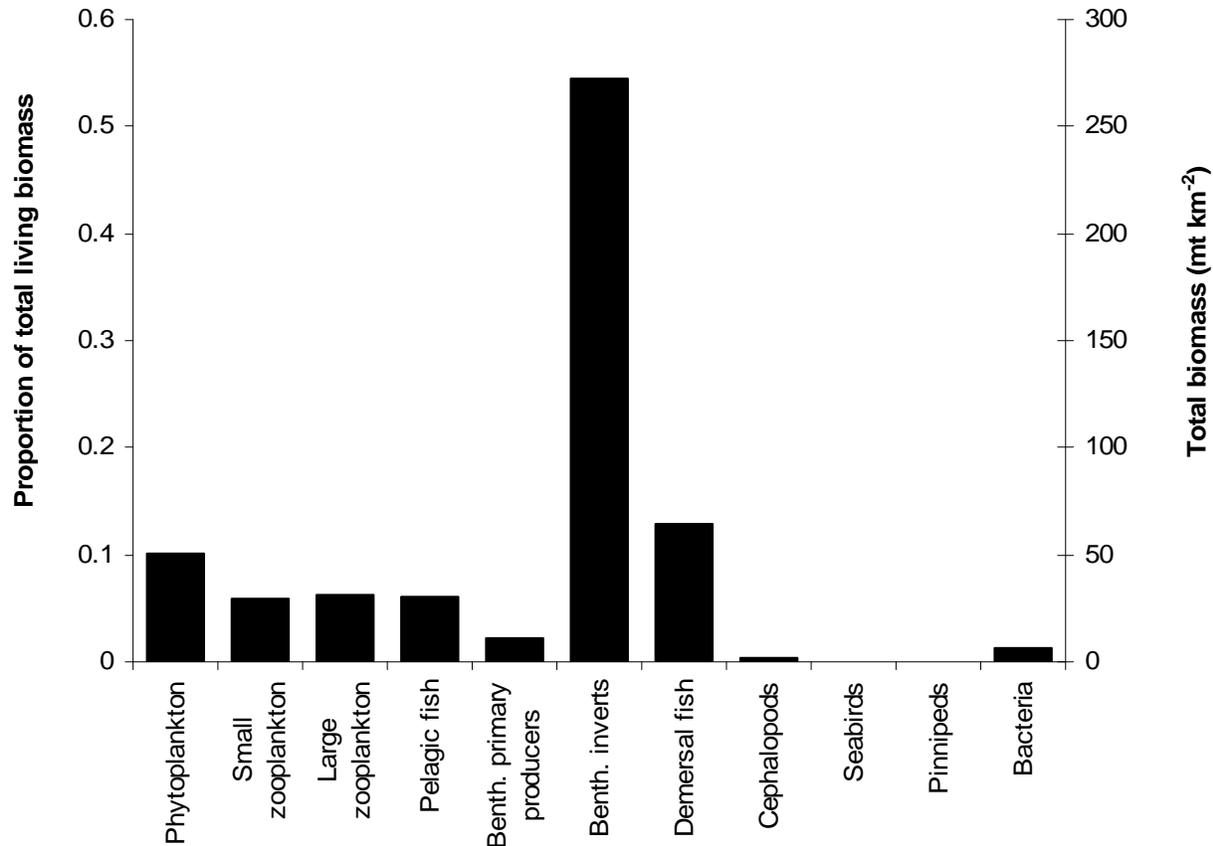


Figure 3. Biomass of coarsely pooled categories of functional groups in the PSCB Ecopath model. Biomass is expressed in relative and absolute terms. Seabird and pinniped biomasses are each greater than zero but are very small relative to other categories.

these ranks (Figure 5). Groups with positive residuals had proportionally greater throughput per unit biomass than would be expected. Notable examples include the seabird groups, bacteria, benthic primary producers, and many of the pelagic fishes and invertebrates. By contrast, those with negative residuals were mostly demersal fishes and benthic invertebrates. Thus, even though most biomass in the system is in demersal pools (Figure 3), relatively high throughputs emphasize the importance of pelagic pools.

Transfer efficiencies of consumer groups spanned a broad range (Table 6). The average transfer efficiency for all consumers, weighted by biomass, was 11.9%, which compares favorably to the Aydin et al. (2002) estimates for transfer efficiency in Bering Sea food webs (12.1 to 13.5%). In general, consumer transfer efficiency decreased with increasing trophic level (Figure 6), which is to be expected as higher consumers become less energetically efficient (i.e., higher respiration) and also less subject to predation by the relatively small biomass pools that occupy the uppermost trophic levels. However, the relationship was very weak, in part because of the large number of functional groups from lower trophic levels that do not experience much predation, and thus have low transfer efficiencies (e.g., herbivorous birds, geoducks, small benthic grazers, tunicates, sea urchins, other deposit feeders). Moreover, the relationship was

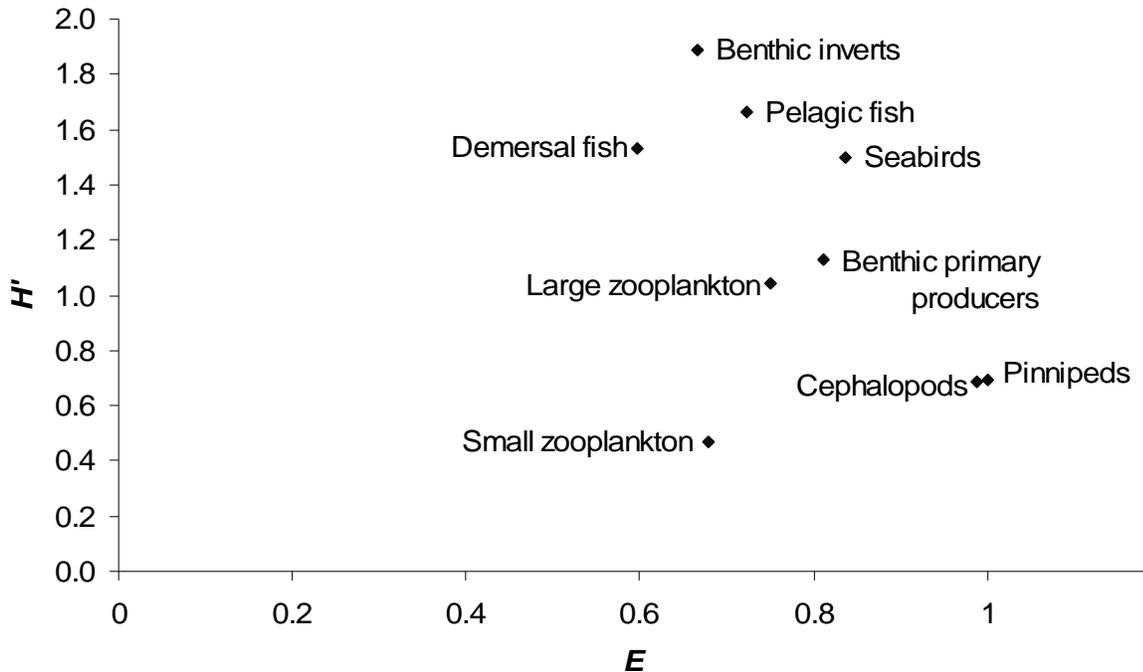


Figure 4. Plot of Shannon diversity index (H') against functional evenness (E) for coarsely pooled categories of functional groups in the PSCB Ecopath model.

weakened by several mid-level consumers (squid, YOY and age 1+ *Cancer* crab) that had very high transfer efficiencies, a result of having both high assimilation efficiencies and also relatively high predation pressure.

Mortality

Allocation of mortality is a function of factors such as the values of P/B and EE , the Q/B of an organism's predators, and the magnitude of F . As explained earlier and also in Appendix A, we were forced to input estimates of EE for many functional groups, and inputting EE is based more on coarse guidelines than on empirical information (e.g., Christensen et al. 2005). For all such groups, the proportion of total mortality allocated to M_0 (i.e., $1-EE$) was therefore a direct result of our assumptions, and should be regarded with care until better estimates of missing parameters such as biomass enable mass-balance estimation of EE .

For functional groups not targeted by fisheries, the relative importance of predation and M_0 was taxonomically dependent (Figure 7a). Seabirds, with the exception of gulls, primarily experienced M_0 , which reflects their relative lack of predators and tendency to spend large portions of the year outside the model domain. Gulls and resident diving birds had higher predation mortality than other birds because they spend more time in PSCB and they are more heavily targeted by raptors. In all seabird groups except gulls, EE was the parameter estimated in the mass-balancing step of Ecopath (Table 3), so the EE -related issue alluded to in the preceding paragraph generally does not apply.

Table 6. Biomass (mt km⁻²), throughput (mt km⁻² yr⁻¹), and transfer efficiency of functional groups. Transfer efficiencies are for consumers only.

Functional group	Biomass		Throughput		Transfer efficiency
	Value	Rank	Value	Rank	
Harbor seals	0.024	58	0.59	59	0.0020
Sea lions	0.024	58	0.58	60	0.0010
Gulls	0.0622	54	10.74	39	0.0004
Resident diving birds	0.0112	60	1.33	54	0.0005
Migratory diving birds	0.0414	57	4.93	45	0.0002
Nearshore diving birds	0.0846	50	17.36	33	0.0001
Herbivorous birds	0.055	55	18.10	32	0.0001
Raptors	0.00131	62	0.05	66	0.0002
Juvenile wild salmon	0.0951	49	2.85	48	0.0373
Subadult wild salmon	11.918	8	83.42	22	0.0283
Juvenile hatchery salmon	0.0819	51	2.46	50	0.0433
Subadult hatchery salmon	6.071	19	42.49	27	0.0291
Juvenile pink salmon	0.0085	61	0.28	65	0.0599
Subadult pink salmon	0.0772	53	1.04	56	0.0117
Juvenile Pacific herring	3.407	28	54.46	24	0.2059
Adult Pacific herring	2.531	32	18.95	31	0.1819
Forage fish	3.461	27	24.22	29	0.1714
Surfperches	3.170	31	19.02	30	0.1733
Spiny dogfish	5.254	21	14.14	36	0.0067
Skates	0.68	39	2.18	51	0.0033
Ratfish	36.1	6	59.67	23	0.0194
Pacific hake	3.405	29	8.86	40	0.1401
Pacific cod	0.2	46	0.76	58	0.0357
Walleye pollock	3.704	25	14.82	34	0.1800
Juvenile lingcod	0.124	48	0.38	64	0.1141
Adult lingcod	0.3	45	0.58	61	0.0204
Juvenile rockfish	0.454	41	1.21	55	0.1078
Adult rockfish	0.327	44	0.47	63	0.0835
Piscivorous flatfish	1.155	35	6.94	41	0.0533
Small-mouthed flatfish	7.962	12	43.89	26	0.0410
Demersal fish	4.565	22	27.39	28	0.1600
Squid	0.902	37	13.53	37	0.3096
Octopus	1.158	34	2.89	47	0.1688
Shrimp	8.134	11	97.61	18	0.1600
YOY <i>Cancer</i> crab	0.757	38	6.21	43	0.2745
Age 1+ <i>Cancer</i> crab	0.547	40	1.69	52	0.4377
Sea stars	0.346	43	0.90	57	0.0250
Sea urchins	0.453	42	4.93	44	0.0230
Other grazers	11.431	9	101.26	17	0.0680
Small crustaceans	38.195	5	954.88	7	0.1228
Large sea cucumbers	0.047	56	0.53	62	0.0609
Predatory gastropods	0.979	36	6.59	42	0.1050
Mussels	3.785	24	11.70	38	0.2700
Barnacles	2.310	33	14.38	35	0.1600

Table 6 continued. Biomass (mt km^{-2}), throughput ($\text{mt km}^{-2} \text{yr}^{-1}$), and transfer efficiency of functional groups. Transfer efficiencies are for consumers only.

Functional group	Biomass		Throughput		Transfer efficiency
	Value	Rank	Value	Rank	
Geoducks	52.442	3	104.88	15	0.0066
Infaunal bivalves	70.506	1	483.91	9	0.2154
Soft infauna	67.899	2	1,493.78	6	0.1137
Deposit feeders	7.512	14	187.80	13	0.0196
Suspension feeders	6.494	15	89.72	20	0.1600
Tunicates	0.157	47	1.61	53	0.0151
Bacteria	6.395	16	1,918.60	3	0.2000
Microzooplankton	5.343	20	1,526.69	5	0.2800
Copepods	24.419	7	1,831.45	4	0.1600
Euphausiids	11.152	10	492.28	8	0.1936
Sm. gelatinous zooplankton	6.388	17	191.63	12	0.2400
Jellyfish	7.958	13	91.51	19	0.1304
Macrozooplankton	6.234	18	218.20	11	0.1600
Phytoplankton	51	4	11,541.0	1	–
Benthic microalgae	4.298	23	429.84	10	–
Benthic macroalgae	3.182	30	47.73	25	–
Overstory kelp	0.08	52	3.44	46	–
Eelgrass	3.558	26	87.32	21	–
Algal/plant material	–	–	103.21	16	–
Salmon carcasses	–	–	2.66	49	–
Detritus	–	–	11,214.0	2	–
Import	–	–	145.32	14	–

Unlike seabirds, nontarget fishes and invertebrates typically experienced far greater predation mortality than M_0 (Figure 7a). Exceptions included functional groups that spend a large portion of time outside of the model domain (juvenile salmon) or groups thought to have few predators (ratfish, sea stars, deposit feeders, tunicates). For most nontarget fish and invertebrate groups, however, EE was an input parameter (Table 3). Thus the EE -related caveat mentioned above should be kept in mind.

Among the primary producers, grazing losses and M_0 were both moderate (i.e., between 30% and 70% of total mortality) for phytoplankton, benthic microalgae, benthic macroalgae, and overstory kelp (Figure 7a). The EE -related caveat applies to benthic microalgae and benthic macroalgae. Eelgrass experienced low grazing relative to M_0 .

Among groups targeted by fisheries (or illegal take, in the case of marine mammals), F generally accounted for a fairly small proportion of total mortality (Figure 7b). The biggest exceptions were large sea cucumbers, for which F was about 50% of total mortality, and three other groups (geoducks, harbor seals, and sea lions) for which F was 30–40% of total mortality. For several fished groups, M_0 represented a large proportion ($\geq 50\%$) of total mortality. These were mostly groups that are top predators (marine mammals, spiny dogfish, lingcod), groups that

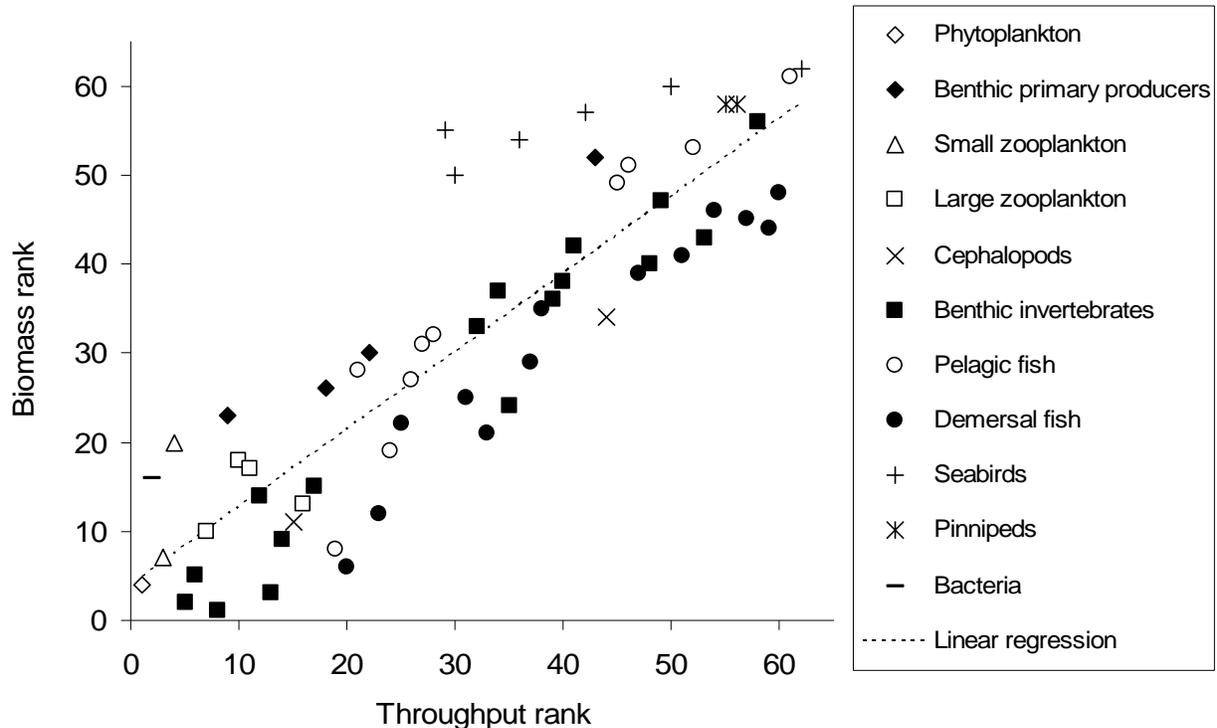


Figure 5. Relationship between the rankings of functional group biomass and functional group throughput in the PSCB Ecopath model. Symbols correspond to coarsely pooled functional categories into which the functional groups fall (as in Figure 3 and Figure 4).

are outside of the system for a large amount of time (subadult salmon), or mid-trophic level groups that have few predators (skates, geoducks).

Among these groups, the aforementioned caveat regarding *EE* is once again relevant, most notably for pelagic fishes and several types of benthic invertebrates (Table 3). In contrast, the allocation of mortality in marine mammals, most demersal fish, geoducks, and infaunal bivalves relies more on empirical data and less on assumed values of *EE*. Also, the proportion of total pinniped mortality derived from illegal take may be an artifact. It assumes that pinniped populations in PSCB are closed, which seems unlikely for sea lions, which are migratory, and harbor seals, which are thought to be at or near carrying capacity at the scale of the entire Puget Sound basin (Jeffries et al. 2003).

Of particular interest for targeted groups is the comparison between predation and fishing mortality, as predators and humans are often considered competitors for harvestable biomass. For the largest fisheries by landings (wild and hatchery Pacific salmon, geoducks), total biomass removed by the fishery exceeded, by one or more orders of magnitude, the amount removed by predators within the model domain (Figure 7b). Adult lingcod also experienced greater fishing mortality than predation. For all other groups targeted by both predators and fisheries, predators were the more important source of mortality, sometimes by several orders of magnitude. In most of those cases, predation mortality was inflicted by a variety of fishes and invertebrates, seabirds to a lesser extent, and marine mammals to a much lesser extent (data not shown). Fishery vs.

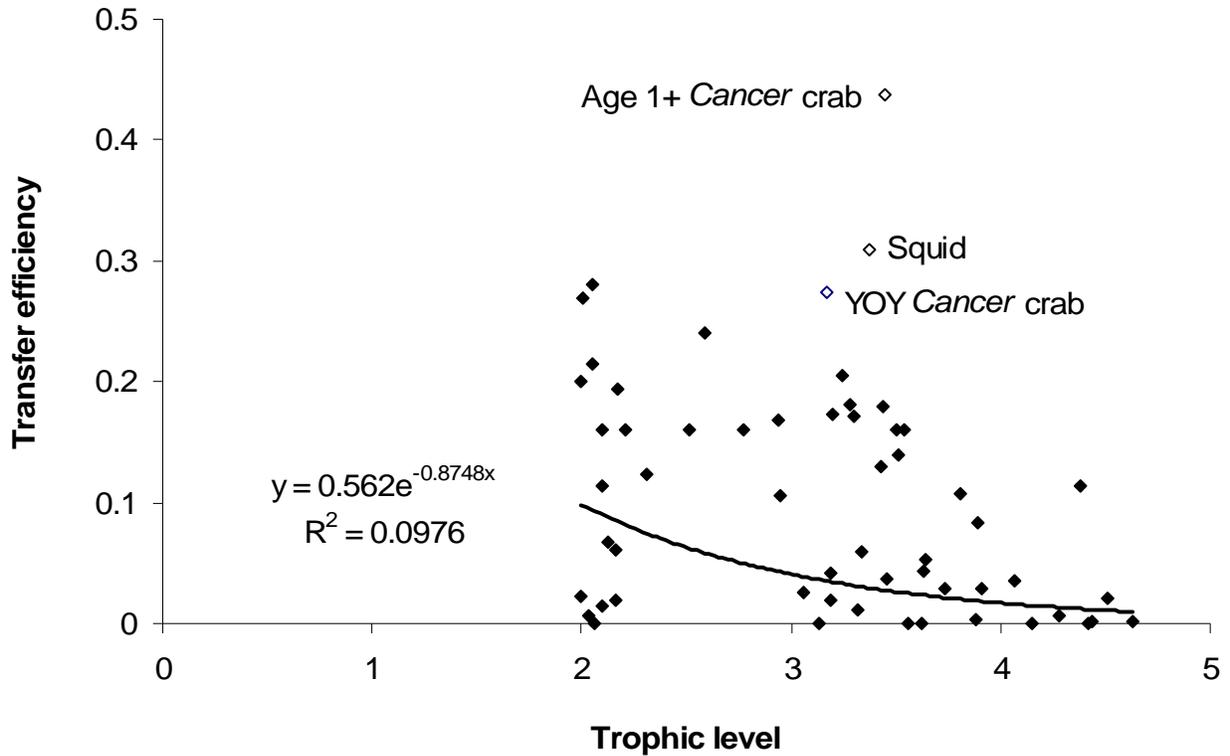


Figure 6. Transfer efficiency as a function of trophic level for consumer groups in the PCB Ecopath model. Open symbols signify substantial outliers (see Throughput and Transfer Efficiency subsection above).

predation comparisons should be viewed with some caution, however: first, recreational fishing and bycatch mortality have likely been underestimated for many groups due to lack of data; and second, as alluded to earlier, sources of mortality occurring outside the model domain are not accounted for, which could bias results for migratory species such as salmon.

Some predation mortality estimates in the mass-balanced Ecopath food web imply particularly strong predator-prey linkages. These are interactions in which a predator accounts for a large portion ($\geq 25\%$) of the total mortality of a prey group. Spiny dogfish are the most noteworthy predator in this case. They account for equal to or greater than 25% of the total mortality of 6 different functional groups, including 2 for which they account for equal to or greater than 50% and one for which they account for more than 85% (Table 7). The groups that they depredate include major species like Pacific herring, Dungeness crab, and the flatfish complex. Another notable predator is the small crustaceans group, which imparts substantial predation mortality on four groups (including via intraguild cannibalism); however, that output derives in part from small crustacean omnivore diet composition that is rather arbitrary in nature (Appendix A). Three groups (Pacific hake, walleye pollock, and mussels) appear twice as prey species in Table 7; that is, they experience substantial predation mortality from two different functional groups. Five groups in Table 7 (jellyfish, squid, small crustaceans, Pacific hake, and juvenile lingcod) experience substantial predation mortality due to intraspecific or intraguild cannibalism. Four groups (soft infauna, piscivorous flatfish, walleye pollock, and surfperch) appear in Table 7 in both the predator and prey columns in noncannibalistic relationships.

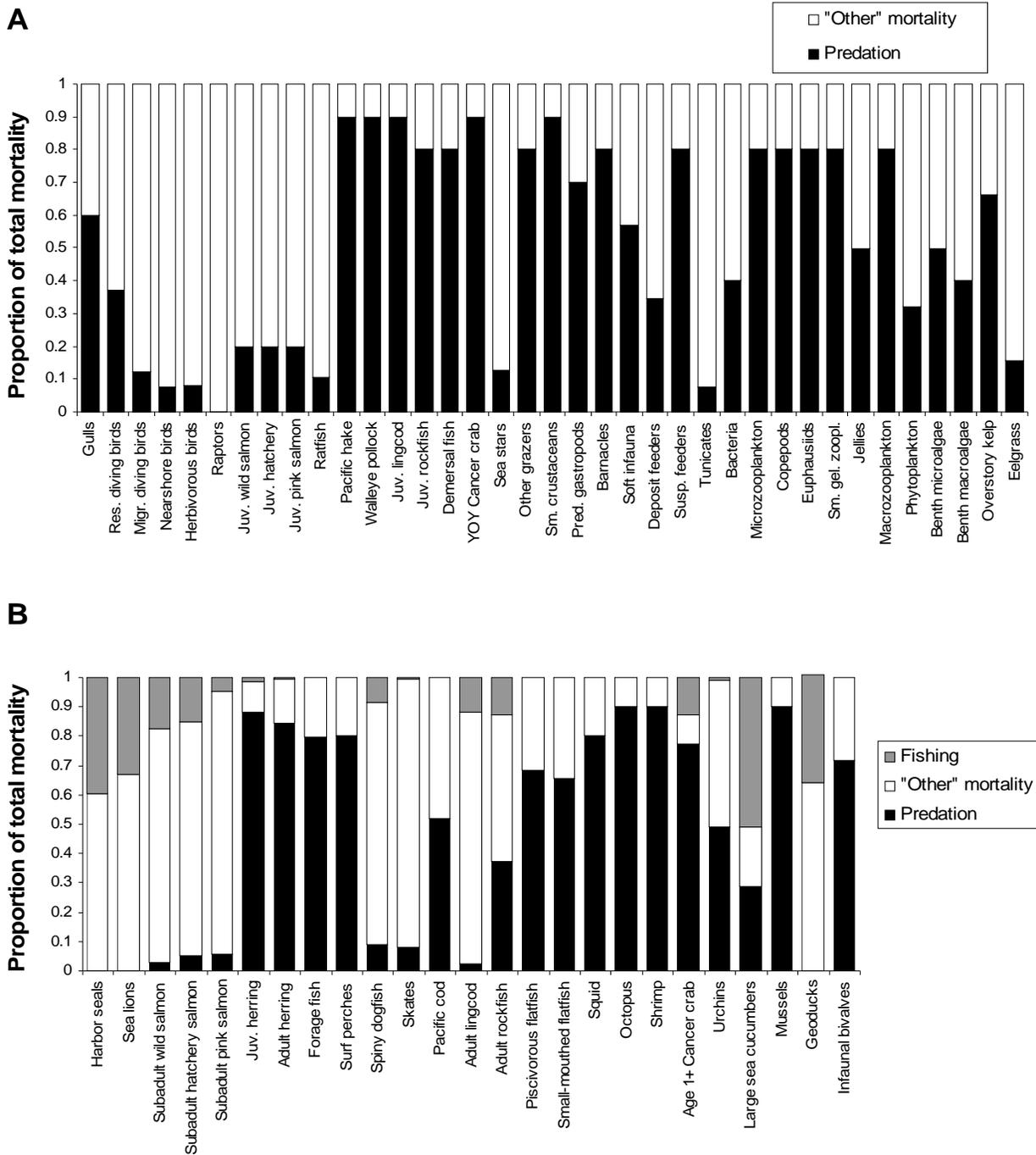


Figure 7. Allocation of mortality to fishing (gray), predation (black) or other sources (white), that is, mortality sources not dynamically modeled in EwE. Panel A is nontarget functional groups and panel B is functional groups targeted by one or more fisheries.

Table 7. Trophic relationships in the Ecopath model where a predator accounts for at least 25% of the total predation mortality experienced by a prey group.

Predator	Prey	Predation mortality %
Spiny dogfish	Adult Pacific herring	34.9
	Small-mouthed flatfish	37.1
	Walleye pollock	42.0
	Piscivorous flatfish	52.4
	Age 1+ <i>Cancer</i> crabs	53.4
	Octopus	86.7
Small crustaceans	Soft infauna	32.0
	Infaunal bivalves	32.9
	Small crustaceans	36.7
	Suspension feeders	53.2
Adult lingcod	Pacific cod	25.6
	Juvenile rockfish	45.4
	Juvenile lingcod	56.6
Raptors	Resident diving birds	31.2
	Gulls	58.6
Ratfish	Walleye pollock	34.2
	YOY <i>Cancer</i> crabs	44.1
Surfperch	Mussels	27.1
	Barnacles	33.1
Jellyfish	Jellyfish	38.3
	Small gelatinous zooplankton	39.0
Nearshore diving birds	Mussels	35.6
Pacific hake	Pacific hake	28.9
Walleye pollock	Pacific hake	32.2
Piscivorous flatfish	Surfperch	28.6
Squid	Squid	50.0
Predatory gastropods	Sea urchins	29.1
Copepods	Microzooplankton	68.5
Other grazers	Overstory kelp	58.9
Soft infauna	Benthic microalgae	34.8

Dynamic Model Responses

Phytoplankton Variability

Stochasticity in phytoplankton production resulted in variation in biomass throughout most of the food web (Figure 8). All but 5 groups experienced substantial displacement (i.e., a change of at least 10% from their initial [Ecopath] biomass values at some point during the 50-year simulation). In fact, the average CV for the biomass of functional groups in this simulation was 18.2%. The magnitude and rate of change varied among groups. Groups with relatively low P/B rates, for example, tended to respond more slowly and to a lesser relative magnitude than groups with high P/B rates. In addition to P/B ratios, trophic relationships influenced the response of some groups to phytoplankton variability. The variability of phytoplankton rippled through all trophic levels, but various feedbacks caused by factors such as dietary overlap or

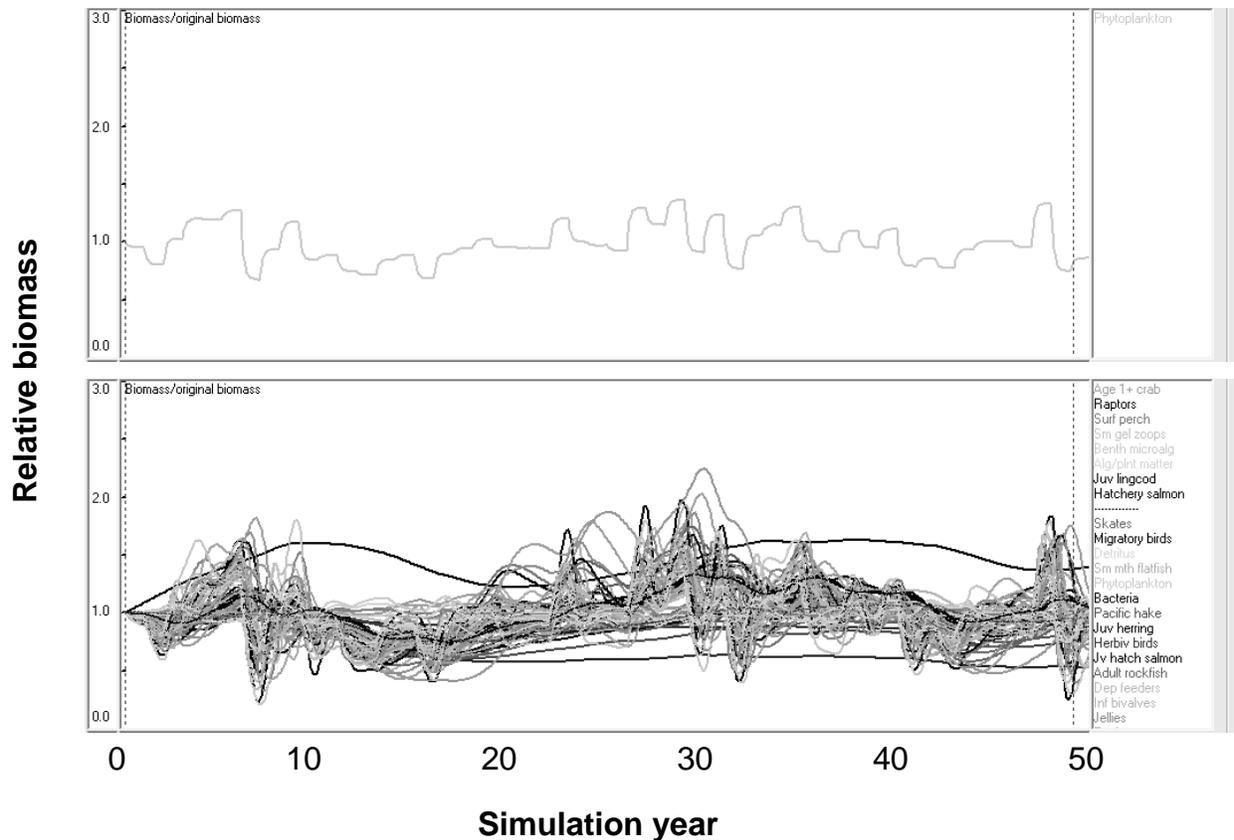


Figure 8. Screen captures from 50-year Ecosim simulation of PCB food web (lower panel) responding to stochastic variability in phytoplankton biomass (upper panel). Each line represents a functional group's relative biomass (i.e., biomass at time t relative to the original biomass from the Ecopath model, as in Table 3). Rates, directions, and magnitudes of change are dependent on inherent vital rates and on trophic linkages.

differences in response rates of predators, prey, and competitors altered the extent of the responses.

Time-series analyses (MAR modeling) confirmed significant bottom-up effects of phytoplankton on most functional groups in the ecosystem, at multiple time lags (Table 8). The best models (i.e., $R^2 > 0.8$) included negative (competitive) effects of phytoplankton on other primary producers, and positive effects of phytoplankton at 1-year time lags (on gulls, subadult pink and wild salmon, Pacific hake, walleye pollock, small-mouthed flatfish, and demersal fish) and 4-year and 5-year lags (on herbivorous birds).

By far the highest number of significant models described effects of phytoplankton at a 1-year time lag, and the number of significant models decreased with increasing time lag. However, significant interactions were observed between phytoplankton and upper trophic levels (e.g., pinnipeds and birds) at all time lags. Interestingly, the bottom-up effects of phytoplankton on some functional groups were delayed, with significant interactions only observed at 3-year, 4-year or 5-year time lags (e.g. spiny dogfish, raptors, sea urchins, herbivorous birds).

Table 8. Results of pairwise MAR analyses of relationships between phytoplankton and each functional group at lags of 1–5 years. Results are interaction coefficients for the effects of phytoplankton on each group (H_{12}) and for the effect of density dependence (H_{22}). Coefficient values in MAR models typically range from -1 to 1 (H_{12}) and 0 to 1 (H_{22}). H_{12} values close to $|1|$ indicate strong interactions, and H_{22} values close to 0 indicate strong density dependence. Zeros indicate no significant interactions. Only models with measurable effects (i.e., either H_{12} or $H_{22} \neq 0$) and $R^2 > 0.5$ are shown; other models are left blank.

Functional group	Lag = 1 year			Lag = 2 years			Lag = 3 years			Lag = 4 years			Lag = 5 years		
	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2
Harbor seals				0.34	0.84	0.62	-0.26	0.86	0.62	0.48	0.61	0.55	0.48	0.48	0.52
Sea lions				0.25	0.92	0.51	-0.10	1.03	0.58	0.41	0.77	0.56	0.41	0.67	0.53
Gulls	0.09	0.96	0.85	0.14	0.91	0.72	0.00	0.91	0.68	0.18	0.78	0.65	0.18	0.70	0.66
Resident diving birds				0.30	0.79	0.56	0.05	0.75	0.61	0.46	0.52	0.58	0.43	0.39	0.55
Migratory diving birds	0.18	0.91	0.51	0.35	0.79	0.59	0.00	0.62	0.58	0.49	0.53	0.51			
Nearshore diving birds	0.23	0.89	0.60	0.43	0.76	0.69	0.00	0.74	0.58						
Herbivorous birds				0.00	0.89	0.61	0.00	0.83	0.70	0.07	0.75	0.80	0.10	0.68	0.86
Raptors										0.43	0.43	0.58	0.49	0.25	0.65
Juvenile wild salmon															
Subadult wild salmon	0.36	0.83	0.90	0.45	0.67	0.57									
Juvenile hatchery salmon	0.87	0.00	0.65				-0.32	0.81	0.52						
Subadult hatchery salmon	0.47	0.70	0.73	0.64	0.38	0.64									
Juvenile pink salmon															
Subadult pink salmon	0.58	0.63	0.95												
Juvenile Pacific herring															
Adult Pacific herring	0.75	0.27	0.77												
Forage fish	0.55	0.39	0.52												
Surfperches	0.48	0.65	0.61												
Spiny dogfish							-0.03	0.98	0.53	0.47	0.68	0.52	0.52	0.56	0.51
Skates	0.33	0.84	0.66	0.52	0.63	0.67	0.00	0.62	0.51						
Ratfish	0.26	0.87	0.69	0.43	0.73	0.62	0.00	0.68	0.52						
Pacific hake	0.79	0.34	0.87												
Pacific cod				0.42	0.70	0.57	-0.34	1.02	0.53						
Walleye pollock	0.43	0.72	0.80												
Juvenile lingcod				0.48	0.60	0.53	0.10	0.91	0.57						
Adult lingcod															
Juvenile rockfish	0.31	0.79	0.54	0.54	0.53	0.59	0.00	0.68	0.55						
Adult rockfish				0.36	0.73	0.51									
Piscivorous flatfish	0.27	0.84	0.66	0.41	0.68	0.51									
Small-mouthed flatfish	0.32	0.85	0.88	0.40	0.70	0.53									
Demersal fish	0.67	0.50	0.82												
Squid	0.99	-0.41	0.79												

Table 8 continued. Results of pairwise MAR analyses of relationships between phytoplankton and each functional group at lags of 1–5 years. Results are interaction coefficients for the effects of phytoplankton on each group (H_{12}) and for the effect of density dependence (H_{22}). Coefficient values in MAR models typically range from -1 to 1 (H_{12}) and 0 to 1 (H_{22}). H_{12} values close to $|1|$ indicate strong interactions, and H_{22} values close to 0 indicate strong density dependence. Zeros indicate no significant interactions. Only models with measurable effects (i.e., either H_{12} or $H_{22} \neq 0$) and $R^2 > 0.5$ are shown; other models are left blank.

Functional group	Lag = 1 year			Lag = 2 years			Lag = 3 years			Lag = 4 years			Lag = 5 years		
	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2	H_{12}	H_{22}	R^2
Octopus															
Shrimp	0.81	0.00	0.78				-0.29	0.54	0.68	-0.36	0.00	0.68			
YOY <i>Cancer</i> crabs	0.53	0.64	0.78												
Age-1+ <i>Cancer</i> crabs				0.60	0.38	0.58									
Sea stars	0.28	0.84	0.56	0.53	0.62	0.66	0.00	0.90	0.54						
Sea urchins										-0.55	0.37	0.51			
Other grazers							0.10	0.00	0.60	-0.66	0.00	0.70	-0.51	0.00	0.61
Small crustaceans	0.87	-0.20	0.56												
Large sea cucumbers	0.48	0.60	0.67												
Predatory gastropods	0.58	0.62	0.77	0.65	0.00	0.60	0.00	0.88	0.54						
Mussels	0.55	0.51	0.68												
Barnacles	0.62	0.40	0.67												
Geoducks	0.17	0.93	0.61												
Infaunal bivalves															
Soft infauna															
Deposit feeders	0.62	0.42	0.73												
Suspension feeders															
Tunicates															
Bacteria															
Microzooplankton	0.83	0.00	0.51												
Copepods							-0.34	0.00	0.54						
Euphausiids							0.00	0.29	0.56						
Sm. gelatinous zooplankton															
Jellyfish															
Macrozooplankton															
Benthic microalgae	-0.99	-0.10	0.98												
Benthic macroalgae	-0.69	0.43	0.66				0.00	0.79	0.59	0.56	0.00	0.60			
Overstory kelp										0.65	0.00	0.60	0.62	0.00	0.58
Eelgrass	-0.87	0.00	0.87				-0.23	0.66	0.63	0.30	0.00	0.50			
Algal/plant material	-0.86	0.00	0.87				-0.30	0.48	0.63	0.33	0.00	0.52			
Salmon carcasses	0.31	0.82	0.78	0.42	0.66	0.51									
Detritus															

MAR models revealed generally increasing density dependence with time lag in upper trophic level functional groups (pinnipeds, birds), as expected in longer-lived species. By contrast, no density dependence was observed in most of the primary producer functional groups. The absence of significant models between phytoplankton and known grazers (copepods, small gelatinous zooplankton, euphausiids) is likely owing to a mismatch between life cycle duration and an annual time lag; that is, for some functional groups with very short turnover rates, a 1-year time lag is likely too long to capture predator-prey dynamics. Some indirect effects of phytoplankton were observed at multiple time lags, including on shrimp at 3-year and 4-year lags, and on other grazers at 4-year and 5-year time lags.

Bald Eagle Impacts

The strong negative press perturbation on the raptor group caused trophic cascade dynamics (*sensu stricto*, Carpenter et al. 2008) in portions of the food web. The initial response of raptors in the scenario was a gradual increase to a new carrying capacity relative to the Ecopath state (Figure 9). This was the result of having a positive *BA* term for raptors in the Ecopath model (Table 3, see also the Raptors description in Appendix A for detail). Changes in several other groups accompanied the initial increase in raptors. The severe decline in raptor biomass beginning in simulation year 20 caused profound changes to other groups, and it generally reversed the signs of the biomass trajectories caused by the earlier increase in raptors.

In general, raptor biomass was negatively related to biomass of all other bird groups (Figure 10, Table 9), but that negative relationship was complex, probably because of the interrelationships between the other birds. Raptors prey on all other bird groups in the model, but gulls also prey on resident diving birds, and there is generally high diet overlap among gulls and diving birds (Table 4). Thus the effect of raptors on any one bird group was mediated through several other bird groups. In turn, many prey items of gulls and diving birds declined, notably juvenile wild salmon, juvenile pink salmon, herring, forage fish, mussels, and demersal fish; by contrast, the trophic cascade did not extend to the major food of herbivorous birds, benthic macroalgae (Figure 10). Macrozooplankton and shrimp, which are preyed upon by many small pelagic and demersal fish, increased by at least 10% and were the only invertebrate groups to demonstrate a pronounced increase.

The effects spread even further. Because juvenile wild and pink salmon declined, subadult wild and pink salmon declined as well, resulting in a decrease in salmon carcasses (Table 9). Because salmon carcasses are a major food source for raptors, the decrease in salmon carcasses may have further exacerbated the raptor decline and contributed more to the nonlinearity of the output. Finally, declines in demersal fish biomass appear to have contributed to declines in Pacific cod and lingcod, which rely on demersal fish for a major portion of their diet. That may be an artifact of lumping so many species of demersal fish into a single functional group, though, as it is questionable as to whether diving birds and predatory fishes would be feeding on the same species of demersal fishes.

Of course, more subtle fluctuations in bald eagle biomass may not produce detectable changes in the rest of the food web. However, both raptors and their major prey (other seabirds) have very high *Q/B* ratios, and thus they have relatively large ecological footprints for groups

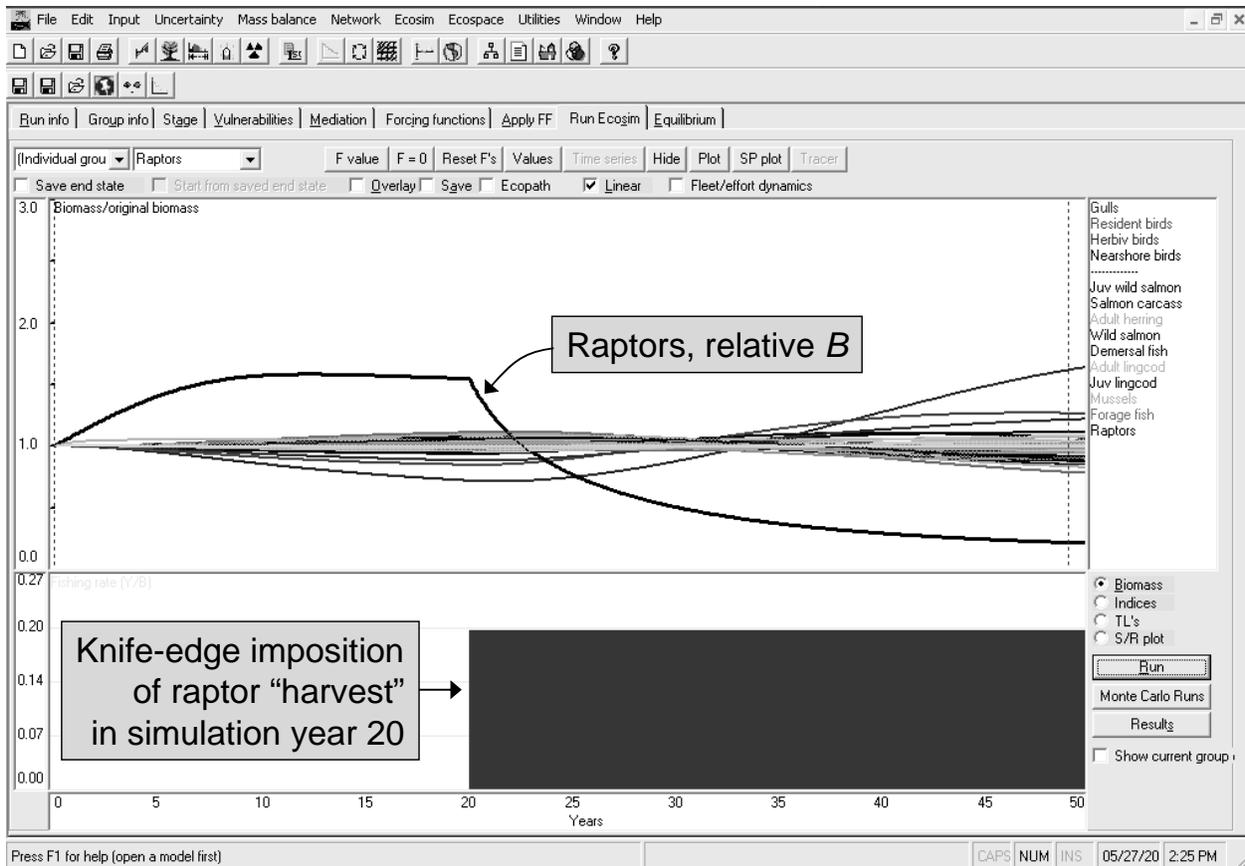


Figure 9. Screen capture from 50-year Ecosim simulation of PSCB food web responding to a sharp reduction in raptor (bald eagle) biomass. Each line in the central panel of the screen capture represents a functional group's relative biomass (i.e., biomass at time t relative to the original biomass from the Ecopath model, as in Table 3). The knife-edge function at the bottom represents harvest mortality increasing from 0 to 0.20 yr^{-1} beginning in simulation year 20, causing precipitous decline in raptors and leading to responses in many other functional groups. Rates, directions, and magnitudes of change are dependent on inherent vital rates and on trophic linkages.

with such small biomasses. Moreover, the seabirds have low P/B ratios, implying that any changes they experience will likely persist for many years.

System-wide Fishery Closures

Closing all fisheries in simulation year 1 caused responses in many target groups and in some groups that are linked to target species via predator-prey interactions or life history (Figure 11). However, most functional groups experienced fairly small changes in biomass relative to a baseline simulation where fishing mortalities were held at the initial values from the Ecopath model. If we assume that a change must be on the order of at least 10% in order to be empirically distinguishable relative to background variability, then only 13 out of 65 functional groups experienced a distinguishable change (Table 10). Most of the groups that increased measurably did so either because of reduced fishing mortality (sea cucumbers, subadult wild and hatchery salmon, geoducks, and age 1+ *Cancer* crabs), an increase in prey availability (raptors),

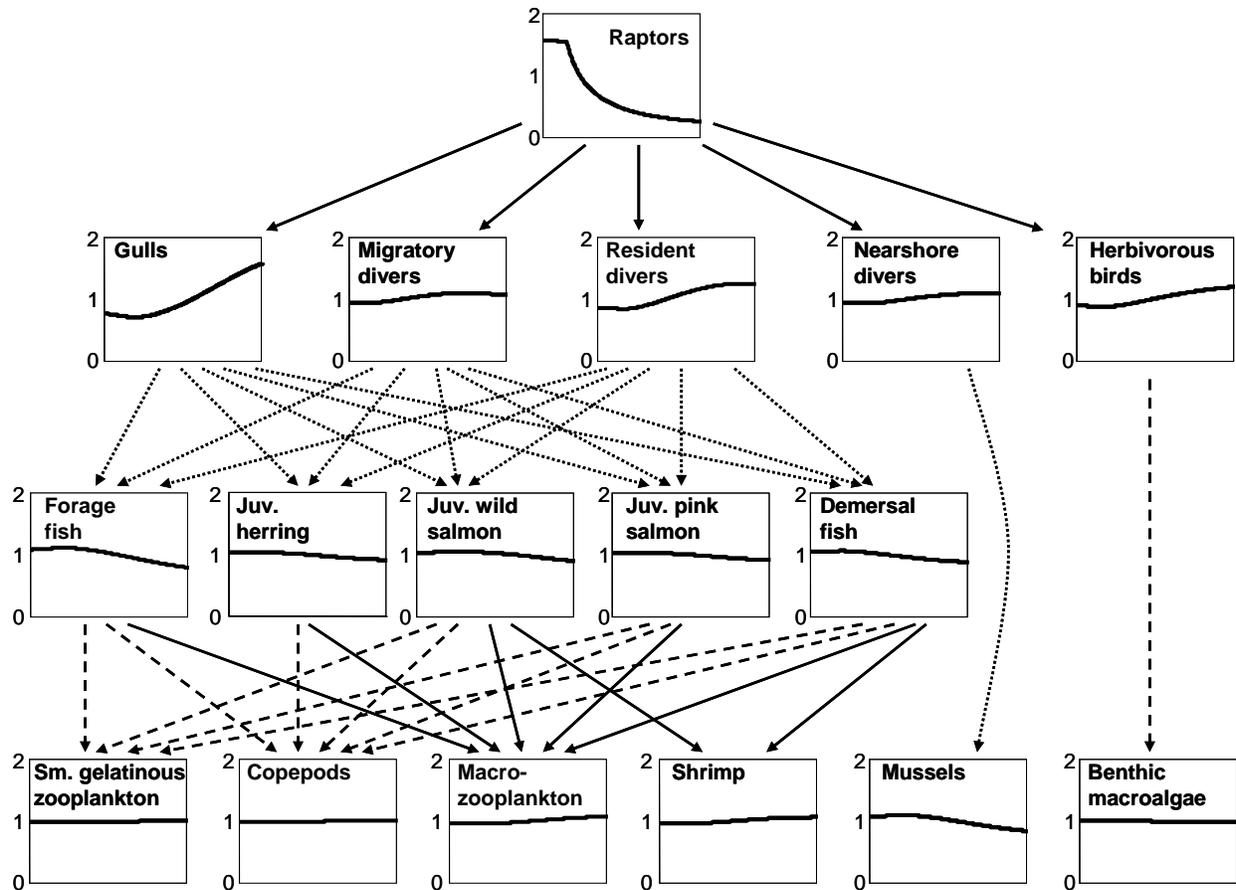


Figure 10. Ecosim outputs representing trophic cascade dynamics caused by a decline in raptor biomass. The x-axis in each panel begins at year 15 (5 years prior to the onset of the raptor decline) and ends at year 50 of the 50-year scenario shown in Figure 9. The y-axis in each panel represents the relative biomass (B_t / B_0) for a functional group, scaled between 0 and 2-fold greater than B_0 . Arrows link predators to prey. Solid arrows indicate relationships in which prey increased by at least 10%, dotted arrows indicate relationships in which prey decreased by at least 10%, and dashed arrows indicate relationships in which the prey changed by less than 10%.

or a combination of both factors (harbor seals and sea lions). Some groups increased due to life history linkages (YOY *Cancer* crabs, juvenile wild salmon, and salmon carcasses). Two groups, walleye pollock and Pacific cod, experienced measurable decreases, likely due to increased predation pressure by functional groups such as spiny dogfish, adult lingcod, and pinnipeds.

Equilibrium Yield Curves

The equilibrium yield curves for functional groups that are now or have historically been targeted showed wide variation in levels of F_{MSY} (Table 11), ranging from very low (0.01375 for geoducks) to quite high (1.1 for squid). As a general rule, target groups with relatively low P/B ratios also had low F_{MSY} . These groups were comprised, by and large, of slow-growing or long-lived species evolved to have relatively low adult mortality rates (profiles in Appendix A), and

Table 9. Groups that changed by at least 10% following the raptor decline in year 20 of the raptor simulation. Values represent the percent change in biomass from year 20 (the start of the raptor decline) to year 50 (the final year of the simulation).

Functional group	Percent decline	Functional group	Percent increase
Raptors	-83.3	Shrimp	10.0
Forage fish	-28.2	Migratory diving birds	12.4
Mussels	-23.0	Macrozooplankton	12.5
Juvenile lingcod	-19.6	Nearshore diving birds	17.8
Adult lingcod	-18.5	Herbivorous birds	36.4
Demersal fish	-16.8	Resident diving birds	48.0
Subadult wild salmon	-15.4	Gulls	120.3
Salmon carcasses	-14.9		
Adult Pacific herring	-14.6		
Juvenile wild salmon	-13.9		
Pacific cod	-13.3		
Octopus	-13.2		
Subadult pink salmon	-12.6		
Juvenile Pacific herring	-12.1		
Subadult hatchery salmon	-11.9		
Juvenile pink salmon	-11.0		

thus have a lesser capacity to handle the mortality brought on by intense fishing. Groups with higher P/B ratios had higher rates of F_{MSY} (Figure 12), consistent with their shorter generation times or greater productivity. A linear regression of $\ln(F_{MSY})$ as a function of $\ln(P/B)$ was highly significant ($r^2 = 0.899$, $p < 0.001$).

Most of the F values that were originally input into the Ecopath model ($F_{initial}$) fell well below the F_{MSY} values (Table 11), which is consistent with our sense that fisheries are currently not exerting much pressure on the PSCB community. Among the groups with the highest landings (Table 5), the $F_{initial}/F_{MSY}$ ratios of wild salmon and geoducks were just below one and *Cancer* crabs were well below one. In just three functional groups, $F_{initial}/F_{MSY}$ was one or greater (harbor seals, sea lions and large sea cucumbers). As previously noted, the pinniped results may be an artifact because of the implicit and unlikely assumption that both pinnipeds populations in PSCB are closed. Large sea cucumbers appear to be slightly overfished, and were the only functional group in the entire model with $F_{initial}$ that was greater than natural mortality (predation + M_0). This result may suggest the need for more precautionary fishing of sea cucumbers. It also highlights the need to better quantify sea cucumber biomass and production, both of which were parameterized indirectly in the Ecopath mass-balancing process (Appendix A).

One issue that arose during this exercise was the difficulty in calculating F_{MSY} for the two herring groups. In initial runs, the F_{MSY} of adult Pacific herring was unreasonably high (≈ 2.4) and skewed to the right rather than parabolic in shape (data not shown). The likely cause was constant replenishment of biomass from the large and productive juvenile herring biomass pool. Likewise in initial runs, F_{MSY} for juvenile herring was high (≈ 1). Our short-term solution to this

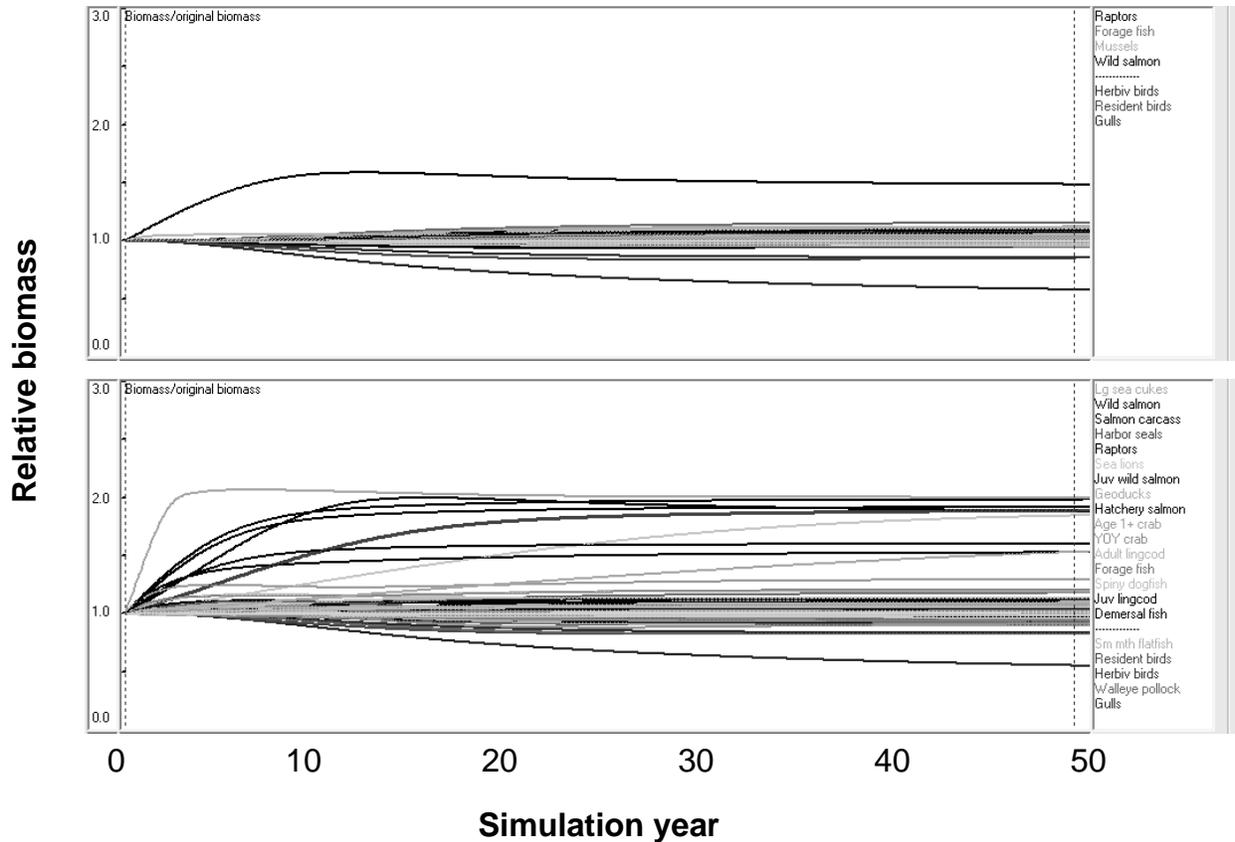


Figure 11. Screen captures from 50-year Ecosim simulations of the PSCB food web subjected to either baseline fishing mortality (upper panel) or a closure of all fisheries in year 1 (lower panel). Each line represents a functional group’s relative biomass (i.e., biomass at time t relative to the original biomass from the Ecopath model, as in Table 3). Rates, directions, and magnitudes of change are dependent on inherent vital rates and on trophic linkages.

Table 10. Groups that changed by at least 10% following a closure of all fisheries in year 1. Values represent the percent difference in biomass from year 50 (the final year of the fishery closure simulation) relative to year 50 of a baseline scenario in which all fisheries remained open and were held constant at their initial exploitation levels (Figure 11).

Functional group	Percent decline	Functional group	Percent increase
Walleye pollock	-10.0	Large sea cucumbers	106.8
Pacific cod	-14.4	Subadult wild salmon	81.1
		Salmon carcasses	74.0
		Sea lions	72.1
		Harbor seals	56.3
		Geoducks	53.4
		Juvenile wild salmon	48.8
		Subadult hatchery salmon	44.1
		Raptors	26.7
		Age 1+ <i>Cancer</i> crab	26.1
		YOY <i>Cancer</i> crab	16.6

Table 11. Productivity (P/B), fishing rates (F), and MSY for targeted groups, according to equilibrium fishing scenarios as described in the text. Groups are sorted by P/B ratios. F rates are for the initial (Ecopath) condition and for the MSY condition, determined iteratively for each functional group (see Methods section). Large $F_{\text{initial}}/F_{\text{MSY}}$ ratios are boldfaced for emphasis.

Functional group	P/B (yr ⁻¹)	F_{initial} (yr ⁻¹)	F_{MSY} (yr ⁻¹)	$F_{\text{initial}}/F_{\text{MSY}}$	MSY (mt km ⁻² yr ⁻¹)
Geoducks	0.0363	0.013	0.01375	0.966	0.696
Sea lions	0.076	0.025	0.025	1.000	0.001
Spiny dogfish	0.103	0.009	0.04	0.223	0.137
Harbor seals	0.126	0.050	0.045	1.111	0.001
Skates	0.127	0.0003	0.03	0.010	0.009
Adult rockfish	0.24	0.031	0.11	0.279	0.020
Pacific cod	0.26	0.00003	0.0625	0.000	0.007
Lingcod	0.28	0.033	0.24	0.139	0.036
Small-mouthed flatfish	0.345	0.0001	0.06	0.002	0.265
Pacific hake	0.405	0	0.125	0.000	0.201
Piscivorous flatfish	0.467	0.001	0.1	0.009	0.058
Sea urchins	0.5	0.005	0.09	0.059	0.023
Walleye pollock	0.8	0	0.15	0.000	0.282
Octopus	0.86	0.00001	0.175	0.000	0.112
Large sea cucumbers	0.86	0.439	0.375	1.171	0.022
Mussels	0.927	0.00003	0.2	0.000	0.444
Wild salmon	0.989	0.171	0.2	0.854	2.321
Surfperch	1.3	0.00003	0.3	0.000	0.531
Forage fish	1.5	0.002	0.35	0.006	0.733
Age 1+ <i>Cancer</i> crab	1.5	0.193	0.55	0.351	0.186
Pink salmon	1.577	0.072	0.25	0.286	0.011
Infaunal bivalves	2.059	0.0005	0.45	0.001	17.938
Shrimp	2.25	0.001	0.5	0.002	2.235
Squid	3.0	0.0002	1.1	0.000	0.503
Juvenile herring	3.656	0.060	0.89	0.068	1.916

issue was to simultaneously fish both juvenile and adult herring by incrementally varying fishing pressure on the primary fishing gear that targets them (i.e., other net gear, Table 5) and then to determine the F_{MSY} only for the juveniles, which are the major component of herring landings. That result is given in Table 11. Nevertheless, it is apparent that our parameterization of Pacific herring is currently insufficient to accurately represent all fishing situations. We may need to revisit our estimates for herring P/B or add BA terms in Ecopath,³ or we may need to reconsider some of the values that govern the herring delay-difference relationship between the juvenile and adult pools (Appendix A and Appendix D).

³ See footnote 2.

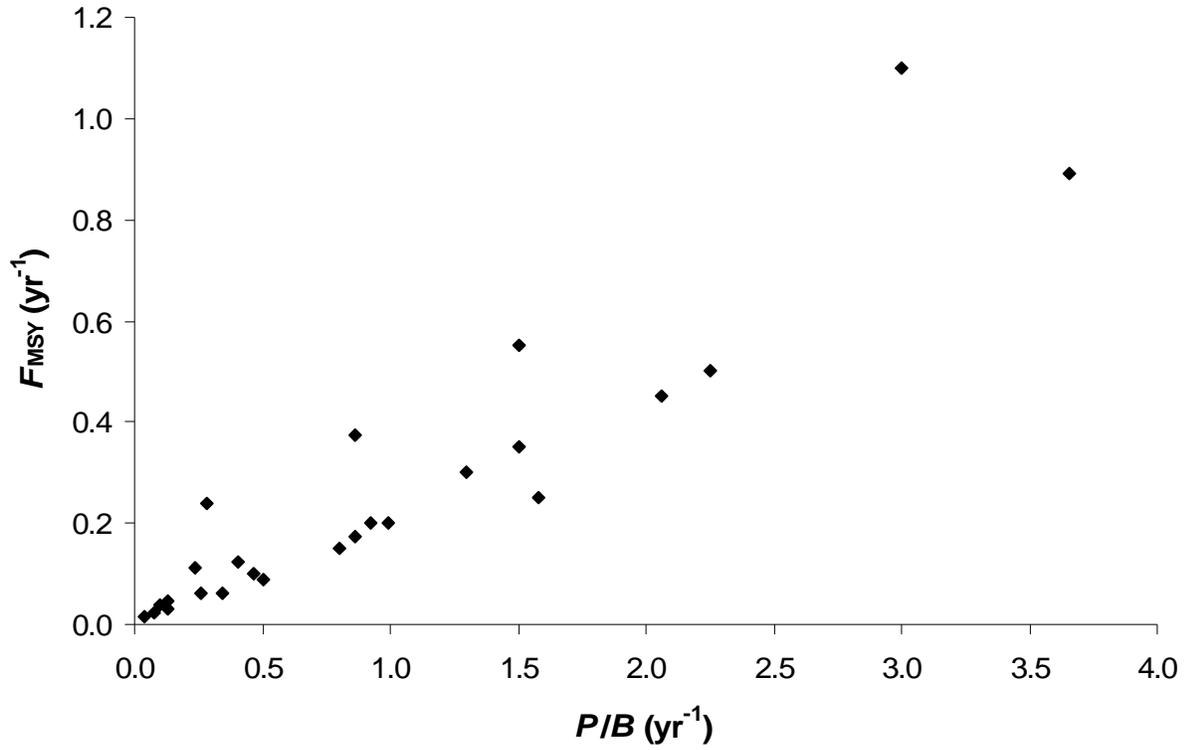


Figure 12. Relationship between F_{MSY} and P/B for targeted functional groups in the PSCB Ecosim model. F_{MSY} estimates derived from single-group equilibrium yield curve analyses.

Discussion

The EwE model presented here is a first attempt at meeting the objectives described in the introduction of this report. Though the model encompasses a considerable amount of the species diversity, total production, and ecological linkages in the PSCB, it remains a simplification of the system and it also reflects many assumptions and biases on the part of the model designers. Nevertheless, it is a foundational step forward in developing ecosystem-scale models of Puget Sound with which to ask meaningful ecological and management-related questions, and it can only improve with time and additional information.

Objectives 1 and 2: Model Development and Assessment

Objectives 1 and 2 of this project were to build a model that represents the current understanding of the PSCB food web, which would enable us to ask basic ecological questions based on the best available information. It also enables us to make broad assessments about how management actions might be expected to influence the community via direct effects on the managed species and indirect effects created through food web interactions and feedbacks.

We addressed these objectives throughout the iterative mass-balancing phase of model development (i.e., the Ecopath model), and further through a series of dynamic heuristic simulations (the Ecosim model). The mass-balancing phase involved identifying the most important functional groups and compiling relevant data into a quantitative arena so that we could evaluate the importance of intergroup dynamics and linkages at the scale of the entire community, something that is profoundly difficult to evaluate empirically. The dynamic simulations provide an initial idea of the sensitivity of the model food web to perturbations at different trophic levels. This is essential for evaluating model performance. It allows us to answer basic questions, such as:

- Do perturbations propagate in a believable manner, given past observations?
- Do groups with short generation times respond and recover more quickly than groups with long generation times?
- Do minor perturbations lead to dynamic instability, including explosions or collapses of multiple groups?

These simulations may also offer a preview of groups that will be important indicators of ecosystem processes.

In essence, the contemporary PSCB food web appears to be a community dominated in terms of biomass by benthic/demersal species, although the relatively high energy throughput in the pelagic community somewhat offsets its lower biomass. Phytoplankton is the major source of primary production and supplemental production (via the large amount of detritus generated by dead phytoplankton). Although we have represented many functional groups, overall biomass

is highly aggregated within a subset of seven groups from low and intermediate trophic levels; only one of these groups is a vertebrate (ratfish). Bottom-up forcing, through phytoplankton production for example, appears to be a dominant trophic structuring mechanism. Top-down control was apparent in some instances and may even lead to complex trophic cascades that span several trophic levels. Such was the case in the raptor scenario. In all of the dynamic simulations, time lags related to differences in production and life history extend the influence of trophic interactions for many years. We intend to extend the MAR model analysis approach to more thoroughly examine the structure of time lags, including subannual time steps. We will also use the same method to stochastically vary other groups and examine their pairwise interaction strengths so that we can gauge the relative influence of top-down and bottom-up forcing in the system.

Some initial diagnostic analyses produced encouraging outputs in terms of model structure and stability. Obviously we achieved mass balance in the Ecopath model, and in many exploratory Ecosim simulations (not described above), we saw no evidence of unreasonable population extinctions or explosions, or of high-amplitude oscillatory behavior. Knife-edge fishery closure did not cause explosions or extinctions in any group (Figure 11). The equilibrium yield curves for currently or formerly targeted functional groups showed that F_{MSY} was a function of P/B (Figure 12), which is in line with expectations (Walters and Martell 2004). Less encouraging was the rather equivocal analysis of diversity and evenness (Figure 4), which implies that this model may not be informative in identifying useful ecosystem indicators related to species diversity.

Overall, fishing mortality does not appear to be a major structuring force in the contemporary PSCB food web, although contemporary food web structure may be a byproduct of heavier fishing in previous decades. While F is substantial for Pacific salmon, the heavy fishing pressure on Pacific salmon does not ripple down to lower trophic levels because subadult Pacific salmon are outside of the model domain for most of their lives. It probably does affect food availability for pinnipeds and raptors. Two other groups support large landings: geoducks and *Cancer* crabs. Although an important mortality source for geoducks themselves, the geoduck fishery has little effect on the rest of the system because geoducks are fairly disconnected from the rest of the food web. Extraction of *Cancer* crabs, while apparently sustainable, likely affects the biomass of some *Cancer* crab prey groups.

Our model suggests that simply terminating fishing would not restore depleted populations of gadoids (Pacific hake, Pacific cod, walleye pollock) to historic levels of abundance (e.g., Gustafson et al. 2000). That output has several possible explanations: we may lack the data to properly characterize current gadoid stocks or biomass trends; our model may not cover some ecological processes that are influential to gadoid populations; a fundamental system shift may have occurred, in which the carrying capacity of gadoids has changed; or some combination of the above.

The simulations presented in the Results section and summarized above are certainly preliminary, pending testing of the model against time series data to see how effective it is in re-creating historic trends. Testing Ecosim models against time series is a useful technique for estimating the relative importance of drivers such as primary production, fishing intensity, recruitment variability, and the relative strength of donor/recipient control within individual

predator-prey interactions (e.g., Walters and Martell 2004, Christensen et al. 2005). Ongoing development of this model includes the gathering of time series data related to multiple trophic levels. Data include estimates or indexes of abundance, total landings, and catch-per-unit-effort, as well as values related to water quality and total phytoplankton. We will subsequently attempt to fit Ecosim model outputs to all available biomass estimates or indexes by incorporating time series of fishing, by incorporating primary production and recruitment, and through further fine-tuning by adjusting the strength of predator-prey interactions.

Objective 3: Identifying Data Gaps

Objective 3 of this work was “to identify significant data gaps that could potentially constrain model development or increase uncertainty in the outputs.” Meeting this objective is absolutely critical for developing an ecosystem model if it is to gain credibility with scientists, managers, and stakeholders who care about the ecosystem that the model is designed to simulate (Townsend et al. 2008, Levin et al. 2009). A key distinction, however, is that data gaps and uncertainty are not indications that the model is not yet ready. Models can be used responsibly in spite of data gaps and uncertainty, provided that users carefully consider data quality, model structure, and model assumptions as they interpret and apply the model. Uncertainty is an inherent quality of all ecosystem models, even the best ones. They are simplifications of true ecosystems, and thus purposefully omit many components and processes in order to efficiently simulate core dynamics of interest. One of our obligations is to minimize uncertainty that can be attributed to missing data or poorly understood model elements. Below is a summary of some critical data gaps that have become clear through the process of parameter development. These might be thought of as high priorities for future monitoring programs, and would be appropriate elements to examine in more formalized sensitivity analysis of this model.

A major data gap is the absence of biomass estimates for many functional groups. We typically addressed this issue by using *EE* as an input and allowing Ecopath to estimate biomass. That method was applied to 39 (60%) of 65 functional groups (Table 3), including some of great ecological or social value. For example, we used Ecopath to estimate biomass of the salmon groups, most forage fishes, and several groundfish, including groups of conservation concern (rockfish, Pacific hake, and walleye pollock). Nearly all invertebrates were handled this way. Trophic linkages spanning multiple trophic levels were affected by this issue. For instance, juvenile herring and copepods have Ecopath-based biomass estimates. Because juvenile herring are a major copepod predator and copepods are major grazers of phytoplankton, the mass-balance estimate of juvenile herring biomass ultimately influences phytoplankton *EE* and the production of phytoplankton-derived detritus.

In all such cases, the mass-balancing solution for biomass places heavy reliance on our perception of *EE*, our estimates of those groups’ *P/B* ratios, and how well we characterized top-down (predatory and fishery) demands. There are guidelines for assigning *EE* values to groups at different trophic levels (Christensen et al. 2005), but estimating *EE* is obviously inexact and assumption laden. Having credible biomass estimates for most groups is more concrete and desirable. This will require expanded, prioritized monitoring, to the extent that research budgets allow. For some groups, biomass will be extremely difficult to estimate through empirical monitoring due to logistical sampling constraints (examples in Appendix A). For other groups

(e.g., salmon), biomass data are available, but the data themselves have issues (e.g., interagency reporting compatibility) or are challenging to interpret due to complex spatial dynamics.

A second and related data gap is the availability of multidecadal time series data on abundances or biomasses of major biota. Time series of biomass data are powerful assets in development of EwE models. First, recent trends enable the user to estimate biomass accumulation (BA in Equation 1 and Table 3). That leads to better description of the reference state of the food web by allowing functional groups to be at nonequilibrium if that is appropriate; we have only done so with two functional groups (raptors and tunicates). Second, time series biomass data allow the user to tune predator-prey interaction strengths to better fit model output to historic observations. Such tuning includes adjusting the vulnerability parameters in Ecosim that affect the rate at which predators diminish prey pools (Christensen et al. 2005). That tuning process will, in all likelihood, also involve further iterative changes to the parameters described herein. We have been successful in locating time series of fisheries-independent, survey-based biomass data for some functional groups, but in general there are few groups for which such data are available, uninterrupted, and collected at the scale of the basin for long time spans. Identifying and incorporating such time series are central efforts in our ongoing model development.

For many groups, diet compositions are a critical data gap, as they represent the principal means by which functional groups are linked in this model. For many groups, we were unable to locate mass-based or volume-based data on diet proportions in the PSCB (Appendix A). In some cases, there were no quantitative data in the literature. In other cases, data were reported as frequency of occurrence of different prey, and frequency of occurrence data are very difficult to translate into diet proportions for input into the Ecopath diet matrix. For higher trophic levels, we generally addressed these issues by using data from adjacent basins in Puget Sound. For lower trophic levels, our approach ranged from using estimates drawn from field research or Ecopath models from nearby systems to making arbitrary assignments based on anecdotal information in the general literature.

The groups for which we found quantitative diet data from research in Central Puget Sound were primarily fishes, including adult herring, all salmon groups, some surfperches, Pacific hake, walleye pollock, both flatfish groups, spiny dogfish, ratfish, skates, and the catch-all demersal fish group. Other groups for which we found local, quantitative diet data were geoducks, resident and nearshore diving birds, and raptors. Obviously many functional groups and trophic levels are poorly represented in these lists, including almost all invertebrates and the marine mammals. Still other groups are examples of cases where we know relatively little about their predators. For example, we know little about how juvenile salmon contribute to the diets of nearshore fishes. This forces most juvenile salmon predation mortality in our model to be caused by bird groups (especially gulls and migratory divers), which may be a misrepresentation.

The fact that there are gaps in diet data is not to say that the diet compositions are right or wrong, but rather that they may need adjustments in order to improve model performance. Some adjustments are likely to have pronounced effects. For example, groups with substantial intraguild cannibalism (squid, juvenile *Cancer* crab, Pacific hake, small crustaceans) may be responsive because changing the magnitude of cannibalism will strongly affect the mass balance of that group. Another example is higher predators that prey on highly aggregated prey groups,

such as the small crustaceans or some of the zooplankton groups. Aggregating prey groups may result in competition for the aggregated prey pool when in fact no real competition exists in situ. Also, we should carefully examine groups that impart considerable predation mortality on one or more other groups. Some such predators have diet compositions based on recent seasonal stomach content analysis from samples collected in PSCB (e.g., spiny dogfish). By contrast, many have diet compositions that were derived arbitrarily (e.g., small crustaceans). The predator-prey linkages listed in Table 4 are potentially very strong and influential, as they highlight groups with large biomasses and throughputs at several trophic levels (e.g., spiny dogfish, ratfish, small crustaceans, copepods) or with the potential for disproportionate influence via trophic cascades (e.g., raptors).

Fishery mortality is also a data gap, although perhaps of lower overall priority than others identified above. With the exception of a few functional groups, F values in PSCB appear to be fairly low relative to total mortality or historic levels of exploitation, due to fishery closures and diminished effort for a variety of reasons (e.g., Palsson et al. 1998, Ruckelshaus and McClure 2007, PSP 2008). The major gaps are recreational catches of certain groups and bycatch mortality from all gears.

Aside from biomass, diets, and fisheries, there are many explicit and implicit data gaps described in the functional group descriptions (Appendix A). Some of these gaps have to do with concrete quantities that possibly could be estimated with adequate study. Examples include questions such as:

- What are appropriate P/B and Q/B ratios for the main zooplankton species?
- What proportion of subadult wild, hatchery, or pink salmon reside in PSCB for the entirety of their marine phase?
- Where do adult Pacific herring populations from PSCB and adjacent basins disperse following spawning?
- What is the magnitude and trend of mortality experienced outside the model domain by migratory groups like seabirds?

On the other hand, there are implicit information gaps related to assumptions of functional group structure (e.g., Christensen et al. 2005). That is, we may misrepresent the importance of some species by lumping them into broad functional groups. For example, we have one functional group that contains all phytoplankton, which deemphasizes the role of inedible species, harmful algal blooms, and competition for resources such as dissolved nutrients and light. Similarly, the roles of individual species are blurred in catch-all groups such as small crustaceans, macrozooplankton, infaunal bivalves, and demersal fish.

Formal sensitivity analyses will aid in estimating the robustness of model outputs to groups for which we lack confidence in data. The EwE software contains limited capacity for sensitivity analysis (Christensen and Walters 2004, Christensen et al. 2005). Unfortunately, that capacity has not been applied very broadly in the literature (Plagányi and Butterworth 2004). Essington (2007) conducted perhaps the most formal published analysis of the sensitivity of Ecopath parameter estimation to data assumptions. He concluded that the precision of model estimates (namely estimates of biomass and EE) was similar to the precision of the inputs (P/B ,

Q/B, diet), that iterative adjustments during the balancing process led to only minor improvements in model performance, and that biomass and *P/B* are the most influential input parameters relative to estimation errors. Essington (2007) also concluded that tight food web linkages and cycles—especially ones involving cannibalism, a feature common in highly aggregated groups such as our small crustacean omnivore group—are most likely to produce imprecise or unstable outcomes. As Essington (2007) notes, the impacts of such data gaps are probably greater if the model is being used as a prediction tool to make quantitative estimates of future system states, as opposed to more heuristic applications where the model is being used to screen policy options and identify possible qualitative outcomes to management actions.

Conclusions

This effort documents the initial development of a food web model for the PSCB. It outlines our progress toward synthesizing available information and identifying important data gaps. The next major objective we hope to accomplish will be to formally use the model in support of EBM. As a first step, we hope to identify meaningful indicators of how the food web responds to ecosystem changes and to human-derived pressures. This objective is intended to support the PSP's stated goal of identifying appropriate indicator species that will reflect the status of the biological community in response to management actions designed to restore Puget Sound ecosystem health (PSP 2008). Indicator identification will be undertaken using methods developed by NWFSC scientists (Samhuri et al. 2009, Samhuri et al. 2010).

The model described here is and will continue to be a work in progress. Ideally, model development should be an ongoing process that is complemented by experiments, field research, and monitoring. Experimental and empirical approaches will provide data that improve our input data; in turn, model simulations will identify hypotheses and data gaps integral in devising future research plans. Further development and improvement of this model would also be fostered by broad engagement of managers and stakeholders in simulation development. That level of engagement increases the critical scrutiny of the model and enhances the likelihood that its major shortcomings will be identified and addressed. Additionally, broad engagement helps ensure that the most important research and management questions are taken into account as model development ensues. Finally, we plan to use the model in manuscripts that will be submitted to the primary literature, in order to ensure that the structure and performance of the model and the assumptions of its makers are subject to appropriate scientific peer review. This data-based, stakeholder-engaged, and peer-reviewed approach is essential to producing robust and reliable models that are qualified to evaluate alternative strategies in an ecosystem approach to management (e.g., Levin et al. 2009).

Even as EwE model development continues, we are beginning work on a more complex ecosystem model intended to address questions at the scale of the Salish Sea (Puget Sound, the Strait of Georgia, and connecting waters). This next generation of ecosystem model will use the Atlantis software developed by scientists at CSIRO-Australia (Fulton et al. 2004, Fulton et al. 2005, Smith et al. 2007). This model framework offers several advances relative to the EwE approach. It is spatial in nature, wherein the user divides the model domain into discrete three-dimensional spatial units to account for spatial and temporal patchiness of processes, habitats, life histories, and species distributions. It incorporates abiotic drivers such as oceanographic fluxes, nutrient cycles, hypoxia, and terrestrial inputs of water, nutrients, and sediment. It has

broad capabilities to simulate age structure, recruitment dynamics, habitat preferences, and dietary ontogeny in different functional groups. It also simulates human dimensions such as fisheries, ecosystem monitoring and assessment, and management decision rules.

The Atlantis approach, although more sophisticated, is extremely data-intensive and will require much longer to develop than the model described here. It is our hope that this model will continue to improve as the parallel Atlantis model is developed. This will allow us to address relevant objectives with the EwE model even as the other model is being developed. Moreover, once both models are functional, we will have two distinct conceptual modeling frameworks with which to address important ecological and management questions.

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Appendix A: Species and Functional Group Descriptions

In the sections that follow, we outline the basic biology and ecology of the functional groups included in our Ecopath models. The descriptions and associated model parameters are based on published research in the Puget Sound basin where available, but are also informed by expert opinion, discussions among the authors and with colleagues, and Ecopath with Ecosim (EwE) models from neighboring ecosystems. In many cases, they reflect simplifying assumptions that will require additional work to validate. For the sake of organization, functional group descriptions are pooled at very general levels (e.g., primary producers, benthic invertebrates, etc.). Many species have been omitted from the model, including some iconic ones (e.g., killer whales), mostly because they are rare or more important to the ecology of neighboring basins than they are to the ecology of the Puget Sound Central Basin (PSCB). Those species are briefly noted in Appendix B, and will likely be incorporated into future models (e.g., Atlantis) built at the scale of the entire basin.

The parameter descriptions below are meant to describe the baseline model state. In the body of this document, deviations from this baseline may have been considered in judging the model's overall stability and sensitivity to assumptions and perturbations.

Primary Producers

Phytoplankton

Phytoplankton in Puget Sound is highly productive relative to most marine environments on earth, due in large part to seasonal and spatial patterns of tide-, river-, and wind-driven mixing and stratification (Strickland 1983). The phytoplankton community is mostly comprised of diatoms, dinoflagellates, and phytoflagellates, each of which can play different ecological roles. Diatoms can be solitary or chain-forming; dominant genera are *Skeletonema*, *Chaetoceros*, *Thalassiosira*, and *Coscinodiscus* (Strickland 1983). These species are important components of spring blooms that drive production in the early part of the growing season. Dinoflagellates and phytoflagellates are better adapted to waters that are warm and highly stratified; phytoflagellates may dominate in the dark, well-mixed conditions of winter (Strickland 1983). Dinoflagellates include representatives such as *Gymnodinium* and *Gonyaulax*, the latter being responsible for paralytic shellfish poisoning, while phytoflagellates include taxa such as *Pyramimonas* and *Dichtyocha* (Strickland 1983). Taxonomic representation among phytoplankton can vary throughout the year and also over relatively short periods of time. For example, in Hood Canal during 2002, surface diatoms dropped from 70% to less than 10% of the abundance within a week in February, rose to 70% of the abundance within a week in late March and stayed at greater than 60% for two more weeks, then crashed to less than 10% a week later (Horner et al. 2005).

Estimates of steady-state phytoplankton biomass reflect properties such as standing stock, doubling rate, grazing by herbivores or predators, and loss by sinking; each of these properties can be highly variable in space and time. Three studies in the PSCB spanning nearly 4 decades were considered for a biomass estimate. One study was conducted in the spring of 1966 and 1967 (Winter et al. 1975) and a second study was conducted in both spring and summer of 1975 (Campbell et al. 1977). More recently, Newton and Van Voorhis (2002) monitored four sites in PSCB for 3 contiguous years during all seasons. All studies examined depth-integrated chlorophyll *a* levels, which we converted to biomass by assuming a chlorophyll *a*:carbon ratio of 0.0200 (Robinson et al. 1993) and a total carbon:wet biomass ratio of 0.0828 (Sherr and Sherr 1984). Biomass estimates for the two earlier studies were 14 and 22 mt km⁻², respectively, assuming in each case that spring-summer values were applicable for 6 months and that a light-limited value of 12 mg chlorophyll *a* m⁻² was applicable for the other 6 months. The Newton and Van Voorhis (2002) study, however, yielded a mean annual biomass of 51.0 mt km⁻². We used this value for our initial phytoplankton biomass because it is based on more comprehensive spatial and temporal sampling (n=168 samples) representing contemporary conditions.

Like biomass estimates, production:biomass ratio (*P/B*) estimates for phytoplankton can be highly variable, both in spatiotemporal terms and also by species. The size composition and taxonomy of the phytoplankton community, as driven by environmental conditions, affects productivity. For example, Table A-1 shows productivity derived for oceanic estuaries, comparing nanoplankton (<22 μm size) and net plankton (≥22 μm size), and illustrates a generalized observation on conditions that favor nanoplankton over net plankton: low nutrient levels, higher water temperatures, and high light levels (Malone 1980).

Puget Sound experiences cyclical episodes of plankton blooms throughout the spring and summer. Blooms are often extensive; for example, a multiship survey found that the spring bloom in 1969 covered most of the Central Basin (Munson 1970). Individual ¹⁴C assimilation studies to estimate production in PSCB have shown significant variations from month to month, probably due to the bloom-bust cycles of growth during spring and summer. Annual production measurements suggest a trend of increasing production in PSCB. Mean annual production in 1966 and 1967 was 2,462 and 2,314 g wet weight m⁻², respectively (Winter et al. 1975), while in 1975 it was 3,769 g m⁻² (Campbell et al. 1977). Experiments in 1999, 2000, and 2001 found much higher annual production rates of 9,478, 12,334, and 15,570 g m⁻², respectively (Newton and Van Voorhis 2002). The latter study also estimated *P/B* at four PSCB sites. During the summer, mean daily *P/B* averaged 0.92 (0.78 at West Point to 1.02 at Admiralty Inlet), while during the winter, daily *P/B* was a mean of 0.33 (0.27 at West Point to 0.42 at Possession Sound), resulting in a weighted average *P/B* of 0.62 d⁻¹. This equals an annual *P/B* of 226.3 yr⁻¹.

Table A-1. Seasonal production rates of nanoplankton (<22 μm) and net plankton (≥22 μm) in oceanic estuaries, derived from Malone (1980). Values are mean production (with upper and lower limits in parentheses).

Season	Surface temperature (°C)	Nanoplankton production (mg C m ⁻² d ⁻¹)	Net plankton production (mg C m ⁻² d ⁻¹)
Winter	0–8	0.16 (0.08–0.48)	0.67 (0.03–1.94)
Spring	9–17	0.77 (0.11–1.56)	0.88 (0.04–3.80)
Summer	18–26	1.90 (0.49–4.41)	0.23 (0.02–1.45)

Given the inputs for biomass and P/B and the demands of grazers, the Ecopath mass-balancing routine yielded an ectotrophic efficiency (EE) of 0.32. This is in contrast with studies that indicated relatively high rates of grazing compared to other sources of loss (e.g., sinking). In northern Puget Sound, zooplankton grazing rates were lower in fall and winter (35% d^{-1}) and higher in spring and summer (71% d^{-1}), with an annual rate of 64% (Strom et al. 2001). Peak rates of grazing by microzooplankton reached approximately 80% during blooms (Strom et al. 2001). The annual rate of 64% is double our EE , but is similar to the 62% observed in Norwegian fjords (Archer et al. 2000). It is possible that the Strom et al. (2001) results for northern Puget Sound are not directly transferable to PSCB, but it is also possible that we have underrepresented grazing pressure (e.g., by copepods and microzooplankton), which would result in an underestimate of the true EE .

Phytoplankton is grazed upon by numerous filter-feeding invertebrate groups (Table 4). It is also the largest contributor to the detritus pool. The benthic components of the food web are supported in large part by phytoplankton production that is uncoupled from the pelagic food web by virtue of the fact that phytoplankton production is patchy in space and time, and the fact that larger pelagic grazers in Puget Sound (copepods, euphausiids) do not respond to blooms as rapidly as is seen in some marine systems. Much of the initial production in spring blooms ends up sinking, as detritus, to the benthos (Strickland 1983).

Benthic Microalgae

The benthic microalgae group is comprised of the microphytobenthos found on a variety of substrates (sand, rock, mud) or on the surfaces of other primary producers such as macroalgae and seagrasses. Representatives such as benthic or epiphytic diatoms are highly productive species that support a variety of benthic grazers (Lie 1974) and underlie production of many higher consumers, including fish (e.g., Simenstad and Wissmar 1985).

These species have high turnover rates and their standing stocks have rarely been measured in Puget Sound (e.g., Thom and Albright 1990). Thus we assumed that the most pragmatic approach was to make assumptions about their P/B ratio and EE , and allow the model to estimate biomass based on mass balance. We assumed a P/B of 100 yr^{-1} , which is considerably lower than the P/B for phytoplankton. It is also conservative relative to published values for P/B of microphytobenthos from other systems, such as the Baltic Sea (range of annual means = 140–185.7 yr^{-1} , calculated from data in Urban-Malinga and Wiktor 2003) and the St. Lawrence Estuary (range of values = 87.6–332.9 yr^{-1} , calculated from data in Roux et al. 2002).

We assumed an EE of 0.5. This implies that benthic microalgae experience modest grazing pressure. Our assumption is that benthic grazers are relatively slow-moving and cannot exert as much sustained pressure on a widespread area of benthic algal growth. In addition, some stands of benthic microalgal growth (e.g., epiphytes on seagrasses) may not be accessible to all sizes of benthic grazers.

The mass-balancing routine of Ecopath yielded a biomass estimate of 4.298 $mt\ km^{-2}$. This value should be viewed as hypothetical. We note that this biomass must be concentrated in waters where light penetration is sufficient to support benthic primary production.

Benthic microalgae are fed upon by small crustaceans, other grazers, sea urchins, and deposit feeders (Table 4). Trace amounts are eaten by herbivorous birds.

Benthic Macroalgae

The benthic macroalgal functional group consists of intertidal and subtidal green algae (phylum Chlorophyta), red algae (phylum Rhodophyta), and brown algae (phylum Ochrophyta, class Phaeophyceae). These range from leafy or filamentous species to species that can grow several meters in length. Benthic macroalgae are abundant in littoral areas. They are major sources of food, detritus, and habitat for a wide variety of species in the euphotic zone (Mumford 2007). Generally speaking, this functional group's role in the system is not well-known and the underlying biology (e.g., biological rates, standing stocks, grazing pressure) is poorly described. Thus we must exercise caution when interpreting model outputs where benthic macroalgae experience marked changes or strongly influence other groups.

The diversity in this functional group is quite high (Waaland 1977, Gabrielson et al. 2006, Mumford 2007). Representative species cover a wide range of sizes, basic morphologies, longevities, and seasonal growth and abundance patterns. (The canopy-forming species bull kelp [*Nereocystis luetkeana*] is considered its own functional group; see Overstory Kelp subsection below.) Growths can be extensive; for example, Mauzey et al. (1968) report dense mats of *Ulva* in sandy areas of Puget Sound out to a depth of 40 m.

We are unaware of large-scale attempts to assess benthic macroalgae abundance or production in PSCB, and thus we rely on gross assumptions for the purpose of parameter development. We elected to allow Ecopath to estimate biomass based on mass balance, given our coarse estimates of P/B , EE , and grazer demands.

We derived P/B estimates from studies of production of species that occur in Puget Sound or are closely related to Puget Sound species. Research on *Ulva* in this region suggests its annual production rate is $200 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Thom 1984, Thom et al. 1984). Assuming that carbon is approximately 30% of *Ulva* dry biomass (Harvey unpubl. data), annual dry weight production (P) = $666.67 \text{ g m}^{-2} \text{ yr}^{-1}$. Early in the growing season, the dry biomass of green algae in nearshore Puget Sound sites is $14 \text{ g m}^{-2} \text{ yr}^{-1}$ (Thom et al. 1984, Thom 1989). These estimates yield a P/B ratio of 47.619 yr^{-1} . In contrast, published data for red and brown macroalgae suggest lower P/B ratios. Red and brown algae in the Black Sea range from 2 to 8 yr^{-1} (Khailov and Burlakova 1969), while species of *Laminaria* at temperate latitudes in the North Atlantic range from 3 to 5.2 yr^{-1} (Brady-Campbell et al. 1984, Beavis and Charlier 1987). The P/B of *Laminaria* in the Alaskan high arctic is much lower (0.8 to 1.7 yr^{-1} , Dunton and Schell 1986). We do not know the biomass ratios of *Ulva* to brown and red algae in Puget Sound; thus it is difficult to weight these disparate P/B ratios. In the interest of being conservative with our estimates, we set P/B at 15 yr^{-1} for the time being. We also assumed moderate grazer pressure on benthic macroalgae by setting their EE at 0.4.

Ecopath's initial estimate of benthic macroalgal biomass, given the estimates of P/B and EE and the pressure of grazers, is 3.182 mt km^{-2} . This is approximately fortyfold greater biomass density than overstory kelp (see Overstory Kelp subsection below), consistent with

surveys in PSCB that indicate much greater coverage by small brown algae than by bull kelp (Mumford 2007).

Benthic macroalgae are fed upon by sea urchins, other grazers, small crustaceans, herbivorous birds, migratory diving birds, and nearshore diving birds (Table 4). Trace amounts are eaten by various fish, possibly inadvertently. Many consumers feed on algal/plant material, a detrital pool to which benthic macroalgae is a major contributor.

Overstory Kelp

Overstory kelp is comprised of bull kelp, the only true overstory alga in the PSCB (Mumford 2007). It is a brown alga with a life history alternating between a microscopic, haploid gametophyte stage and an enormous, floating, diploid sporophyte stage. In a single growing season in Puget Sound, bull kelp sporophytes grow from microscopic to as much as 40 m in length from the holdfast to the tip of the blade (Mumford 2007). The length of a sporophyte is a function of the depth it inhabits, with the stalk growing until the gas-filled pneumatocyst and the trailing blade reach the water surface. After releasing spores in the fall, most sporophytes die off in the high wave energy of winter storms. The die-off produces detritus that is transported via wave dynamics to adjacent marine systems and may support scavengers and detritus-based food webs.

Recruitment of bull kelp sporophytes to an area is dependent on many features (Mumford 2007, Springer et al. 2007). A habitat must have appropriate light penetration, temperature, nutrient concentrations (particularly dissolved NO_3 , which is the preferred form of dissolved nitrogen), and wave energy. It must have hard substrate to which holdfasts can firmly attach. Bull kelp can be controlled by grazer pressure from benthic herbivorous invertebrates; however, if grazers are in low numbers, then perennial understory or midwater canopy-forming algae may proliferate and outcompete bull kelp for settlement habitat or light. Bull kelp can tolerate lower salinities than many kelps, but is sensitive to sedimentation (Mumford 2007).

Overstory kelps such as bull kelp provide important habitat for many other species (Mumford 2007). Epiphytic algae and invertebrates grow on them. Juvenile fishes, including rockfishes (*Sebastes* spp.), recruit to them (e.g., Bodkin 1986, Haldorson and Richards 1987). A variety of observational studies (summarized by Springer et al. 2007) suggest that adult fish densities of some species are positively correlated with bull kelp density. Calvert (2005) experimentally manipulated bull kelp abundance and found that its density was positively correlated with density of some benthic fishes, but negatively correlated with density of pelagic, schooling fishes. Finally, large bull kelp beds can dampen wave energy within the canopy and on the shoreward side of the canopy (Springer et al. 2007), which may affect species composition, shoreline disturbance and erosion, and other features in nearshore habitats.

Estimating standing stock biomass of overstory kelp is difficult, owing to the tremendous seasonal variability in individual size (Foreman 1984, Springer et al. 2007). We developed a biomass estimate for overstory kelp based on both areal surveys and measures of biomass density in bull kelp beds. Bailey et al. (1998) surveyed the proportion of shoreline and intertidal area covered by a number of habitat types including “kelp,” which we used as the proxy for bull kelp. They estimated that kelp coverage accounted for 0.2% of Central Puget Sound’s intertidal zone.

We assumed comparable coverage for the subtidal zone out to 10 m depth, which is approximately the lower range of depths at which most Puget Sound bull kelp attachment occurs.⁴

We then assumed a density of 1.5 sporophytes per m² in kelp beds, according to estimates from several studies (Thom 1978, Stober and Chew 1984, Shaffer and Parks 1994). Furthermore, we assumed an average individual mass of 20 g (dry weight), based on measures of Puget Sound bull kelp by Stober and Chew (1984), and a dry:wet ratio of 0.103, based on estimates by Foreman (1984). Thus 1 m² of kelp bed habitat would contain $1.5 \times 20 / 0.103 = 291.26$ g wet weight. If that biomass density of bull kelp occupies 0.2% of the 0–10 m depth contour, which accounts for 13.75% of the total area of PSCB, then overstory kelp biomass equals 0.08 mt km⁻². (Note: This implies that an average bull kelp sporophyte is a small plant that has not yet grown to its large, climax size; for example, in British Columbia waters, sporophytes with stipe lengths of 5.5–7.5 m typically weighed between 3,000 and 5,000 g [Foreman 1984]). The extraordinary growth capacity of an individual sporophyte is captured in its high *P/B* ratio, not its biomass estimate.

The *P/B* estimate for overstory kelp comes in part from Thom (1978), who estimated that bull kelp can produce 10 kg m⁻² of biomass in a growing season. Thus a plot with 0.291 kg m⁻² of bull kelp would have a *P/B* of 34.364 yr⁻¹. We increased this rate because of the work of Khailov and Burlakova (1969), who found that algal production estimates based on biomass changes alone were underestimates, due to release of dissolved organic matter (DOM) that increases the overall production estimate by an additional 23–39%. We elected to use an increase of 25%, yielding an adjusted *P/B* of 42.955 yr⁻¹. This may be a conservative estimate; Foreman (1984, his Figure 1) estimated that approximately one-half of total bull kelp production was lost to attrition or mortality.

In the mass-balancing step, Ecopath estimated an *EE* of 0.661 for overstory kelp, indicating moderately high grazing pressure, most likely on smaller sporophytes.

Overstory kelp is consumed by sea urchins and other grazers (Table 4). Its detrital fate is mixed: 75% of its dead material is assumed to ultimately become fragmentary organic matter that flows to the algal/plant material pool. The remaining 25% is the DOM loss described above; this flows to the general detritus pool.

Eelgrass

Eelgrass (*Zostera marina*) plays several vital roles in the Puget Sound ecosystem. It is a primary producer, a key source of fish and invertebrate habitat, and a source of detrital organic matter. It provides food for grazing invertebrates and many birds, and surface area on which many small epiphytic algae and bacteria grow. Its rhizomes and roots promote stabilization and influence water chemistry of underlying sediments, which promotes habitat quality for many sediment-dwelling species (e.g., Kendrick et al. 2005, Ferraro and Cole 2007, Mumford 2007). Eelgrass is an important substrate on which many fish species spawn, notably Pacific herring. The eelgrass functional group is primarily intended to represent the native intertidal and subtidal

⁴ T. Mumford, Washington Dept. Natural Resources, Olympia, WA. Pers. commun., 12 March 2009.

eelgrass, although an invasive species, Japanese eelgrass (*Z. japonica*), has become well established in the upper intertidal zone in many areas of Puget Sound. Related species of surfgrasses (*Phyllospadix* spp.) also occur in Puget Sound, but primarily in rocky areas with high wave energy, and those habitats are essentially absent in the Central Basin (e.g., Mumford 2007).

To estimate eelgrass biomass, we first assumed that it occupies 11.7% of the intertidal area of the Central Basin, which is based on an estimate that 11.7% of the coastline of the main basin of Puget Sound had eelgrass between 1975 and 1989 (Thom and Hallum 1990). The intertidal zone area is approximately 31.88 km² (WDF no date); 11.7% of this area = 3.73 km². To convert areal coverage to biomass, we first elected to only model aboveground biomass, which varies seasonally from approximately 50% (winter) to 80% (summer) of total eelgrass biomass; we assumed a constant value of 70% biomass to be aboveground. In a subtidal meadow in the San Juan Islands, Nelson and Waaland (1997) estimated total eelgrass biomass to average 256.3 grams dry weight (gdw) m⁻², or 179.4 gdw m⁻² of aboveground material. Similarly, Webber et al. (1987) found aboveground biomass densities of 50–230 gdw m⁻² in Padilla Bay (Whidbey Basin, Puget Sound). Both studies were of plots with 100% eelgrass coverage (i.e., saturated shoot density). If we multiply 179.4 gdw m⁻² by 3.73 km² and apply conversion multipliers of 8.05 (to convert from dry weight to wet weight, Keser et al. 2003) and 0.5 (assuming that 50% shoot density is more reasonable over the full range of eelgrass distribution), we get a total biomass estimate of 2,693.4 mt. After dividing by the total model domain area of 757.08 km², our eelgrass biomass estimate is 3.558 mt km⁻². This value represents a coarse estimate and should be confirmed via field study.

We derived eelgrass *P/B* estimates from Nelson and Waaland (1997). Annual production in the meadow they examined was 1,767 gdw m⁻² y⁻¹, a weighted value that accounts for variation ranging from 1.5 gdw m⁻² d⁻¹ (December–January) to 9.8 gdw m⁻² d⁻¹ (August–September). We divided the annual production rate by the mean January biomass density (72.2 gdw m⁻²) to get a *P/B* of 24.542 y⁻¹. This estimate may well be inaccurate: It is based on a 2-year study at one site, and the simplicity of our estimation method does not account for shoot recruitment that occurred after January or old shoot mortality (e.g., Olesen and Sand-Jensen 1994). Production rates of eelgrass also may vary from site to site: Ruesink et al. (2006) calculated a 40% coefficient of variation for production in Willapa Bay eelgrass meadows. Eelgrass *P/B* is clearly a parameter for which we should evaluate model sensitivity.

In the mass-balancing step, Ecopath estimated an *EE* of 0.156 for eelgrass, suggestive of low grazing pressure.

Eelgrass is grazed by herbivorous birds, other grazers, and small crustaceans (Table 4). Small amounts of eelgrass occur in some fish stomachs and in *Cancer* crabs. Senescent eelgrass contributes to the algal/plant material pool.

Zooplankton and Pelagic Invertebrates

Copepods

Copepods are among the most important grazers of phytoplankton, and thus are a principal means by which phytoplankton production is transferred into the planktonic food web.

They have relatively rapid turnover rates, often with several generations occurring per year, which helps maintain the flow of phytoplankton-derived production into the food web (Strickland 1983). Copepods are among the most important food sources to fishes. Many schooling fishes feed primarily on copepods throughout their lives (Penttila 2007). Additionally, copepods are a major prey resource for early pelagic stages of many fishes, including benthic fishes such as rockfish and flatfish (Emmett et al. 1991, Love et al. 2002).

Copepods are the largest component of the zooplankton standing stock throughout the year in Puget Sound (Strickland 1983). The copepod functional group in this model is made up primarily of calanoids. In biomass terms, the most important species is probably *Calanus pacificus*; the genera *Acartia*, *Pseudocalanus*, *Paracalanus*, and *Eucalanus* are also abundant (Strickland 1983, Dey et al. 1988). Most Puget Sound copepods experience peaks in biomass and reproductive effort just after phytoplankton blooms, notably in the spring. By contrast, all but the smallest species are relatively dormant in the less productive winter months, possibly entering diapause (Strickland 1983). This fact plays a role in the uncoupling hypothesis whereby the initial production in spring phytoplankton blooms is largely uneaten because copepods and other grazers are not present, allowing the production to sink to the benthic food web (Strickland 1983).

(Note: We excluded some abundant copepod species because they are mostly carnivorous. These include *Corycaeus anglicus* and *Epilabidocera longipedata* [Dey et al. 1988]. We will assume that they are in the macrozooplankton pool, described below.)

We found no extensive, survey-based copepod biomass estimates for PSCB in the literature, and thus allowed Ecopath to estimate copepod biomass through the mass-balancing procedure. To facilitate this, we assumed that copepod $EE = 0.8$, implying that 80% of copepod production is consumed by modeled predator groups in the initial state of this model.

Similarly, we are unaware of P/B or Q/B estimates for Puget Sound copepods. We derived our estimates from the EwE model of the California Current by Field (2004). Field's copepod group includes many of the same genera, although many of the species are cold-water copepods that are also common in Alaska waters. One species that is abundant in Puget Sound, *Calanus pacificus*, is referred to by Field as a warm-water species that is most common in California Current waters during the winter, when the warm, northerly flowing Davidson Current becomes dominant. It seems appropriate, then, to assume slightly greater Q/B ratios for our copepods than Field used (70 yr^{-1}), given the relative warmth of Puget Sound waters; we set copepod Q/B at 75 yr^{-1} . Assuming a P/Q of 0.2, we arrived at a P/B estimate of 15 yr^{-1} .

With these parameters in place, the mass-balancing routine of Ecopath yields an initial copepod biomass of $24.419 \text{ mt km}^{-2}$. This value is one-third lower than a historic copepod biomass estimate in Puget Sound waters. Damkaer (1964) examined copepod biomass in Dabob Bay (Hood Canal Basin) and found a biomass density of approximately 36 mt km^{-2} .

Based on the general description of Puget Sound copepods by Strickland (1983), we assumed that their diets were primarily composed of phytoplankton and supplemented by microzooplankton (Table 4). This is similar to the diet assumed by Field (2004) for northern California Current copepods. Copepods are eaten by most of the smaller pelagic fish species,

and also by walleye pollock (*Theragra chalcogramma*), juvenile rockfish, demersal fish, shrimp, squid, barnacles, euphausiids, small gelatinous zooplankton, jellyfish, and macrozooplankton. They are taken at trace levels by ratfish (*Hydrolagus colliei*), juvenile lingcod (*Ophiodon elongatus*), piscivorous flatfish, and small-mouthed flatfish.

Microzooplankton

The microzooplankton functional group consists of small planktonic invertebrates that feed primarily on small phytoplankton and respond rapidly to changes in phytoplankton production (Strickland 1983). The group is made up primarily of unicellular heterotrophic protozoans (ciliates, dinoflagellates, foraminiferans, and radiolarians), early pelagic larval stages of many benthic invertebrates, and a few species of rotifers. These small grazers collectively serve several vital roles in the pelagic ecosystem. They are a natural trophic link that connects phytoplankton production to higher consumers, including pelagic larvae of numerous invertebrates and fishes. In addition, their dissolved nitrogenous waste products may be taken up by phytoplankton in the upper layer of the water column. Such nutrient cycling further tightens the coupling between the microzooplankton and phytoplankton functional groups.

We are unaware of any quantitative sampling of microzooplankton biomass in PSCB, and it is likely that any such sampling would reveal intense variability due to spatial patchiness and the rapid temporal responsiveness of these organisms to changes in phytoplankton availability. We used the Ecopath mass-balancing routine to estimate microzooplankton biomass. We first assumed a high EE (0.8), which implies that 80% of microzooplankton production is consumed by other model groups in the initial model state.

We followed the lead of Field's (2004) EwE model of the California Current ecosystem and assumed a microzooplankton P/B ratio of 100 yr^{-1} , consistent with organisms capable of rapid increases in biomass and high mortality in the absence of resources. Our estimate is consistent with work by Landry and Calbet (2004), who observed that overall microzooplankton production typically is 28 to 55% of total primary production. Our microzooplankton P/B estimate is 44.2% of the phytoplankton P/B estimate of 226.3 yr^{-1} (see Phytoplankton subsection above).

Lacking data on Q/B ratios for these species, we instead estimated P/Q (the production to consumption ratio, the rough equivalent of food conversion efficiency). Our estimate of 0.35 was taken from Landry and Calbet (2004) and results in a remarkable Q/B of 285.714 yr^{-1} . Although a very high rate, this estimate is only slightly less than the 300 yr^{-1} estimated by Field (2004) for California Current microzooplankton.

The above parameter estimates coupled with the demands of predators result in a mass-balanced biomass estimate of 5.343 mt km^{-2} for microzooplankton.

This group's diet is dominated by phytoplankton (Table 4), with small contributions from bacteria and detritus. We arbitrarily assigned this initial diet based on descriptions of Puget Sound's pelagic food web (Strickland 1983, Strom et al. 2001). Microzooplankton in turn are eaten by macrozooplankton, small gelatinous zooplankton, euphausiids, copepods, tunicates, suspension feeders, infaunal bivalves, barnacles, and mussels.

Macrozooplankton

The macrozooplankton pool includes many diverse taxa, including chaetognaths, pelagic shrimp (e.g., families Sergestidae and Pasiphaeidae), hyperiid amphipods, the pelagic larval stages of benthic macroinvertebrates, and large predatory copepods. This is something of a catchall group, incorporating species that are not included in other, more taxonomically defined large zooplankton groupings (e.g., euphausiids, small gelatinous zooplankton, jellyfish). In making this grouping, we acknowledge the perceived importance of these species as both consumers and prey. This broad grouping also belies our general lack of information on these taxa in Puget Sound. Pooling such diverse taxa undoubtedly means that we will lose some information as we try to characterize a representative macrozooplankton. Thus the scenarios that are sensitive to changes in macrozooplankton should be evaluated cautiously.

To our knowledge, quantitative sampling of these species for estimating abundance has not been done in Puget Sound in any comprehensive manner. In fish stomach contents collected in multiple seasons, hyperiid amphipods and decapod larvae were highly abundant (Reum 2006, Reum unpubl. data). If fish are unbiased samplers of macrozooplankton, then hyperiids and decapod larvae are important representatives; however, this does not give us a biomass estimate. We therefore estimated biomass using the mass-balancing step of Ecopath, first assuming an *EE* of 0.8 (reflecting the importance of these species in predator diets).

Our estimates for macrozooplankton *P/B* and *Q/B* are poorly founded and represent an area of potential improvement through empirical study and monitoring. We reasoned that *P/B* rates for these organisms should be equal to or greater than rates for similar benthic taxa (e.g., small crustaceans, $P/B = 3.41 \text{ yr}^{-1}$) and older stages of related taxa (e.g., YOY *Cancer* crabs, $P/B = 2.50 \text{ yr}^{-1}$; shrimp, $P/B = 2.25 \text{ yr}^{-1}$), because we would assume that the mortality rates for younger, smaller, pelagic animals are higher. We set the macrozooplankton *P/B* at 7.00 yr^{-1} , following the estimate used by Beamish et al. (2001) for an Ecopath model of the nearby Strait of Georgia ecosystem. This value is somewhat greater than a value estimated for chaetognaths (5.6 yr^{-1} , Banse and Moser 1980). Based on our *P/B* estimate, we set *Q/B* at 35.00 yr^{-1} , in order to hold conversion efficiency (*P/Q*) at 20%. Given the input parameters and the consumptive demand of higher trophic levels, macrozooplankton biomass was estimated by Ecopath to be 6.234 mt km^{-2} , a value that should certainly be confirmed by empirical study.

We made generalizing assumptions about macrozooplankton diets. We assumed that phytoplankton and copepods each comprised approximately one-third of the diet, with substantial contributions from bacteria, microzooplankton, and euphausiids (Table 4). Lesser amounts were contributed by detritus, small gelatinous zooplankton, and jellyfish. Macrozooplankton are preyed upon by most of the fish groups in this model, as well as by gulls and jellyfish.

Euphausiids

Euphausiids represent still another critical trophic bridge between the primary producers and consumers on which they feed and the higher trophic levels that consume them in turn. Considerable research in Pacific Ocean ecosystems has demonstrated their importance in the marine food web structure and their value as indicators of ecosystem processes (e.g., Brodeur

and Percy 1992, Ainley et al. 1996, Keister et al. 2005). In the Puget Sound–Georgia Basin, euphausiids are comprised primarily of one species, Pacific krill (*Euphausia pacifica*) (Bollens et al. 1992, Romaine et al. 2002). They occupy deep midwater habitats (≈ 75 m) during the day and then move to surface waters at night to feed, mainly on larger chain diatoms, copepods, and microzooplankton (Strickland 1983, Ohman 1984).

To our knowledge, no euphausiid abundance surveys are conducted in Puget Sound. We used the Ecopath mass-balancing function to estimate euphausiid biomass. To facilitate estimation of biomass, we assumed an *EE* of 0.8, implying that most euphausiid production is consumed by other functional groups in the model.

Euphausiid *P/B* was based on research by Tanasichuk (1998), who studied productivity of Pacific krill in Barkley Sound, British Columbia, during the 1990s. He developed annual estimates of *P/B* for adult Pacific krill, accounting for production devoted to both growth and molting. The average over the 6 years was 10.683 yr^{-1} . This is nearly double the *P/B* ratios used for euphausiids in Ecopath models of several nearby systems (e.g., Beattie 2001, Ainsworth et al. 2002, Field 2004). However, Field (2004) did not include the molting component of production in his model, and there is no evidence that the other models did either. Molting was approximately 40–60% of total production in the Pacific krill adults studied by Tanasichuk (1998).

Absent actual estimates of consumption rates for euphausiids in PSCB, we derived a *P/Q* estimate from work by Ikeda and Iguchi (1999), who studied Pacific krill in Toyama Bay in the southern Sea of Japan. They calculated total production (including somatic growth and molting) and daily consumption rates; their annual estimate was $P/Q = 0.242$. Our *P/B* estimate divided by 0.242 yields a *Q/B* of 44.145 yr^{-1} ; because our *P/B* estimate was high relative to EwE models in nearby models, our *Q/B* estimate is also greater.

Based on these parameter estimates and the demands of euphausiid predators, Ecopath estimated the initial euphausiid biomass to be $11.152 \text{ mt km}^{-2}$.

Euphausiid diets (Table 4) were inferred based on the work of Ohman (1984), who found that Puget Sound Pacific krill grew more effectively when feeding on diatoms than on copepods. We allocated most of their diet to phytoplankton, with lesser amounts of copepods, detritus, microzooplankton, and bacteria. Euphausiids are eaten by resident diving birds, most pelagic and demersal fishes, shrimp, squid, small gelatinous zooplankton, jellyfish, and macrozooplankton.

Small Gelatinous Zooplankton

The small gelatinous zooplankton group is a taxonomically diverse assemblage that includes small hydromedusae (phylum Cnidaria); comb jellies (phylum Ctenophora); urochordates (phylum Chordata), including larvaceans (class Appendicularia) and pelagic salps (class Thaliacea); and thecosomes and gymnosomes (aka pteropods, phylum Mollusca). These animals are primarily filter feeders. Most are soft and gelatinous, but some pteropods have more solid bodies, possibly even shells, and surround themselves in a mucous net that helps them to trap food particles. Small gelatinous zooplankton can quickly form patches of high biomass

when conditions are favorable (Strickland 1983, Field 2004). They are capable of consuming very large amounts of phytoplankton, microzooplankton, marine snow, and other suspended organic materials (Madin et al. 2006). Given their low energy content and their rarity in stomachs of vertebrates, some have considered them a dead end of energy flow in marine food webs (e.g., Greve and Parsons 1977). However, that perception has stemmed in part from the fact that gelatinous organisms are difficult to detect in fish stomach contents, and there is growing recognition of the importance of these organisms as prey for generalist consumers (Arai 1988, Purcell and Arai 2001).

Members of this group may also be important indicators of global climate change. Thecosome pteropods are a focal group in studies of ocean acidification because of the potential for lowering ocean pH to hinder development of their aragonite shells (Orr et al. 2005). On the other hand, pelagic salps may serve as a major carbon sink in areas where they swarm to immense numbers, consume large quantities of phytoplankton, and transport that carbon to the ocean floor via rapidly sinking fecal pellets (Madin et al. 2006).

We are unaware of biomass surveys for small gelatinous zooplankton in Puget Sound, nor do we expect any to be forthcoming in the near future; these organisms are difficult to sample due to their fragility. Thus we input P/B , Q/B , and EE and allowed the Ecopath mass-balancing routine to estimate their initial biomass.

Small gelatinous zooplankton are short-lived and grow rapidly, with life spans likely on the scale of weeks to months (e.g., Mills 1993). Growth rates can be quite rapid, particularly during seasonal bloom events, although those growth rates may not reflect growth or production trends at a full year scale (Heron and Benham 1985). Following the example of Ruzicka et al. (2007), who developed Ecopath models for the Oregon upwelling zone and drew particular attention to the role of gelatinous zooplankton, we assumed a P/B ratio of 9.0 yr^{-1} for this group.

For consumption estimates, we used Q/B and assimilation efficiency estimates from Madin and Purcell (1992). They suggested that salps have high Q/B ratios ($\approx 30 \text{ yr}^{-1}$). They also found that salps lose approximately 40% of ingested food as fecal material, which is double the ratio of unassimilated:assimilated food assumed for most consumers.

Given the above parameters, predation pressure from other functional groups, and our assumed EE of 0.8 (which implies high predation pressure, similar to Field [2004]), Ecopath calculated an initial biomass of 6.388 mt km^{-2} for small gelatinous zooplankton.

We assigned small gelatinous zooplankton an initial diet dominated by a mix of phytoplankton, copepods, detritus, bacteria, and microzooplankton (Table 4). Minor prey include euphausiids, functional group cannibalism, and a trace of newly pelagic medusae of the jellyfish group. This reflects both the herbivorous tendencies of salps and also the omnivorous or carnivorous tendencies of hydromedusae, ctenophores, larvaceans, and pteropods. Besides cannibalism, small gelatinous zooplankton are preyed upon by jellyfish, macrozooplankton, demersal fish, forage fish, small-mouthed flatfish, juvenile and subadult wild salmon, and juvenile pink salmon.

Jellyfish

The jellyfish group contains large members of the cnidarian class Scyphozoa. Generally, species in this group produce medusae with bells tens of centimeters in diameter and trails of prominent, nematocyst-filled tentacles (Wrobel and Mills 1998). In recent years, scyphozoans have received worldwide attention due to an apparent increase in the frequency of major blooms, which have had negative impacts on coastal fisheries, aquaculture, industrial facilities, recreational activities, tourism, and public perception of ecosystem health (Mills 2001, Purcell and Arai 2001, Purcell et al. 2007). They may compete with or prey upon pelagic fish species (Purcell and Arai 2001). Human alterations of food web structure, habitat, water chemistry, and regional climate patterns are widely held to be responsible for large jellyfish blooms in coastal waters (Purcell et al. 2007). Some human impacts, such as coastal zone hypoxia, may exacerbate resource competition between scyphozoans and other species (Rutherford and Thuesen 2005).

Jellyfish can comprise a major, or even dominant, component of pelagic community biomass in Puget Sound during summer months (Rice 2007). Their abundance in Puget Sound varies by location and year, is strongly influenced by latitude and Julian day, and was inversely related to biomass and diversity of the pelagic fish community in 2003 (Rice 2007). Prominent jellyfish species in Puget Sound include the crystal jelly (*Aequorea victoria*), moon jelly (*Aurelia labiata*), lion's mane jelly (*Cyanea capillata*), and fried egg jelly (*Phacellophora camtschatica*). These species appear to be more tolerant to hypoxia than many other co-occurring scyphozoans (Rutherford and Thuesen 2005). Zooplankton, particularly copepods, are major prey for these species (Wrobel and Mills 1998, Purcell 2009). Some species have symbiotic relationships with macrozooplankton (e.g., pelagic amphipods, Wrobel and Mills 1998).

The seasonal aspect of jellyfish abundance in Puget Sound (Rice 2007) and the inherent difficulty of quantitatively sampling these fragile animals makes direct biomass assessment problematic. We thus estimated jellyfish biomass by the Ecopath mass-balancing routine. We assumed an *EE* of 0.5, suggesting a moderate degree of predation, most of which is presumably focused on small medusae that have recently detached from the sessile polyp stage. We essentially took the other main parameters (*P/B* and *Q/B*) from prior Ecopath models of northeast Pacific waters (Pauly and Christensen 1996, Aydin et al. 2003, Field 2004), with slight modification. We used their *P/B* value of 3 yr⁻¹ (which spreads their high summer production evenly over the course of a full year), but increased their *Q/B* estimate from 10 yr⁻¹ to 11.5 yr⁻¹. The increased *Q/B* stems from an assumption that Puget Sound waters are 2° warmer and a consumption *Q*₁₀ of about 2.0 (Appendix C), which is approximately that observed for digestion times of scyphozoans (Purcell 2009).

Given these parameters and the demands of predators, Ecopath estimated a jellyfish biomass of 8.483 mt km⁻². That estimate exceeds the summer biomass estimate for large jellyfish in coastal waters off Oregon (3.269 mt km⁻², Ruzicka et al. 2007). It is lower than the total estimated biomass of pelagic fishes (Pacific herring, forage fish, and juvenile Pacific salmon, Table 3), which contrasts with the findings of Rice (2007). At an annual time scale, however, this may be acceptable, given that jellyfish biomass is likely close to 0 mt km⁻² in PSCB for many months each year. Empirical biomass estimates would certainly help the model to represent this functional group more reasonably.

We adapted our jellyfish diet estimates from the work of Ruzicka et al. (2007). Jellyfish prey primarily on copepods, small gelatinous zooplankton, and eggs and larvae of euphausiids (Table 4). Macrozooplankton comprised a small portion of their diet. We also assumed a small amount of intraguild cannibalism, as we have witnessed fried egg jelly preying on small lion's mane jelly in Puget Sound waters (G. Williams, NWFSC, field observation). We currently assume no predation by jellyfish on small fishes in Puget Sound.

Squid

Squid are truly nektonic (free-swimming), unlike most of the other more planktonic organisms presented thus far. They are another example of a key link between lower trophic levels and vertebrate predators in marine food webs, and they are also valued by fisheries. Smaller species such as the opalescent, aka market, squid (*Loligo opalescens*) are indicators of oceanographic changes, by virtue of their relatively short life spans and their strong growth responses to environmental conditions (Jackson and Domeier 2003). Market squid, the major squid species in Puget Sound, are generally dispersed and pelagic, except during spawning periods when they aggregate in nearshore, soft-bottomed habitats. Adults die after spawning (Morris et al. 1980, Jackson 1998). Their maximum life span is believed to be about 2 years, but in some areas they can complete their life cycle in less than a year (Jackson 1998, Jackson and Domeier 2003). Other squid species are also present, most often the small North Pacific bobtail squid (*Rossia pacifica*).

Small squid such as market squid are very difficult to sample for the purpose of stock size estimation (Jackson 1998) and, to our knowledge, no attempts have been made to estimate squid biomass in Puget Sound. We chose to allow the Ecopath mass-balancing step to calculate squid biomass. Similarly, data on squid mortality and consumption were not available for this area, so we incorporated the P/B and Q/B values (3.0 yr^{-1} and 15.0 yr^{-1} , respectively) for small squid in the Eastern Subarctic Gyre Ecopath model of the north Pacific Ocean (Aydin et al. 2003).

We assumed that intense predation would lead to a high proportion of mortality directly related to other model components, and hence set the squid EE at 0.8. Given these parameters and the diet and fishery configuration of the model, Ecopath estimated squid biomass to be 0.902 mt km^{-2} in PSCB.

Squid diet estimates derive from work by Karpov and Cailliet (1979) on market squid near Monterey Bay. We especially followed their findings on stomach contents from squid captured in less than 40 fathoms (73 m) of water, except for samples collected on the spawning grounds. Karpov and Cailliet (1979) reported indices of relative dietary importance based on frequency of occurrence and number of prey items eaten, rather than on prey mass or volume, so we were forced to make some assumptions about relative mass of prey eaten. We assumed the majority of squid diet to be euphausiids, along with juvenile Pacific herring and minor contributions from copepods, macrozooplankton, and forage fish (Table 4). Squid are also cannibalistic (Karpov and Cailliet 1979). Other squid predators include harbor seals (*Phoca vitulina*), sea lions, resident and migratory diving birds, lingcod, piscivorous flatfish, small-mouthed flatfish, and demersal fish. Fisheries take a very small amount of squid (Table 5, also Appendix C).

Benthic Invertebrates

Sea Stars

Sea stars are a diverse group of predatory and scavenging echinoderms (class Asteroidea) found at all depths in Puget Sound. Examples include short-spined pinkstar (*Pisaster brevispinus*), flat mud star (*Luidia foliolata*), six-rayed star (*Leptasterias hexactis*), rose star (*Crossaster papposus*), sunflower sea star (*Pycnopodia helianthoides*), and morning sun star (*Solaster dawsoni*). Sea stars feed on a variety of organisms, ranging from bryozoans to other sea stars (Morris et al. 1980, Lambert 1981). Many invertebrates have developed escape responses elicited by the touch or chemical stimulus of an attacking sea star. These are predator-specific: benthic invertebrates may respond strongly to some sea stars while ignoring others (Mauzey et al. 1968). At patch scales, sea stars are known to be important consumers that can shape community composition through top-down control (e.g., Paine et al. 1985).

We based sea star biomass estimates on data from trawl surveys of northern Puget Sound and southern Strait of Georgia, as described by Palsson et al. (2003). Trawls were conducted using a depth- and region-stratified design, and ranged from approximately 10 m to 220 m depths. The width of the trawl opening was between 10.8 m and 13.7 m, and the mesh size ranged from 10 cm (main body) to 3.2 cm (codend liner). Palsson et al. (2003) reported catching 14 different species of sea star, most of which were predatory. They reported bathymetrically scaled biomass estimates for four study regions. The average biomass density (weighted by the total areas of their study regions) was 0.346 mt km⁻², which we are going to assume is also consistent for PSCB. This conclusion has several caveats. First and probably most importantly, it implies that there is no basin effect on biomass density of sea stars in the Salish Sea, which is tenuous (e.g., Palsson et al. [2003] found rather large differences between their four sampling regions). Second, it implies that the trawl gear of Palsson et al. (2003) was an effective way to representatively sample sea star biomass. Third, it implies that the biomass density of sea stars in the intertidal and subtidal zones (i.e., shallower than the bathymetric contours sampled by Palsson et al. [2003]) is similar to the biomass density in deeper waters. These assumptions will require empirical monitoring in PSCB to validate.

For sea star P/B , we used the Robertson (1979) method to estimate P/B based on longevity (Appendix C). Longevity data are sparse for the species common to Puget Sound, but studies suggest that both purple ochre sea star (*Pisaster ochraceus*) and rose star life spans exceed 20 years in natural conditions (Morris et al. 1980, Carlson and Pfister 1999). If we use 20 years as our representative longevity, the Robertson equation yields a P/B of 0.519 yr⁻¹.

We estimated sea star Q/B based on the assumption that their conversion efficiency (P/Q) was equal to 0.2; this yields a Q/B ratio of 2.595 yr⁻¹. This Q/B estimate may be too low, given the seemingly voracious nature of many sea stars (notably sunflower sea star) coupled with a presumed long life span, factors that would imply a higher Q/B ratio. On the other hand, Mauzey et al. (1968) observed some extremely long handling times by sea stars that were attacking prey. Attacks sometimes lasted hundreds of hours, and often did not result in a predation event if the target was too large. Mauzey et al. (1968) also observed extended periods of starvation by sea stars when preferred prey were not available.

The Ecopath mass-balancing step estimated the *EE* of sea stars to be 0.125, reflecting a very low level of predation pressure that comes from intraguild cannibalism.

Sea star diets are very diverse. Some species are specialists while diets of others vary by habitat, season, and prey community structure (Mauzey et al. 1968, Lambert 1981). Important prey groups across sea star species were bivalves, snails, barnacles, sea pens (*Ptilosarcus gurneyi*), chitons, sea urchins, small crabs, sponges, bryozoans, and carrion; some common species also specialize on everything from algae to other sea stars. We attempted to represent this dietary breadth by making the sea stars a very generalist group (Table 4). Bivalve groups (infaunal bivalves, mussels, and a small amount of geoducks) collectively made up more than 40% of the initial sea star diet. The remainder of the diet included other grazers, deposit feeders, suspension feeders, barnacles, detritus, sea urchins, other sea stars, benthic microalgae, small crustaceans, large sea cucumbers, and predatory gastropods. A trace of predation on tunicates was also included (Mauzey et al. 1968).

Large Sea Cucumbers

Although there are many species of sea cucumber in Puget Sound (Kozloff 1983), this functional group has only one species, the California sea cucumber (*Parastichopus californicus*). Other holothurians, which are considerably smaller, are pooled into the deposit feeders, described below. The California sea cucumber is distinguished by its size, reaching a length (>40 cm) more than twice that of the next largest sea cucumber (Kozloff 1983). It is also the only sea cucumber in Puget Sound that is commercially harvested. California sea cucumbers are easily recognized by their ruddy, reddish-brown skin and many conical papillae. The California sea cucumber is found from intertidal waters down to 90 m (Morris et al. 1980). It inhabits both soft and hard substrates. Research in other systems has noted higher densities on substrates such as boulders, gravel, shell debris, and sand (Woodby et al. 2000).

As there are no survey data for California sea cucumber biomass or abundance in PSCB, we used the Ecopath mass-balancing step to estimate biomass for large sea cucumbers. We assumed an *EE* of 0.8, implying that predation (particularly from sea stars such as sunflower sea star and morning sea star, Lambert 1981, Cameron and Fankboner 1989) and fishing pressure (Table 5) accounted for a substantial removal of California sea cucumber annual production.

We inferred large sea cucumber *P/B* using the Robertson (1979) estimation method, where *P/B* is a function of longevity (Appendix C). According to Bruckner (2004),⁵ the life span for California sea cucumber is 8–12 years; the middle of that range (10 years) yields a *P/B* of 0.86 yr⁻¹ in the Robertson method.

Large sea cucumber *Q/B* was estimated using data from Yang et al. (2005), who measured daily consumption rates in the Japanese sea cucumber (*Apostichopus japonicus*), a relatively large sea cucumber from the western Pacific Ocean. When the daily consumption rates (in kJ d⁻¹) of small, medium, and large Japanese sea cucumbers at temperatures of 10°C and

⁵ Bruckner (2004) stated that these data appeared in J. L. Cameron and P.V. Fankboner (1989, *Journal of Experimental Marine Biology and Ecology* 127:43–67), but we could not find these data in the Cameron and Fankboner paper; Cameron and Fankboner have published other papers and documents on this sea cucumber species, however, and it is possible that Bruckner (2004) simply misattributed the data.

15°C were converted to mass-specific annual rates of total mass ingested, they ranged between approximately 12.6 yr⁻¹ and 32.7 yr⁻¹. An approximate middle point would be 22.6 yr⁻¹. We divided this rate in half (11.3 yr⁻¹) because the California sea cucumber does not feed for most of the fall, winter, and early spring months (Lambert 1997).

Given these parameters and demands from predators, Ecopath estimated the large sea cucumber biomass to be 0.0471 mt km⁻². This estimate is slightly greater than estimates of California sea cucumber biomass derived from surveys in the geoduck management tracts in Central Puget Sound. Those surveys were conducted by WDFW from 2005 to 2009 (Sizemore et al. unpubl. data).

The California sea cucumber is a deposit-feeding detritivore that also ingests small infaunal organisms (Morris et al. 1980). We assumed a diet consisting mostly of detritus, but with measurable contributions from bacteria, benthic microalgae, suspension feeders, and other grazers (Table 4). Based on a review of predation on holothurians (Francour 1997), we assume that large sea cucumbers are preyed upon by sea stars, and at a trace level by demersal fish. Young California sea cucumbers are preyed upon occasionally by greenlings (family Hexagrammidae).

Sea Urchins

This group pools two sea urchins of the genus *Strongylocentrotus*: the green sea urchin (*S. droebachiensis*) and the red sea urchin (*S. franciscanus*). The green sea urchin far outnumbers the much larger red sea urchin in PSCB waters.⁶ The two species have distinct feeding preferences; green sea urchins are often found climbing and feeding on live algae, whereas red sea urchins typically feed on detached algal detritus or crustose coralline algae. The nutritional quality of the algal species on which they feed directly influences rates of growth, maturation, and gonadal production (Vadas 1977). Inclusion of this functional group is certainly important, as it is capable of exerting strong grazing pressure on kelp species, and thus can affect habitat availability for a number of species. The role of sea urchins in regulating kelp forest biomass and structuring nearshore communities on the west coast of North America is well documented (Estes and Duggins 1995, Tegner 2001).

Sea urchin biomass has not been surveyed in PSCB to our knowledge, and we used the Ecopath mass-balance procedure to estimate biomass for this group. We first assumed an *EE* of 0.5, which assumes a moderate degree of production loss to predation; there are also losses of sea urchins to fishery removals, although these are small (Table 5).

To estimate *P/B*, we used the Robertson (1979) relationship of *P/B* and life span (Appendix C). The green sea urchin, the more abundant species, is the shorter-lived of the two. We found no estimates of longevity for green sea urchins in Puget Sound, but in fjords around Greenland, where growth should be relatively slow and life span relatively long, maximum observed ages of green sea urchins ranged from 20 to 45 years (Blicher et al. 2007). We will assume that the maximum age of green sea urchins in PSCB is 20 years. By contrast, red sea urchins may live up to 100 years (Ebert and Southon 2003). These two life spans produce *P/B*

⁶ B. Sizemore, WDFW, Olympia, WA. Pers. commun., 12 March 2009.

estimates of 0.519 yr^{-1} and 0.161 yr^{-1} , respectively, when applied to the Robertson equation. Because the green sea urchin is much more abundant, we assumed a P/B of 0.5 yr^{-1} .

We based our Q/B estimate on laboratory-based daily consumption rates from red sea urchins feeding on eelgrass material at $9\text{--}10^\circ\text{C}$ (McBride et al. 2004). They estimated consumption rates of approximately 1 g (dry weight) per day in both spring and fall. After accounting for variable wet:dry weight ratios of red sea urchin and the sizes of the individuals in the spring and fall trials (McBride et al. 2004), then converting all units into wet weights and annual time scales, we concluded that Q/B was approximately 10.88 yr^{-1} .

The Ecopath mass-balance routine calculated that sea urchin biomass = 0.453 mt km^{-2} , based on the above parameters and the demands of predators.

We made coarse estimates of sea urchin diets (Table 4), assuming that the green sea urchin, a live algae feeder, is more abundant than the red sea urchin, which feeds on drifting algal detritus and microalgae. Benthic macroalgae were the dominant food source, followed by benthic microalgae and lesser amounts of overstory kelp and algal/plant material. Sea urchins are preyed upon by sea stars and predatory gastropods. As mentioned, a small diver-based fishery exists.

Other Grazers

This functional group primarily contains small gastropods (snails, limpets) and chitons (the large gumboot chiton [*Cryptochiton stelleri*] as well as smaller species like black katy [*Katharina tunicata*], *Tonicella lineata*, and *Mopalia* spp.). The primary food sources of these species are leafy algae, coralline algae, benthic or epiphytic diatoms, eelgrass, and detritus. This group is quite diverse along the west coast, particularly the snails (Morris et al. 1980).

We lack information on biomass density of this group, and thus chose to initialize biomass using the Ecopath mass-balancing routine. We begin with an assumption that $EE = 0.8$, which implies that most annual production is lost to predation by other functional groups in the model.

P/B estimates were generated using the Robertson (1979) method, where P/B is a function of maximum life span (Appendix C). Longevity data for several representative or related species were culled from a number of sources, and ranged from 3 years (the chiton black katy and *Homalopoma sangareense*, a Russian congener of the common snail *H. luridum*) to more than 20 years (the gumboot chiton, the keyhole limpet [*Diodora aspera*], the black turban snail [*Tegula funebris*], and the exotic snail [*Ilyanasa obsoleta*]). We opted to apply an average life span of 12 years to this functional group; using the Robertson (1979) relationship, this produces a P/B estimate of 0.753 yr^{-1} . This estimate is within the range of empirical observations from at least one other marine system: Taylor (1998) found that P/B values for grazing gastropods in New Zealand ranged from 0.262 to 1.375 yr^{-1} .

The P/B estimate also formed the basis for our Q/B estimate, because we opted to estimate P/Q rather than Q/B . A P/Q of approximately 0.1 is near the low end of the range of typical consumers in Ecopath (Christensen et al. 2005), which seems appropriate for consumers with a relatively low-quality diet of benthic algae and detritus. In a recent study of the slipper

limpet (*Crepidula fornicata*), Arbach Leloup et al. (2008) determined dry weight values of consumption and production rates; the P/Q ratio from their measurements was 0.067. From these two sources, we assumed an intermediate P/Q ratio of 0.085; these estimates seem reasonable for relatively long-lived, slow-growing grazers. Our P/B estimate divided by 0.085 yields a Q/B of 8.859 yr^{-1} .

With the parameters outlined above and the estimated loss of production to predation, Ecopath estimated the initial biomass of other grazers to be $11.431 \text{ mt km}^{-2}$. This is a large biomass estimate, and may be an overestimate stemming from our assumption about P/B .

Diets for other grazers (Table 4) come from anecdotal information about their feeding habits, as described by Morris et al. (1980) and Kozloff (1983). We assume that nearly half of their diet is benthic microalgae, with substantial contributions from detritus, bacteria, algal/plant material, and benthic macroalgae. Lesser dietary items were eelgrass and overstory kelp. We also assigned a small portion of the diet to suspension feeders, as there is evidence that some grazers, such as snails of the genus *Calliostoma* and chitons of the genus *Mopalia*, occasionally feed on hydroids and bryozoans (Morris et al. 1980, Kozloff 1983). In turn, other grazers are preyed upon by predatory gastropods, sea stars, *Cancer* crabs, octopuses, shrimp, large sea cucumbers, surfperches, demersal fish, both flatfish groups, ratfish, skates, herbivorous birds, nearshore diving birds, migratory diving birds, and gulls (Table 4).

Predatory Gastropods

The predatory gastropod group is comprised of predatory snails and nudibranchs. Noteworthy predatory snails include the moon snail (*Polinices lewisi*), the hairy triton (*Fusitriton oregonensis*), and the leafy hornmouth (*Ceratostoma foliatum*), as well as exotic species like the Japanese oyster drill (*Ocenebrellus inornatus*) and the eastern oyster drill (*Urosalpinx cinerea*). Predatory snails typically feed on bivalves, barnacles, ascidians, sponges, gastropods, and dead animal matter (Morris et al. 1980, Kozloff 1983). Nudibranchs, elaborately colored and ornate sea slugs, feed to a large extent on sessile consumers such as bryozoans, sponges, hydroids, and sea anemones, although some feed on mobile invertebrates including other nudibranchs (Morris et al. 1980, Kozloff 1983). Predatory gastropods are found in many habitats, including intertidal zones, rocky reefs, oyster beds, mud flats, kelp beds, docks and piers, or sand flats (Kozloff 1983).

There is little background information for parameter development of this functional group. We used the Ecopath mass-balancing routine to estimate initial biomass, as we are unaware of comprehensive surveys of predatory gastropod biomass in Puget Sound. We began with the assumption that $EE = 0.7$; we are thereby assuming that predation by functional groups within the model accounts for a moderately high amount of annual production. Predation on nudibranchs is somewhat constrained by the fact that they are toxic or foul tasting to many consumers (Morris et al. 1980).

Our P/B estimate was derived using the Robertson (1979) relationship between P/B and longevity among benthic invertebrates (Appendix C). This estimate required some assumptions, though: the age range of this group is broad, from the majority of nudibranchs at one extreme (typically ≈ 1 year) to leafy hornmouth at the other (16 years). Other known ages for

representative species include moon snails (“several years”), *Urosalpinx* (5–8 years), and the intertidal predatory dire whelk (*Lirabuccinum dira*) (15 years) (all ages from Morris et al. 1980). We assigned a median longevity of 8 years, which produces a P/B of 1.01 yr^{-1} . This assumption deemphasizes the relative importance of the short-lived nudibranchs on the overall parameter values of this group. To estimate Q/B , we assumed a P/Q ratio of 0.15, which seemed appropriate for small, slow-growing, moderately long-lived carnivores. Given our P/B estimate, the P/Q ratio yields a Q/B of 6.733 yr^{-1} . The mass-balancing routine of Ecopath yielded a biomass estimate of 0.979 mt km^{-2} .

The diet of predatory gastropods is diverse, owing to the range of sizes and substrate types characteristic of the representative species (e.g., Kozloff 1983). Based on anecdotal information from a number of sources, particularly Morris et al. (1980) and Kozloff (1983), we assumed that the major prey groups were infaunal bivalves, suspension feeders, detritus, and other grazers (Table 4). Other prey included barnacles, deposit feeders, mussels, sea urchins, and tunicates. A small amount of their diet is functional group cannibalism, mainly to account for nudibranch predation on other nudibranchs.

Assigning predatory impact on this group is difficult. Studies on feeding habits often report “gastropods” without necessarily specifying the type of gastropod that was fed upon, and predation on predatory gastropods could be misappropriated to the other grazers group (above), or vice versa. We consider our assignments to be preliminary. Functional groups that feed on predatory gastropods include sea stars, *Cancer* crabs, octopuses, surfperches, demersal fish, both groups of flatfish, adult lingcod, ratfish, nearshore diving birds, and gulls (Table 4). As mentioned previously, there is a small amount of functional group cannibalism.

Octopuses

There are two common species of octopus in Puget Sound: the red octopus (*Octopus rubescens*) and the Pacific giant octopus (*Enteroctopus dofleini*). The latter, as its name suggests, is considerably larger than the former. The Pacific giant octopus reportedly reaches a maximum of approximately 270 kg in mass (Morris et al. 1980), compared to 0.4 kg for the red octopus (Anderson et al. 1999). Both species are generalist predators of invertebrates and fishes (Morris et al. 1980, Anderson et al. 1999), and are in turn fed upon by large fishes and marine mammals. Although the vast difference in size implies that these two species are quite distinct in terms of their functional role in the Puget Sound ecosystem, we pool them into a single group for the sake of simplicity and under the assumption that they are more similar to one another than either is to other, more taxonomically distant species. Furthermore, biological data on these species are scant, and we have elected to compartmentalize that uncertainty into a single box.

We opted to use the Ecopath mass-balancing step to solve for octopus biomass. There are surveys of octopus abundance in Puget Sound, particularly a volunteer-based annual Pacific giant octopus census coordinated by the Seattle Aquarium, but such data cannot be effectively translated into a basin-scale biomass estimate. Because octopuses spend much of their time in dens, they are not particularly vulnerable to gears that might otherwise allow some estimate of biomass per unit area sampled.

Direct empirical measures of octopus P/B , such as mortality data, were not available in the literature for either species. Two theoretical estimation methods, based either on age of maturation (Rikhter and Efanov 1976) or life span (Hoenig 1983), provide natural mortality estimates ranging from 0.53 to 0.86 yr^{-1} for Pacific giant octopus (Connors and Jorgensen 2008). In all likelihood, the P/B for red octopus would be even greater because the red octopus has a life span of 2–3 years (Dorsey 1976) compared to 5–7 years for the Pacific giant octopus (Morris et al. 1980). For now, pending further information, we will assume a P/B of 0.86 yr^{-1} for octopus, which is the upper estimate for the Pacific giant octopus but is probably conservative for the red octopus.

Consumption rate data for the red octopus and Pacific giant octopus were also unavailable. We estimated Q/B using a bioenergetics model for the common octopus (*O. vulgaris*) in the Mediterranean Sea (Aguado Giménez and García García 2002). According to their model, a 100 g common octopus feeding on crab prey at the optimal growth temperature (17.5°C) has a Q/B of approximately 2.75 y^{-1} . We assumed a Q/B of 2.5 y^{-1} for octopus in PSCB, owing to lower temperatures in Puget Sound and larger body sizes of typical Puget Sound octopuses; both factors should lower mass-specific bioenergetic rates. We do not know if the bioenergetics model of Aguado Giménez and García García (2002) fairly represents either the temperature-specific or the mass-specific bioenergetics of the two Puget Sound species. However, the estimates of P/B (0.86 y^{-1}) and Q/B (2.5 y^{-1}) result in a P/Q ratio of 0.344, which is at the upper end of the range of conversion efficiencies observed by Aguado Giménez and García García (2002).

We assumed that octopus $EE = 0.9$, implying that a considerable amount of octopus production is consumed by predators in the model. A small amount of octopus is also landed in PSCB fisheries (Table 5). Given our general feeling that octopuses are solitary animals with populations limited by available den habitat, we are thus assuming that their total numbers are not high enough to vastly outpace the demands of higher trophic levels. The mass-balancing routine of Ecopath estimated the initial octopus biomass to be 1.158 mt km^{-2} .

Octopus diets have been characterized to different degrees for the two species. Anderson et al. (1999) examined the contents of middens around glass bottles occupied by red octopuses in Puget Sound. Most prey were small gastropods and barnacles. Red octopuses that occupied bottles were probably juveniles, and may have been at an early stage of their dietary ontogeny (Anderson et al. 1999). Other diet information is descriptive in nature. Morris et al. (1980), for example, describe both species as predators of shrimp, crabs, bivalves, gastropods, and fishes, with a possible preference for crabs. The Pacific giant octopus is clearly capable of feeding on larger prey (e.g., abalone, moon snails, large crabs, rockfish) than the red octopus. Given the largely qualitative nature of these data, we were forced to arbitrarily estimate octopus diets (Table 4). Major prey groups were infaunal bivalves, other grazers, *Cancer* crabs, and small crustaceans; lesser groups were shrimp, predatory gastropods, mussels, and demersal fish.

Octopuses are eaten by spiny dogfish (*Squalus acanthias*), lingcod, and harbor seals (Table 4).

Cancer Crabs⁷

The *Cancer* crab group is significant owing to its abundance, its role in the system as a major large-bodied consumer and scavenger throughout the benthic zone, its provision of prey to a wide range of other consumers, and the substantial fisheries that it supports (Pauley et al. 1986). The focal species in this functional group is the Dungeness crab (*C. magister*), an abundant species that is highly prized for its flavor and fishery value. Several other *Cancer* species inhabit Puget Sound, including the red rock crab (*C. productus*), the graceful crab (*C. gracilis*), and the pygmy rock crab (*C. oregonensis*). These species are not valued as highly as Dungeness crab because of their smaller size, their lower abundance, or (as is the case with red rock crab) their relatively heavy shell (Kozloff 1983).

This functional group has two life history stages, which are dynamically linked in EwE software by a stage-based reproduction function (Appendix D). We chose to divide *Cancer* crabs into those with carapace width (cw) less than 30 mm (young-of-the-year crabs, aka, YOY *Cancer* crabs) and with cw more than 30 mm (age 1+ *Cancer* crabs). YOY *Cancer* crabs settle from the plankton in the summer and feed on benthos in nearshore soft sediments, around beds of eelgrass (*Zostera* spp.), or on fields of bivalve shell hash. They are preyed upon by seabirds, fishes, and macroinvertebrates. Once cw is greater than 30 mm (typically in the spring following settlement, Fisher and Velasquez 2008), age 1+ *Cancer* crabs move out of this habitat into deeper waters, and may change distributions seasonally in relation to spawning timing or feeding and growing conditions.

Mature individuals (generally with cw greater than 100 mm) produce larvae, and males with cw greater than 159 mm (typically age 4+) are fished intensively with several commercial and recreational gears. In fact, due to their complex life history, it may be more appropriate to separate them into even more stages. For example, larval stages, which are pelagic, feed on phytoplankton and zooplankton and are a key prey source for many fishes and seabirds. Also, among post-settled crabs, the primary sources of mortality (predation, fishing, senescence) change dramatically with increasing size. However, our initial attempts to divide *Cancer* crabs into more than two stages produced badly unrealistic outcomes from Ecopath's mass-balancing algorithm.

We opted to use the Ecopath mass-balancing function to estimate biomass for both stages of *Cancer* crab. We do not know of quantitative, basin-wide surveys for *Cancer* crab population abundance at any life history stage. We can make loose estimates of the biomass of older age classes by, for example, extrapolating annual harvested biomass by a factor of two (to account for the fact that only males are harvested) and then adjusting upward slightly to account for the fact that not all harvestable males are actually captured; however, this would only give us an estimate of a portion of the age 1+ *Cancer* crabs. Thus we used the model to estimate biomass. We assumed *EE* of 0.9 for both YOY and age 1+ *Cancer* crabs, which presumes a high degree of production loss each year to predation or to fishing, in the case of old, large males.

⁷ Recently, Ng et al. (2008) recommended reclassification of *C. magister* and *C. gracilis* into the genus *Metacarcinus*. As this nomenclature is not yet widely practiced in the research literature on either species, we use *Cancer* to avoid confusion.

To calculate *Cancer* crab P/B , we used stage-specific mortality estimates from the Wainwright et al. (1992) study of Dungeness crab population biology in Grays Harbor, located on the outer coast of Washington. For post-settled YOY crabs, Wainwright et al. (1992) found an annual mortality rate of 2.5 yr^{-1} , which we used as the P/B for the YOY stage. Older age classes of crabs had instantaneous natural mortality rates of 1.2 yr^{-1} (Wainwright et al. 1992), and we adjusted this upward slightly to 1.5 yr^{-1} for the age 1+ to account for an increase in mortality after maturation. This is reasonable because of the sudden onset of intense fishing pressure directed at male Dungeness crab with cw greater than 159 mm.

Cancer crab Q/B was estimated using a Dungeness crab bioenergetics model originally developed by Holsman et al. (2003) and recently validated using data from temperature-specific feeding experiments (Holsman unpubl. data). The model estimated daily consumption rates as a function of individual crab cw and water temperatures for appropriate age-specific seasonal depth distributions. These temperatures were based on monitoring in the PSCB conducted by the Washington Department of Ecology (WDE no date). The presumed diets in the models were as described in Table 3. The energy density of the diets were $3,300 \text{ Joule (J) g}^{-1}$ for YOY crab diets and $4,000 \text{ J g}^{-1}$ for age 1+ crabs, based on calorimetric conversion data (Thayer et al. 1973, Wacasey and Atkinson 1987, Brey et al. 1988, Perez 1994, Foy and Norcross 1999, Cauffopé and Heymans 2005).

Models were run for approximately 13 molting stages, which exceeded the point at which crabs had reached harvestable size (158.75 mm cw). Growth in each simulation was constrained by predicted growth rates based on algorithms from published temperature and size-specific growth rates for Puget Sound (Wainwright and Armstrong 1993) by adjusting daily feeding rates, which were always below the maximum physiological feeding rate for a given size and temperature. The resulting Q/B ratios, after rescaling to an annual time step, were 8.197 yr^{-1} for YOY crabs and 3.084 yr^{-1} for age 1+ crabs. These Q/B ratios result in P/Q ratios of 0.305 and 0.401 for the two stages, respectively. Although those are high growth efficiencies, they are consistent with the high food absorption efficiencies that Holsman et al. (2003) observed in Dungeness crabs.

Given the above parameter inputs plus the demands of predators and fisheries, Ecopath's mass-balancing step calculated biomass of 0.757 mt km^{-2} for YOY *Cancer* crabs and 0.547 mt km^{-2} for age 1+ crabs.

Diet information on Puget Sound *Cancer* crabs is limited to qualitative observations, and little has been published. Studies from other systems often only report frequency of occurrence of prey items in *Cancer* crab diets (e.g., Butler 1954, Gotshall 1977, but see Stevens et al. 1982), which presents problems for generating Ecopath diets based on mass or volume. Some patterns emerge from the various studies, namely that there are differences related to size, habitat, and season (Butler 1954, Gotshall 1977, Stevens et al. 1982). Bivalves and crustaceans are clearly important, but the role of fish ranges from very important (e.g., Gotshall 1977, Stevens et al. 1982) to almost entirely absent (Butler 1954). When present, fishes consisted largely of forage fish (e.g., osmerids), flatfish (sanddabs), and demersal fishes from many families. Stevens et al. (1982) note that many authors consider Dungeness crabs to be opportunistic generalists feeding on invertebrates and fish that are associated with benthic substrates.

We used the aforementioned studies (Butler 1954, Gotshall 1977, Stevens et al. 1982) as rough guides, but made some arbitrary adjustments to account for differences among the studies (e.g., in the importance of fish) and to account for the relative abundance of common prey items in our model. For YOY *Cancer* crabs, we closely considered the Stevens et al. (1982) data for small (15–60 mm cw) crabs and Butler’s (1954) data for less than 100 mm cw crabs. Their diet consisted primarily of bivalves and crustaceans (primarily small species such as amphipods, mysids, and barnacles, plus a small amount of *Crangon* spp. and some cannibalism), a small amount of fish, and other items. We also added small amounts of detritus, algal/plant material, eelgrass, benthic macroalgae, and other invertebrate functional groups that were observed (Table 4).

For age 1+ *Cancer* crabs, we considered the Stevens et al. (1982) data for medium and large crabs (61–100 mm cw and 100–162 mm cw, respectively), Butler’s (1954) data for crabs with greater than 101 mm cw, and all crabs sampled by Gotshall (cw range: 67–200 mm). The resulting diet was approximately 28% fishes (mainly forage fish and demersal fish, with smaller amounts of surfperch, piscivorous flatfish, small-mouthed flatfish, and trace amounts of juvenile Pacific herring [*Clupea pallasii*] and juvenile lingcod). Infaunal bivalves were a substantial diet item (30%). The balance of their diet was made up of many of the same groups as YOY *Cancer* crabs, and included cannibalism on both YOY and age 1+ *Cancer* crabs (Table 4).

Predators of YOY *Cancer* crabs include resident diving birds, spiny dogfish, skates, ratfish, adult rockfish, small-mouthed flatfish, demersal fish, octopus, and cannibals (Table 4). For age 1+ *Cancer* crabs, the predator pool is limited to spiny dogfish, skates, octopuses, and other age 1+ *Cancer* crabs. In addition, there is a substantial fishery take (Table 5). Commercial fisheries in PSCB land approximately $0.091 \text{ mt km}^{-2} \text{ yr}^{-1}$, according to data from 1998 to 2007 (Appendix C). Still more are taken by recreational fisheries. Fisher and Velasquez (2008) reported that approximately 16.3% of Dungeness crabs landed in Puget Sound are taken by recreational harvest, which implies an additional $0.015 \text{ mt km}^{-2} \text{ yr}^{-1}$ taken by recreational crabbing.

In Ecosim simulations, the YOY and age 1+ pools of *Cancer* crabs are linked by a delay-difference equation (Appendix D) that uses several life history parameters. Key among these are the age at transition from YOY to age 1+ (0.75 year, derived from Pauley et al. 1986, Fisher and Velasquez 2008), the ratio of the weight of an average age 1+ crab to the weight of an individual at the transition (≈ 10 , derived from Stevens and Armstrong 1985), and the k parameter of the von Bertalanffy growth equation (0.3, derived from Stevens and Armstrong 1985). All other values are the Ecosim default values (Appendix D).

Shrimp

The shrimp group consists of large decapod crustaceans that are primarily benthic. The group has numerous species, many of which are important prey for higher trophic levels. Seven of these species, all of the genera *Pandalus* and *Pandalopsis* (family Pandalidae), support important commercial and recreational fisheries throughout Puget Sound. This group also includes several species of sand shrimp (genus *Crangon*). Shrimp are found at most depths, associated with a variety of natural and man-made substrates (Wicksten 2008). Depths and activity levels likely vary on a diel basis, with many species more active at night and some

moving up into the water column to forage. Some species may change depths as a function of seasonal temperature or reproductive status (Siegfried 1989). As this group is comprised of benthic, nonburrowing species, it does not include intertidal thalassinidean burrowing shrimps (Appendix B), nor does it include pelagic shrimps such as members of the family Sergestidae (see Macrozooplankton subsection above) or mysids (see Small Crustaceans subsection below).

As there are no surveys for biomass of benthic shrimp species, we allowed Ecopath to estimate shrimp biomass via the mass-balancing routine. We assumed an initial *EE* of 0.9, recognizing the heavy predation on shrimp by fishes and other predators as well as the small removal pressure by fisheries (Table 5, Appendix C).

We adapted the *P/B* estimates that Field (2004) used for the pandalid and benthic shrimp groups in his model of the northern California Current. He assumed a *P/B* of 2.0 yr⁻¹ for pandalid shrimp and 2.5 yr⁻¹ for benthic shrimp, a group that includes *Crangon* spp. We used the average (2.25 yr⁻¹) of these values, although there are potential problems with this estimate. Field (2004) notes that there have been few attempts to measure *P/B* in these shrimp species. Hannah (1995) estimated the annual natural mortality of pandalid shrimp off the U.S. West Coast to be 1.82 yr⁻¹, which is lower than our estimate, and we suspect that fishing mortality is higher for the West Coast shrimp than for shrimp in PSCB; thus, our *P/B* estimate may be too high. Furthermore, WDFW, on its Web site describing regulations for shrimp sportfishing (<http://wdfw.wa.gov/fish/shelfish/shrimpreg/shrimp.htm>), reports that pandalid shrimp in Puget Sound live to be 4 to 5 years old. A life span of 4.5 years applied to the Robertson formula (Appendix C) produces a *P/B* estimate of 1.53 yr⁻¹. However, Field (2004) notes a *P/B* estimate of 3.82 yr⁻¹ for a crangonid from the Atlantic Coast of the United States.

We also followed the lead of Field (2004) in our estimate of shrimp *Q/B*. He assumed *Q/B* values of 10 yr⁻¹ for pandalid shrimp and 12 yr⁻¹ for benthic shrimp, respectively, based primarily on the principle of keeping *P/Q* (growth efficiency) at or near 0.2 (20%). We used the value of 12 yr⁻¹ for our shrimp group, which yields a reasonable *P/Q* (0.1875). A *Q/B* of 12 yr⁻¹ is slightly greater than the average of Field's values; we justify this by the fact that Puget Sound waters are slightly warmer than California Current waters.

Given these parameters, plus the predatory and fishery removals from other components of the model, the mass-balancing routine of Ecopath yielded a biomass of 8.134 mt km⁻². This value is approximately 2.75 times the combined biomasses of pandalid and benthic shrimp in Field's (2004) model of the northern California Current, although that is an open coastal ecosystem with a narrow shelf and considerable slope habitat.

As with other aspects of the shrimp group, we estimated their diets based on the literature surveys done by Field (2004) for shrimp in the northern California Current. Generally, shrimp diets are not well studied and we were unable to find anything other than anecdotal information about shrimp diets in Puget Sound. We assigned most of their diet to soft infauna, detritus, small crustaceans, and euphausiids (Table 4). Minor contributions came from copepods, macrozooplankton, other grazers, and deposit feeders; additionally, 2% of their diet was attributed to intraguild cannibalism.

Shrimp are fed upon by most bird and fish groups, as well as octopuses and both stages of *Cancer* crabs (Table 4). As noted above, shrimp are also cannibalistic.

Small Crustaceans

This abundant and productive functional group is comprised of a variety of small, mobile crustaceans living on or near benthic substrates, macrophytes, pier pilings, or other structures. Key constituents include small brachyuran crabs such as spider crabs (family Majidae), anomurans such as hermit crabs (superfamily Paguroidea) and porcelain crabs (family Porcellanidae), mysid shrimps (family Mysidae), cumaceans (order Cumacea), benthic-oriented amphipods (order Amphipoda, suborders Gammaridea and Corophiidea), isopods (order Isopoda), and tanaidaceans (order Tanaidacea). Members of this group can be found at virtually all depths in Puget Sound and their species diversity is considerable (e.g., Jensen 1995). This is certainly among the most important functional groups in the system in terms of its contribution to food web structure and energy flow. They are key consumers of benthic primary producers and detritus, and are a major food source for a wide variety of higher invertebrates and fishes.

The range of depths and habitats occupied by this group, coupled with a range of behaviors ranging from free swimming to burrowing in soft sediments to hiding under rocks, precludes comprehensive, quantitative biomass surveys. Thus we elected to estimate small crustacean biomass with the Ecopath mass-balancing routine. We began the estimation process with the assumption that their $EE = 0.9$, reflecting their great importance in the diets of numerous species in the community.

We used Robertson's (1979) method that draws on the relationship between production and life span (Appendix C) to estimate small crustacean P/B . A number of amphipod and mysid species, cataloged by McLusky and McIntyre (1988), have life spans of 1 to 2 years, and yield a mean P/B of 3.57 yr^{-1} when analyzed with the Robertson method, although the species listed by McLusky and McIntyre (1988) are mainly from the North Atlantic. Rudy and Rudy (1983) list some species of estuarine isopods in Oregon as having life spans of 1.5–2.5 years, which would yield P/B between 3.41 and 2.35 yr^{-1} with the Robertson method. The P/B of the isopod *Cirolana harfordi*, common in intertidal zones on the open coast, was empirically estimated at 2.4 yr^{-1} (Johnson 1976). We made the simplifying assumption that most biomass in this functional group is comprised of small taxa (e.g., amphipods, mysids, cumaceans) and that their life span is 1.5 years, yielding a P/B of 3.41 yr^{-1} .

For Q/B , we drew from the work of Field (2004) and Aydin et al. (2003), who assumed Q/B ratios of 22 yr^{-1} for comparable functional groups in models from open ocean ecosystems of the Northeast Pacific. As Puget Sound is warmer than those systems, we increased the Q/B to 25 yr^{-1} to account for the higher energetic demands of warmer water.

Given these parameters and the intense predatory demands of upper trophic levels, the mass-balancing function of Ecopath calculated a biomass of $38.195 \text{ mt km}^{-2}$ for the small crustacean pool. That estimate implies that this group is one of the more abundant components of the benthic invertebrate community, the rest of which is largely infaunal (Table 3).

The diversity of this group allows for the occupation of many different trophic niches, and quantitative diet studies on these species are rare. Based largely on anecdotal accounts and assumptions common to other EwE models in nearby systems, we developed an arbitrary initial diet composition (Table 4). The majority of the diet was detritus; the remainder was spread among a variety of benthic and pelagic invertebrates and benthic primary producers. They also engage in some functional group cannibalism. Some predation on invertebrates (e.g., on infaunal bivalves and soft infauna) is assumed to be done by brachyuran and anomuran crabs, and our assumption about the allocation of biomass to crabs (as opposed to smaller consumers like amphipods, mysids, and cumaceans) is crucial in properly representing the diet composition.

Small crustaceans are a major prey pool in the food web (Table 4). They are fed upon by every seabird group and virtually every fish group. In addition, they are preyed upon by shrimp, octopuses, age 0+ *Cancer* crabs, sea stars, and other members of their own functional group.

Barnacles

Barnacles are found from intertidal waters down to at least 90 m (Morris et al. 1980, Kozloff 1983). Shallow-water species such as *Chthamalus dalli*, *Balanus glandula*, and the thatched barnacle (*Semibalanus cariosus*) affix to natural and artificial hard substrates. *C. dalli* is the shallowest, while *B. glandula* is slightly deeper and gradually gives way to the larger thatched barnacle in the middle and lower intertidal regions (Kozloff 1983). *B. glandula* and *C. dalli* may compete for habitat along rocky shores, with densities of tens to hundreds of thousands per m², although predation by the snails *Nucella* spp. can dramatically affect both taxa, particularly *B. glandula*, at local scales (Morris et al. 1980). At greater depths, the giant barnacle (*B. nubilus*) becomes increasingly important. Occurring subtidally to as deep as 90 m (Morris et al. 1980), the giant barnacle may reach a diameter of more than 10 cm and serve as habitat for a variety of other organisms such as sponges (Kozloff 1983) and small fishes (Demetropoulos et al. 1990).

Empirical biomass estimates for the barnacle group are not available. We therefore used Ecopath's mass-balancing routine to estimate barnacle biomass, first inputting an *EE* of 0.8, which implies that a large proportion of barnacle production is lost to predators.

To estimate *P/B* for barnacles, we used the Robertson equation (Appendix C) that correlates benthic invertebrate *P/B* with longevity. The range of longevities among common Puget Sound barnacles is wide: *C. dalli* live an estimated 3 years, *B. glandula* life spans are estimated at 8–10 years, and thatched barnacles live up to 15 years (Morris et al. 1980, Rudy and Rudy 1983). No longevity data have been reported for giant barnacles. We elected to use a longevity of 6 years as a compromise between the larger, deeper-dwelling, long-lived species and the shallower, more short-lived species that may be more vulnerable to predators. Erring on the side of the shorter-lived, depredated species was done in order to keep the barnacle biomass estimate from being unreasonably large. Applying 6 years to the Robertson equation yields a *P/B* of 1.245 yr⁻¹.

We had no information on consumption rates by barnacles, and thus opted to estimate growth efficiency. We made the assumption that barnacle growth efficiency was 20% (i.e.,

$P/Q = 0.2$), as we have similarly assumed for many other primary consumers in this model. This corresponds to a Q/B of 6.225 yr^{-1} , given our P/B estimate.

Given these parameter estimates and the predation pressure exerted on barnacles by other model groups, the Ecopath mass-balancing routine estimated a biomass of 2.310 mt km^{-2} . This estimate seems high given the large portion of the PSCB model area (e.g., soft-sediment habitats and all waters $>90 \text{ m}$ deep, Table 1) that is not inhabited by barnacles. We may have misrepresented the role of barnacles in the diets of some predators, particularly surfperches, which alone account for 42% of barnacle predation mortality.

Barnacle diets were based on thatched barnacle gut and cirri contents in the San Juan Islands by Navarrete and Wieters (2000). The most abundant prey, diatoms and barnacle nauplii, made up 32% and 16% of the total observed items, respectively. Also present were microzooplankton (foraminiferans and mussel postlarvae), copepods, nemerteans, and macroalgal fragments. Based on these observations, we assigned barnacles a diverse diet with equal amounts of phytoplankton and microzooplankton, along with soft infauna, copepods, algal/plant material, and detritus (Table 4). Conversely, barnacles are preyed upon by nearshore diving birds, gulls, spiny dogfish, ratfish, piscivorous flatfish, small-mouthed flatfish, surfperches, demersal fish, predatory gastropods, sea stars, and *Cancer* crabs.

Mussels

The mussel functional group is comprised of the blue mussel (*Mytilus edulis*), a nearshore filter feeder that prefers relatively protected estuarine bays (Kozloff 1983). They are most often found on stable substrates, including anthropogenic structures, between the intertidal zone and waters as deep as 36 m (Emmett et al. 1991). They reach sizes of more than 6 cm, although that is rare (Kozloff 1983, Emmett et al. 1991). Mussels can be extremely dense in areas where conditions are favorable, although predation can drastically drive their numbers down (Emmett et al. 1991). Blue mussels can be cultured or harvested wild for human consumption as well.

We found no data on blue mussel abundance in Puget Sound, and thus used the Ecopath mass-balancing step to solve for biomass. In order to do so, we assumed an EE of 0.9, implying a very high degree of annual production lost to predation.

The P/B estimate for mussels stems from the P/B -longevity relationship described by Robertson (1979) (Appendix C). According to Seed (1976), blue mussels may live to be 18–24 years, but that is primarily in very cold northern areas of slow growth (e.g., Greenland). Longevities in Atlantic systems of latitudes similar to Puget Sound were approximately 7–9 years (Seed 1976). Applying a longevity of 9 years to the Robertson equation yields a P/B of 0.927 yr^{-1} , a value that falls within (but close to the upper end of) the range of blue mussel P/B estimates summarized from other systems (e.g., Seed 1976, Munch-Petersen and Kristensen 2001).

The Q/B ratio for mussels was estimated indirectly, because direct consumption estimates were not available in the literature. However, according to Grant and Bacher (1998), a review of bivalve bioenergetics by Griffiths and Griffiths (1987) concluded that bivalves have a gross

growth efficiency of 30%. If 0.30 is a reasonable estimate of production over consumption (i.e., P/Q), then Q/B for mussels = 3.090 yr^{-1} .

Given these parameters and the predation pressure of other groups, Ecopath's mass-balance function calculated an initial biomass of 3.785 mt km^{-2} for mussels. As with barnacles, this seems like a rather high biomass for mussels, given the relatively low amount of habitat available to them in PSCB (Table 1). If this is an overestimate, it may result from overestimating the amount of mussels in the diets of predators or from underestimating P/B .

Blue mussels primarily consume organic detritus, along with phytoplankton and other microorganisms (Table 4, derived from Morris et al. 1980, Emmett et al. 1991). Mussels are preyed upon by sea stars, *Cancer* crabs, octopuses, predatory gastropods, surfperches, demersal fish, ratfish, nearshore diving birds, gulls, and raptors. We assume a trace level of fishing mortality from recreational shellfish extraction (Table 5).

Infaunal bivalves

Infaunal bivalves include all bivalve mollusks that are found at or below the surface of soft sediments (except for geoducks [*Panopea abrupta*], which are their own functional group, see next subsection below). This group ranges from very small clams, such as *Transennella tantilla*, amethyst gemclam (*Gemma gemma*), Charlotte macoma (*Macoma carlottensis*), and Baltic macoma (*M. balthica*), to large clams, such as the horse clam (*Tresus capax*) and the butter clam (*Saxidomus giganteus*). Members of this group are important filter feeders that can reach exceptionally high densities under favorable conditions; for example, *Macoma* spp. were among the most abundant infaunal invertebrates in deepwater benthic grab samples taken in PSCB from the early 1960s (Lie 1968) and again from 1989 to 2000 (Partridge et al. 2005). Infaunal bivalves supply food for a wide variety of predators, support lucrative fisheries, and are the basis for growing aquaculture programs in Puget Sound and elsewhere.

Infaunal bivalve biomass was estimated directly from data collected by the Washington Department of Ecology (WDE) in benthic grab samples taken at numerous sites and depths between 1989 and 2000 (Partridge et al. 2005). We pooled bivalve density estimates into 20 m depth bins and weighted depth-specific mean abundances by the relative area represented by their depth bin. This yielded a grand mean abundance estimate ($\approx 1,730$ individuals m^{-2}), which we multiplied by an estimated individual biomass for bivalves taken from similar benthic grab sampling done by Lie (1968). His mean individual mass estimate was less than 0.041 g, implying that the typical infaunal bivalve in Puget Sound is a small individual. This yielded a weighted biomass estimate of $70.506 \text{ mt km}^{-2}$. We cannot be certain that this is plausible, because it is possible that the benthic grab did not sample deep enough to efficiently capture large clams that are deep burrowers. Even so, this group is one of the most abundant in the model in biomass terms.

We again adopted the Robertson (1979) method (Appendix C) to estimate P/B as a function of the maximum age. Infaunal bivalve life spans range from relatively short (e.g., 2 years for the exotic amethyst gemclam) to intermediate (e.g., 5–10 years for the exotic Baltic tellin [*Macoma balthica*], 7–8+ years for the Pilsbry piddock [*Zirfaea pilsbryi*] and the littleneck clam [*Protothaca staminea*]) to relatively long (e.g., 16 years for the heart cockle [*Clinocardium*

nutallii] and more than 20 years for the butter clam) (Morris et al. 1980, Chew and Ma 1987, Budd and Rayment 2001). Assuming that most species of infaunal bivalve are small bodied, we assigned a median maximum age of 3 years. This corresponds to a P/B of 2.059 yr^{-1} .

We estimated Q/B based on publications indicating that bivalves typically have a conversion efficiency (P/Q) of 0.3 (Griffiths and Griffiths 1987, Grant and Bacher 1998). Based on our estimate of P/B , this conversion efficiency requires a Q/B of 6.863 yr^{-1} .

With our estimates of the other parameters plus the demands of predators and fisheries, Ecopath estimated the infaunal bivalve EE to be 0.718. This implies a moderately high proportion of production lost to model predators or to fishing each year in the initial model state.

We assumed that the diets of infaunal bivalves are primarily made up of suspended phytoplankton and detritus filtered from water drawn through their siphons. We partitioned these two diet items proportionally according to the proportion of area located above and below the depth of light extinction ($\approx 30 \text{ m}$). About 28% of the PSCB domain is in the euphotic zone (Table 1), thus we assumed that 28% of infaunal bivalve diet is phytoplankton (Table 4). The remainder of their diet is detritus (67%) and bacteria associated with detritus (5%).

Infaunal bivalves are fed upon by predatory gastropods, sea stars, small crustaceans, YOY and Age 1+ *Cancer* crabs, octopuses, demersal fish, surfperches, piscivorous and small-mouthed flatfish, walleye pollock, ratfish, skates, raptors, gulls, and nearshore diving birds. Furthermore, commercial fishing operations removed $0.03 \text{ mt km}^{-2} \text{ yr}^{-1}$ of infaunal bivalves from PSCB between 1998 and 2007 (Table 5, Appendix C). Additional removals must be allocated to recreational harvest and to aquacultural production, but we have not yet located or compiled those data.

Geoducks

Geoducks warrant their own functional group for at least two reasons: first, their unique growth and life history compared to other bivalves in the model domain, and second, their significance as a target species for fisheries and aquaculture in Puget Sound. Geoducks are the largest bivalve found in Puget Sound, achieving weights of more than 3 kg, shell lengths of greater than 200 mm and siphon lengths of more than 1 m, allowing them to burrow deeply into sand and mud sediments beyond the reach of most predators (Goodwin and Pease 1989). Geoducks reach sexual maturity between the ages of 2 and 8 (Andersen 1971, Goodwin and Shaul 1984) and may continue spawning beyond the age of 100 years (Sloan and Robinson 1984). They are found at depths ranging from the lower intertidal to 110 m (Goodwin and Pease 1989).

Geoduck biomass estimates stem from survey work done by WDFW biologists on geoducks in the depth band between approximately 6 and 23 m (Goodwin and Pease 1987, Bradbury and Tagart 2000, Bradbury et al. 2000). Surveys have focused on tracts that are both harvestable and unharvestable. Tracts are classified unharvestable by virtue of having densities below approximately $0.4 \text{ geoducks m}^{-2}$, conflicts with existing use sectors such as passenger ferries, or human health concerns (WDNR and WDFW 2001). Biomass in the tracts can be high: Goodwin and Pease (1987) estimated a mean biomass of $1,482 \text{ g m}^{-2}$ in Puget Sound tracts, with

a maximum of 19,651 g m⁻². Limited information is available on biomass in areas outside of the tracts. We used data from the most recent (2009) survey of tracts in PSCB. Not all tracts are surveyed every year and some go many years or even decades between samplings, so it behooves us to use the most updated data possible.

Surveys indicate a total geoduck biomass of 39,703 mt in the tracts, which cover an area of 37.01 km² (Sizemore et al. unpubl. data). If we conservatively assume that this biomass constitutes the entirety of the geoduck population in PSCB (area = 757.08 km²), we arrive at a biomass of 52.442 mt km⁻². A recent environmental impact assessment of the commercial and tribal geoduck fisheries assumed that deepwater areas adjacent to surveyed tracts had 1.573 times as much biomass as the surveyed tracts, and that inshore areas adjacent to surveyed tracts had 0.5 times as much biomass as the surveyed areas (WDNR and WDFW 2001). Those assumptions would yield a biomass of 161.154 mt km⁻², but we will use the more conservative estimate until widespread empirical estimates of geoduck abundance outside the surveyed tracts become available. The conservative estimate also should promote precautionary levels of fishing mortality in fishing simulations.

To estimate P/B , we began first with an instantaneous rate of natural mortality of 0.023 yr⁻¹, estimated by Bradbury and Tagart (2000) for adult geoducks in Puget Sound from 1979 to 1981. Based on current commercial and tribal harvest rates in the PSCB area (approximately 0.697 mt km⁻² annually from 1998 to 2007, Table 5, also Appendix C) and the current biomass estimates described above, instantaneous fishing mortality is approximately 0.0133 yr⁻¹. The sum of these mortality rates is 0.0363 yr⁻¹, which we used for our P/B estimate.

In the absence of direct measures of geoduck consumption rates, we inferred the Q/B ratio by comparison with the other, smaller bivalve species in this model. Their Q/B values generally fell between 3 and 5 yr⁻¹, and we expect geoduck Q/B should be lower because large animals tend to have lower mass-specific energy requirements than small, taxonomically similar animals (e.g., Jobling 1994). We assumed a Q/B of 2 yr⁻¹, which produced a very low conversion efficiency ($P/Q = 0.018$), although a low conversion efficiency is reasonable for a species as long-lived and slow growing as geoduck.

The mass-balancing routine of Ecopath produced an estimated EE of 0.366 for geoducks. This implies that a moderate amount of geoduck production is lost to other model groups (primarily the geoduck fishery) each year.

The diet of geoducks has only been characterized anecdotally, as summarized by Goodwin and Pease (1989). They are filter feeders and gut content studies from Puget Sound specimens have only revealed phytoplankton, apparently even among individuals collected from below the photic zone. These individuals may persist on phytoplankton that is transported into deep waters by currents or on dead or dying phytoplankton that has sunk (Goodwin and Pease 1989). Here we assume that geoduck diet is mostly phytoplankton (Table 4), following the assumption that most geoduck biomass is found at depths where they have consistent access to living phytoplankton. The remainder of their diet is detritus and associated bacteria.

Although predation on geoduck larvae and juveniles is likely quite high, predation mortality probably becomes inconsequential once they have reached 2 years of age, except for

possible rare predation events due to larger sea star species (Lambert 1981, Goodwin and Pease 1989). Because our model focuses on the adult phase of the geoduck life history, we assume only a small amount of predation pressure, from sea stars.

Soft Infauna

The soft infauna community includes numerous species of annelids, sipunculans, nemertean, and turbellarians. Annelids, particularly polychaetes, are typically the most abundant taxa of worms captured in benthic grab samples in Puget Sound over the past 30–40 years (Nichols 1975, 2003, Partridge et al. 2005). Therefore, all model parameters for the soft infauna group derive from studies of polychaetes.

Biomass estimates were made using benthic grab data collected by WDE at 93 sites in PSCB and adjacent areas in 1998 (Long et al. 2000). Sites ranged from approximately 4 m to 250 m in depth, and the data consisted of abundance estimates per 0.1 m². We converted the counts to areal biomass estimates by assuming a mean individual weight of 0.032 g, the average polychaete weight in Puget Sound benthos samples collected by Lie (1968). We pooled the areal biomass estimates into 20 m depth bins, averaged them by depth bin, then weighted the depth-based averages according to the proportional area of each 20 m bathymetric contour (Table 1). After appropriate unit conversions, the resulting biomass estimate was 67.899 mt km⁻².

Our P/B estimate was taken directly from work done on a numerically dominant polychaete in Puget Sound, *Pectinaria californiensis*. Nichols (1975) measured annual production of *P. californiensis* in deep waters (>100 m) of Puget Sound and found that P/B ranged from 3.3 yr⁻¹ to 5.5 yr⁻¹. We used the mean of this range, 4.4 yr⁻¹.

Not having an estimate of Q/B for any polychaete species, we used a P/Q estimate to infer Q/B . Field (2004) in his model of the northern California Current ecosystem pooled polychaetes into a general group of benthic infauna, for which he assumed a P/Q of 0.2. That ratio coupled with our P/B estimate yields a Q/B of 22.0 yr⁻¹.

The mass-balancing step of Ecopath produces an EE estimate of 0.568 for this group, which implies moderate loss of production to predation. We would have expected a larger number and may have underrepresented soft infauna in predator diets. For example, there may be intraguild cannibalism that we have thus far omitted.

The diet of soft infauna is assumed to be mostly detritus, with important contributions from benthic microalgae and bacteria (Table 4). Soft infauna are eaten by nearshore diving birds, migratory diving birds, spiny dogfish, ratfish, Pacific hake, walleye pollock, juvenile wild and hatchery salmon, adult rockfish, piscivorous flatfish, small-mouthed flatfish, demersal fish, surfperches, shrimp, *Cancer* crabs, small crustaceans, barnacles, and deposit feeders.

Deposit Feeders

This functional group covers deposit-feeding invertebrates apart from those already in other groups listed above. The group is mainly comprised of echinoderms that feed on patches of organic detritus on the seafloor. Some also feed on diatoms and suspended particles; some may opportunistically scavenge dead material or prey on small organisms (Morris et al. 1980,

Kozloff 1983). Representatives include brittle stars (class Ophiuroidea), the heart urchin (*Brisaster latifrons*), a few species of sea star (e.g., mud star [*Ctenodiscus crispatus*]), and the many species of sea cucumber (except for the California sea cucumber, see Large Sea Cucumbers subsection above). These organisms can be found at all depths in Puget Sound on a wide variety of substrates; many of them are burrowing animals found in soft sediments (Nichols 2003).

The role of these organisms in the functioning of the Puget Sound ecosystem is not clear, but the roles of some key species have probably changed in recent decades. Nichols (1975, 2003) measured abundances of two deposit feeders, the heart urchin and the burrowing sea cucumber (*Molpadia intermedia*) at deep stations in PSCB. He found that *Brisaster* numbers fell drastically between the 1960s and 1990s while *Molpadia* numbers increased and then leveled off over the same time period. Whereas *Brisaster* was a dominant component of the benthic community biomass in the 1960s (Nichols 1975, 2003), it was not abundant at any site sampled by the WDE between 1989 and 2000 (Partridge et al. 2005). Apparently, *Brisaster* recruitment has not occurred since approximately 1970 (Nichols 2003). This implies a major shift in benthic taxa and community structure.

The most up-to-date sampling of the benthic community in PSCB is the WDE sampling mentioned above (Long et al. 2000, Partridge et al. 2005). Their data consist of counts of different species per 0.1 m², which we converted to biomass by multiplying by 0.037 g, and the estimated wet weight of brittle stars and sea cucumbers from data in Lie (1968). Expanding the data from g per 0.1 m² to mt km⁻², and weighting according to the bathymetric distribution of samples, we estimated deposit feeder biomass to be 7.512 mt km⁻².

P/B estimates for deposit feeders were made using the Robertson (1979) relationship between life span and production (Appendix C). The range of maximum ages in this functional group is potentially wide. The predominant subtidal brittle star (*Amphiodia urtica*), has a life span of 5 years in Puget Sound (Lie 1968). Small sea cucumbers of the genus *Cucumaria* are common in Puget Sound (Kozloff 1983); *C. curata* and *C. pseudocurata* have been found to have maximum ages of at least 4 or 5 years (Rutherford 1973, Morris et al. 1980). In contrast, Nichols (2003) surmised that heart urchins can live in excess of 20 years, as individuals recruited prior to 1970 were the only remaining individuals in 1992. However, *Brisaster* is no longer an important component of this group (Nichols 2003). If we assume a mean 5-year life span for organisms in this functional group, the Robertson relationship predicts a *P/B* of 1.421 yr⁻¹.

We are aware of no data on *Q/B* rates for these organisms. We assumed that it would be comparable to, but greater than, the *Q/B* of large sea cucumbers by virtue of the latter's larger size and longer life span. We estimated a deposit feeder *Q/B* of 25 yr⁻¹. This estimate, coupled with the *P/B* estimate, yields a *P/Q* (food conversion efficiency) of 0.057, which seems plausible for detritus feeders with multiyear life spans.

The parameters above, coupled with the demands of predators, yield an initial *EE* of 0.344 in the mass-balancing routine of Ecopath. This suggests relatively moderately low predation pressure on deposit-feeder populations.

Based on anecdotal accounts in Morris et al. (1980) and Kozloff (1983), we assigned deposit feeders an initial diet dominated by detritus, along with smaller amounts of bacteria, soft infauna, and benthic microalgae (Table 4). Their predators included shrimp, sea stars, predatory gastropods, age 1+ *Cancer* crabs, surfperches, piscivorous flatfish, small-mouthed flatfish, adult rockfish, and ratfish.

Suspension Feeders

This group features a diverse range of filter-feeding benthic invertebrates not already represented in the functional groups described previously. Major groups include sponges (phylum Porifera), colonial hydrozoans (phylum Cnidaria, class Hydrozoa), sea pens (phylum Cnidaria, order Pennatulacea), tube-dwelling worms such as serpulids (phylum Annelida, class Polychaeta) and horseshoe worms (phylum Phoronida), and bryozoans (phylum Bryozoa). Suspension feeders fill multiple ecological roles: they feed on planktonic organisms and detritus, they are prey for a number of species, and they provide biogenic habitat structure for fishes and invertebrates. Some species of sponges and bryozoans may grow on other species (e.g., on kelp blades, on the backs of crabs, or on the shells of scallops); the resulting effects can be beneficial (e.g., camouflage) or deleterious (e.g., fouling) (Kozloff 1983).

Not knowing quantitative biomass estimates for this diverse group, we used the Ecopath mass-balancing algorithm to estimate biomass. We began the mass-balancing process by assuming an *EE* of 0.8, which implies an initial model state in which 80% of production is lost to predation by other model groups.

Lacking direct measures of production, we developed suspension feeder *P/B* estimates by using the Robertson (1979) method, where *P/B* is a function of maximum age (Appendix C). This was challenging because of the diversity of life histories among constituents of this group. For example, the sea pen (*Ptilosarcus gurneyi*) can live up to 15 years (Birkeland 1974). Published accounts of bryozoans and serpulids worldwide suggest life spans of several years (e.g., Rubin 1985, Medernach et al. 2000, Bianchi and Morri 2001, Hill 2006). Sponges, however, may live a few years in nearshore habitats to decades or centuries in the deep oceans (e.g., cloud sponges). We assumed that the vast majority of the biomass of this functional group in Puget Sound is represented by the relatively short-lived species of bryozoans, sponges, tube worms, and hydroids, rather than the old, deepwater sponges or sea pens; a life span of 2 years results in a *P/B* of 2.763 yr^{-1} in the Robertson equation.

Q/B was estimated based on the simplifying assumption that $P/Q = 0.2$. Given our *P/B* estimate, this assumption yielded a *Q/B* of 13.815 yr^{-1} .

The combination of the above parameter estimates and the top-down demands of predators resulted in an estimated initial biomass of 6.494 mt km^{-2} for suspension feeders.

Suspension feeders were arbitrarily assigned a diet dominated by phytoplankton (Table 4). This implies that their biomass is disproportionately found in the euphotic zone ($\approx 28\%$ of the basin), an assumption that should be tested. The remainder of their diet includes detritus, microzooplankton, and bacteria. Suspension feeders are preyed upon by predatory gastropods, sea stars, small crustaceans, age 1+ *Cancer* crabs, large sea cucumbers, and other grazers.

Tunicates

We chose to include tunicates as a separate group from the other suspension feeders because several nonindigenous tunicates have become established in Puget Sound, and their populations may eventually reach the level of full-blown invasions with measurable effects. The species of concern are the stalked sea squirt (*Styela clava*), solitary sea squirt (*Ciona savignyi*), and *Didemnum* spp. They were likely introduced via ballast water transfer or attached to ship hulls, and *Didemnum* may have also been introduced with aquacultural plantings of nonnative shellfish (PSAT 2007). These species are capable of spreading rapidly and exhibit some resistance to control measures and environmental conditions such as low dissolved oxygen. Numerous agencies, organizations, and fishery stakeholders are concerned that nonnative tunicates will outcompete native species and commercially valuable resources for space and resources.

There are no biomass survey data available for the nonnative tunicates in PSCB; therefore, we used the Ecopath mass-balancing routine to estimate tunicate biomass. We input an *EE* of 0.075, assuming relatively little predation pressure; however, during the mass-balancing step, Ecopath increased *EE* to 0.099 due to the biomass accumulation (*BA*) input (discussed below).

We used the equation proposed by Robertson (1979) (Appendix C) to estimate tunicate *P/B* based on life span. Stalked sea squirt life span is estimated at 1–3 years, according to Cohen (2005). A maximum life span of 3 years, when applied to the Robertson equation, yields a *P/B* of 2.059 yr⁻¹. There were no estimates of tunicate *Q/B* available, so we assumed a trophic transfer efficiency (*P/Q*) of 0.2, leading to a *Q/B* estimate of 10.295 yr⁻¹. (Morris et al. 1980 report that the water filtration rate of the stalked sea squirt is 78–175 ml per gram dry weight per minute in flowing, 10°C seawater; this estimate may lend itself to a more empirical *Q/B* estimate.)

Given the above parameters, the Ecopath mass-balancing routine yielded a biomass estimate of 0.157 mt km⁻², which is considerably lower than the biomass of suspension feeders. This reflects the status of tunicates as newly established, nonindigenous species. However, we included a *BA* term (Equation 1) because these species are expected to spread within the basin via transport on vessel hulls (PSAT 2007). The *BA* rate is assumed to be 0.05 yr⁻¹, that is, an initial 5% annual increase in biomass.

Tunicates have been characterized as “animals deeply committed to a life of filter feeding in the sea” (Morris et al. 1980, p. 177). Finding no quantitative diet estimates, we assumed tunicates to have a diet of 70% phytoplankton, 20% detritus, and 5% each of microzooplankton and bacteria (Table 4). Tunicates are fed upon in small amounts by predatory gastropods, sea stars, adult rockfish, and small-mouthed flatfish. Predation likely focuses on young, recently settled juveniles (Cohen 2005).

Pelagic Fishes

Pelagic fish species are of great importance to food web structure and function in Puget Sound. They are abundant and generally have rapid turnover rates, high activity levels, and

broad habitat use; they therefore account for considerable energy transfer and connectivity across the basin. They serve as a bridge between primary consumers and the upper-trophic-level fishes, marine mammals, and seabirds that feed heavily on them. Some are important commercial, recreational, or subsistence fish, most notably the Pacific herring as well as some species of smelts (family Osmeridae) and surfperches (family Embiotocidae).

Pacific Herring

Pacific herring are one of the most ecologically and economically important species in Puget Sound (Stout et al. 2001, Stick 2005, Penttila 2007). They feed heavily on productive pelagic crustaceans such as copepods and euphausiids, and are fed upon by some of the most iconic species in Puget Sound, including salmon and marine mammals. They support fisheries for their roe (a roe-on-kelp fishery that occurs north of the PSCB model domain), their juveniles (for use as bait, Baraff and Loughlin 2000), and until recently their adults. Although no fisheries in Puget Sound currently target adult Pacific herring (owing to declines in the largest spawning stock, the Cherry Point stock in northern Puget Sound, Stick 2005), such fisheries were large historically and remain so in the Strait of Georgia.

In addition, their spawning habits link the nearshore and offshore habitats: Pacific herring are open water pelagic feeders, but they spawn in intertidal or subtidal waters, usually over macrophytes such as eelgrass or kelp, in the winter and spring months. Their eggs are fed upon by many nearshore species. Pacific herring spawning aggregations are nonrandom: Puget Sound has at least 19 discrete stocks that spawn in predictable locations each year (Stick 2005). Two of these stocks (Port Orchard/Madison and Quartermaster Harbor) have spawning grounds located in PSCB, and several others spawn close to PSCB. After spawning, the stocks disperse to pelagic habitats (Penttila 2007).

The Pacific herring pool has two age groups, juveniles and adults, that are dynamically linked in Ecosim via the delay difference reproduction function (Appendix D). The transition between these groups occurs at age 2–3. We assumed it to occur at age 2, given that, on average, 40–50% of the Pacific herring spawning stock biomass at Quartermaster Harbor and Port Orchard/Madison has been age-2 in recent decades (Stick 2005). We distinguish the juvenile and adult stages because their ecology differs in important ways, as outlined below.

We made separate calculations for the initial state of biomass for the juvenile and adult pools of Pacific herring. We used the Ecopath mass-balancing routine to estimate juvenile Pacific herring biomass, because no empirical data were available. We set *EE* at 0.9, consistent with considerable losses of annual production to predation and fishing. Adult biomass was drawn from Stick (2005), who conducted stock assessments of all Puget Sound spawning stocks based on annual hydroacoustic and trawl surveys of spawning aggregations. Our biomass estimate was equal to Stick's 5-year average spawning stock biomasses for the Quartermaster Harbor and Port Orchard/Madison populations (1,916 mt, or 2.531 mt km⁻²). We assumed no dispersion of adult herring to or from basins adjacent to PSCB. This assumption, which was not informed by empirical evidence, should be revisited and monitored, particularly given the importance of Pacific herring in Puget Sound food webs and fisheries.

P/B for juvenile Pacific herring was taken from a population model for Puget Sound herring (Guerry unpubl. data), based largely on the historic stock assessments by WDFW (e.g., Stick 2005). We set P/B equal to the instantaneous annual total mortality from the Guerry model, weighted by the estimated biomass in age classes 0 and 1. The weighted average mortality was 3.656 yr^{-1} . For adults, we set P/B at 1.6 yr^{-1} , which approximates the natural mortality for the Quartermaster Harbor and Port Orchard/Madison stocks in recent years, as estimated by Stick (2005). This is considerably higher than many published estimates of natural mortality in adult Pacific herring (Lassuy 1989). For example, Trumble and Humphreys (1985) reviewed population biology literature for this species and concluded that instantaneous natural mortality for adults was between 0.4 and 0.5 yr^{-1} . A similar conclusion was reached by Lemberg et al. (1997). However, the age frequency time series data provided by Stick (2005) imply higher levels of mortality in Puget Sound Pacific herring. Stick (2005) concluded that natural mortality of adult herring had increased sharply since the 1970s.

Q/B ratios for both stages are based on bioenergetics models for Pacific herring. We used bioenergetics parameters described by Megrey et al. (2007) to estimate consumption required for Pacific herring to grow according to the von Bertalanffy growth function described for Strait of Georgia herring by Gunderson and Dygert (1988). We assumed water temperatures for the upper 25 m of the water column of PSCB from WDE (no date) and diets corresponding to the proportions described below; resulting prey energy densities were $3,895 \text{ J g}^{-1}$ for juveniles and $4,280 \text{ J g}^{-1}$ for adults. The average annual Q/B , weighted by age groups based on the P/B ratios described previously, was 15.984 yr^{-1} for juveniles and 7.489 yr^{-1} for adults.

The mass-balancing step in Ecopath calculated an EE of 0.851 for adult Pacific herring and a biomass of 3.407 mt km^{-2} for juvenile herring.

Adult Pacific herring diets were derived from stomach content analysis, largely collected in nearby basins (Strait of Juan de Fuca and San Juan Islands, Miller et al. 1977, Miller et al. 1980) but also from the Central Basin (Fresh et al. 1981). From those sources, we estimated an initial diet dominated by copepods and euphausiids, rounded out by macrozooplankton, forage fish, and juvenile Pacific herring (Table 4). For juvenile Pacific herring, we arbitrarily assumed similar diet composition to adults, but changed some proportions to reflect likely ontogenetic differences and changes in habitat. The resulting diet is consistent with published observations (e.g., Stout et al. 2001).

Between the two age classes, Pacific herring are preyed upon by nearly all other vertebrates in the food web, as well as by squid and *Cancer* crabs (Table 4). We currently do not assume measurable predation by jellyfish on Pacific herring. The commercial bait fishery for juvenile Pacific herring produces modest landings (Table 5, also Appendix C).

For the delay-difference equation that links the two age groups (Appendix D), we used values of 2 years for the juvenile-adult transition age (Stick 2005), 2.875 for the weight ratio of an average adult to a transition-age individual (derived from bioenergetics modeling as described above), 0.36 for the von Bertalanffy k parameter (Gunderson and Dygert 1988), and default values (as in Appendix D) for all other parameters.

Forage Fish

Several other planktivorous fishes inhabit pelagic zones of Puget Sound. Major species are the Pacific sand lance (*Ammodytes hexapterus*), surf smelt (*Hypomesus pretiosus*), northern anchovy (*Engraulis mordax*), and longfin smelt (*Spirinchus thaleichthys*) (Monaco et al. 1990, Emmett et al. 1991, Penttila 2007). Sardine (*Sardinops sagax*) and eulachon (*Thaleichthys pacificus*) are present but rare (Monaco et al. 1990). We also include threespine stickleback (*Gasterosteus aculeatus*) in this group. Forage fish are crucial links between lower and upper trophic levels. They are important prey due to their abundance, high energy density, and vitamin content (e.g., Robards et al. 1999). They are also conduits of mass and energy flow between different habitats; for example, longfin smelt migrate into streams to spawn, and sand lance and surf smelt spawn primarily in beach areas (Emmett et al. 1991, Penttila 2007). They support fisheries in PSCB, though of a smaller magnitude than Pacific herring. As they have received less research or management attention than Pacific herring, much about their abundance and ecology in PSCB is unknown (Penttila 2007).

There are no biomass data available for these species in PSCB, because agencies such as the WDFW have devoted most of their pelagic fish stock assessment efforts to Pacific herring (Penttila 2007). In addition, some species' biology and spatial distribution make abundance estimation by traditional methods very difficult; for example, sand lance spend considerable time burrowed into sandy or gravelly bottoms (Penttila 2007) and also do not show up in acoustic surveys because they lack a swim bladder. We therefore used the Ecopath mass-balancing routine to estimate biomass for forage fish. We assumed a high *EE* (0.8), consistent with intense predation. There is but a trace level of fishing mortality (Table 5, also Appendix C).

We adopted the *P/B* and *Q/B* estimates for forage fish species from other EwE models of northeastern Pacific Ocean ecosystems. We took the *P/B* estimate (1.50 yr^{-1}) from the forage fish functional group in the northern California Current model developed by Field (2004). He describes that group as being primarily made up of northern anchovy, Pacific herring, eulachon, surf smelt, sand lance, American shad (*Alosa sapidissima*), and whitebait smelt (*Allosmerus elongatus*). Field (2004) aggregated natural mortality for this group over the life span of all species, thus representing the relatively high *P/B* of larvae and juveniles ($P/B = 5 \text{ to } 25 \text{ yr}^{-1}$), the low *P/B* of adults ($= 0.21 \text{ to } 1.3 \text{ yr}^{-1}$), and intermediate values for subadults.

The *Q/B* estimate was derived from the forage fish group in the northern British Columbia shelf ecosystem model by Ainsworth et al. (2002). We rounded their estimate up from 6.608 yr^{-1} to 7.0 yr^{-1} in order to reflect the slightly warmer water in Puget Sound. This estimate is slightly higher than Field's (2004) estimates for the pelagic forage fish groups in his northern California Current model ($5.0 \text{ to } 6.0 \text{ yr}^{-1}$), and slightly higher than the *Q/B* of 6.15 yr^{-1} determined by Gilman (1994) for Atlantic northern sand lance (*Ammodytes dubius*).

The mass-balancing step of Ecopath calculated a forage fish biomass of 3.461 mt km^{-2} , a standing stock that is somewhat smaller than the standing stock of Pacific herring (Table 3).

The estimated diet composition of forage fish comes from stomach analyses of surf smelt and sand lance. Forage fish stomach contents were sampled in the 1970s and 1980s, largely in the Strait of Juan de Fuca and the San Juan Islands (Miller et al. 1977, Miller et al. 1980),

although some information from Central Puget Sound does exist (Fresh et al. 1981). Surf smelt diets were a mix of copepods, isopods, gelatinous zooplankton, and euphausiids. The diets of sand lance mostly consisted of copepods, along with some pelagic amphipods. Combining these general diet characteristics, we assumed a diet mainly of copepods, along with small crustaceans, small gelatinous zooplankton, euphausiids, macrozooplankton, and a small amount of jellyfish (Table 4).

Forage fish are preyed upon by nearly all other vertebrates, along with squid and *Cancer* crabs (Table 4). We assume no predation by jellyfish.

Surfperches

This group includes several members of the family Embiotocidae. The most notable representatives are pile perch (*Rhacochilus vacca*), shiner perch (*Cymatogaster aggregata*), and striped seaperch (*Embiotoca lateralis*). They are often found schooling around habitats such as kelp stands, rocky reefs, eelgrass beds, and man-made structures. Their preference seems to be areas with high relief, macrophyte cover, and rich invertebrate populations (Fritzche and Hassler 1989). Schools may contain tens to thousands of individuals. Habitat use, depth distribution, and school density may change from day to night and with season (Fritzche and Hassler 1989, Love 1996). Embiotocids are live-bearing (viviparous) fishes with very low fecundity (<100 larvae per female, Love 1996), and their population sustainability depends on relatively high survival rates of newly released larvae and juveniles (Quinnel 1986). They prey upon a variety of invertebrates, and the larger species in this group (pile perch and striped seaperch) have a feeding morphology particularly evolved to feed on benthic invertebrates (Fritzche and Hassler 1989 and references therein). Surfperches are popular target species for recreational anglers fishing from piers, jetties, small boats, or shorelines (Fritzche and Hassler 1989, Love 1996).

There are no comprehensive biomass surveys for surfperches in Puget Sound. Therefore, we used the Ecopath mass-balancing routine to solve for initial surfperch biomass. *EE* was set at 0.8, which presumes a substantial proportion of production lost to predators. Losses to fishing are minor in the current initial model state (Table 5), although we lack data on catches by recreational anglers.

Estimates of surfperch mortality rates on the west coast of North America are limited. Eckmayer (1975, cited in Lane et al. 2002) calculated instantaneous annual mortality rates (*Z*) for walleye surfperch (*Hyperprosopon argenteum*) and white seaperch (*Phanerodon furcatus*) in Anaheim Bay, California. The former species had an average *Z* of 1.280 yr⁻¹, while the latter species' *Z* was age-specific and ranged from 0.588 yr⁻¹ (age 3 fish) to 1.792 yr⁻¹ (age 4 fish). Estimates for the major species in PSCB are unavailable, but they are expected to have life spans of 6–10 years (Baltz 1984, Lane et al. 2002, Shanks and Eckert 2005), which puts them in approximately the same category as Pacific herring. Based on this information, we assumed a *P/B* rate of 1.3 yr⁻¹ for surfperches.

We estimated *Q/B* for surfperches based on Christensen and Pauly's (1992) equation for determining consumption as a function of maximum weight and average temperature (Appendix C). We used maximum weights as described in Lane et al. (2002) for shiner perch (170 g), striped seaperch (870 g) and pile perch (1,160 g). At near-surface annual average temperature

(10.68°C), these weights produce Q/B ratios of 6.83 yr⁻¹, 5.19 yr⁻¹, and 4.95 yr⁻¹, respectively. Given this range of values, we set surfperch Q/B at 6.0 yr⁻¹.

Given the parameter estimates and the top-down demands of predators and fisheries, the Ecopath mass-balancing routine calculated that initial surfperch biomass is 3.170 mt km⁻². Surfperches are most likely associated with benthic habitats between 0 and 30 m depth in Puget Sound, which restricts them to approximately 28% of the study area according to bathymetric data (Table 1). This translates to nearshore densities of 11.321 mt km⁻², which is more than double the standing stock measurements made of embiotocids in Southern California kelp beds (Quast 1968). We lack information to determine the accuracy of our estimate.

Surfperch diets come from numerous studies, many summarized by Fritzsche and Hassler (1989) and Emmett et al. (1991). Haldorson and Moser (1979) examined frequency of occurrence of prey in pile perch and striped seaperch; predominant prey included small benthic crustaceans, mussels, snails, and barnacles. Emmett et al. (1991) summarized shiner perch diets as dependent on copepods and a mix of benthic invertebrates. Reum (2006, unpubl. data) examined stomachs of shiner perch and pile perch from PSCB and found high dependence on copepods, small bivalves, and small crustaceans. Based on these sources, we input an initial diet that emphasizes infaunal bivalves, copepods, and small crustaceans (Table 4). Lesser importance was given to other grazers, mussels, barnacles, shrimp, predatory gastropods, soft infauna, and deposit feeders.

Surfperches are preyed upon by harbor seals, sea lions, resident and migratory diving birds, spiny dogfish, skates, ratfish, lingcod, adult rockfish, piscivorous and small-mouthed flatfish, demersal fish, and *Cancer* crabs (Table 4).

Salmon

Pacific salmon (*Oncorhynchus* spp.) are perhaps the most significant species in Puget Sound and throughout the Pacific Northwest region as a whole, in terms of their ecological, economic, social, and cultural importance. Their complex life histories feature extended residences in diverse habitats and dramatic mass migrations. These habitats link multiple ecosystems together and provide critical sources of prey, energy, and nutrients in communities where salmon rear, migrate, and spawn. Fisheries targeting Pacific salmon are sources of revenue and employment; formerly, salmon fisheries were also vital sources of food for indigenous peoples. Salmon appeal to tourists through opportunities such as recreational fishing, viewing salmon along their spawning migrations (including whale-watching trips that track killer whales as they feed on salmon schools), and regional cuisine. The well-documented declines in many salmon populations (e.g., Ruckelshaus et al. 2002) have also placed them at the epicenter of numerous policy debates related to land and water use, water quality, habitat conservation and restoration, fisheries management, aquacultural practices, and even the nature of protected species legislation (Waples 1991, Waples 1998).

Clearly, it is important that this modeling effort include Pacific salmon functional groups, but the complexity of salmon life histories, migrations, and habitat dependencies is very difficult for the Ecopath with Ecosim software to handle. Among the major constraints, first, the ephemeral nature of habitat use by salmon is difficult to capture in a food web model that lacks

spatially explicit diets, rates of mortality, rates of growth, etc. Second, the scale of salmon migrations means that they may spend large amounts of time outside of the model domain, either in freshwater systems at the beginning and end of their lives or in marine systems during the time when they accumulate most of their growth. Third, the equations that link together multiple life history stages of functional groups (Appendix D)⁸ are not ideal for salmon because salmon do not grow according to von Bertalanffy–style growth trajectories (Lester et al. 2004), and nearly all *Oncorhynchus* species follow a semelparous reproductive strategy that the model was not designed to simulate. Fourth, salmon populations within an ecosystem often have considerable differences in life history and ecology, even when they are of the same species (e.g., Groot and Margolis 1991).

Capturing the full range of life history and ecological variation among all distinct salmon populations might require a large number of salmon functional groups (e.g., Preikshot and Beattie 2001, Harvey and Kareiva 2005). It is unlikely that we would have accurate information on how other species in the system interact (e.g., as prey or predators) with many of these discrete stocks.

Given the importance of Pacific salmon and the modeling challenges that they present, we chose to simplify them into three functional groups: pink salmon (*O. gorbuscha*), wild salmon, and hatchery salmon. The uniqueness of the pink salmon life history warranted distinction as a functional group. The wild and hatchery salmon groups are aggregations of several species (Chinook salmon [*O. tshawytscha*], coho salmon [*O. kisutch*], chum salmon [*O. keta*], and steelhead [*O. mykiss*]). As the names suggest, wild salmon are naturally sustaining populations, whereas hatchery salmon are artificially propagated. Sockeye salmon (*O. nerka*) were omitted altogether, as justified in Appendix B.

Each group has two stages: a juvenile stage that represents the months following entry into the marine environment when they tend to use nearshore habitats (e.g., Fresh 2006), and a subadult stage that begins when they move into more pelagic habitats and continues until they return to freshwater to spawn. This compromise is far from perfect. It is an attempt to represent salmon as components in the ecosystem without expending exhaustive effort on a larger number of salmon functional groups that would be very difficult to model with an acceptable degree of realism. Clearly, the salmon groups are ones where improvement will be needed, and where caution will be necessary as output is interpreted.

Pink Salmon

Pink salmon have the simplest, most specialized life history of Pacific salmon (Heard 1991). Following emergence from redds, fry rapidly move into estuarine or nearshore marine environments, where they remain for a period of weeks to months, then quickly pass through coastal systems to the open North Pacific Ocean. After approximately 18 months at sea, they

⁸ Difficulties with handling the discrete stages of salmon life history were compounded by problems we encountered with a feature of EwE that allows the user to break life history into three or more stanzas. Having that ability would potentially allow much greater realism in terms of representing salmon as semelparous species that spend discrete time periods in different habitats. However, we were not confident in many of the parameter values that Ecopath forcibly estimated when we used the multistanza feature. We therefore used the simpler feature that enables separation into two stanzas.

return to their natal streams in the fall, spawn, and die. This two-year life history is fixed. Virtually all pink salmon in Puget Sound are odd year stocks, meaning that adults spawn in odd calendar years (Heard 1991). More than 99% of Puget Sound pink salmon are of wild origin (PFMC 2008).

The adult population is large but variable. Recent run sizes (i.e., numbers harvested plus numbers that escaped to spawn in rivers and streams throughout all basins of Puget Sound) have ranged from 440,000 adults in 1997 to 3.5 million adults in 2001 (PFMC 2008). Most are destined for watersheds located north of the PSCB domain (e.g., the Skagit and Stillaguamish rivers in the Whidbey Basin), but several notable populations move through PSCB: the Puyallup River and Green River populations (both of which spawn within the PSCB drainage) and the Nisqually River population (which spawns in the South Puget Sound drainage), although the Nisqually stock has declined steeply (stock description online at http://wdfw.wa.gov/webmaps/salmonscape/sasi/full_stock_rpts/4585.pdf). The Green River population has increased markedly over the last decade from negligible levels to a sizeable run (Hard et al. 1996, PFMC 2008).

We divided pink salmon into juvenile and subadult stages, with the transition occurring at 2 months of age. We assigned this transition age based on the Simenstad et al. (1982) review of literature on juvenile pink salmon residence times in Puget Sound estuaries and basins. The juvenile stage includes the estuarine and nearshore marine rearing periods following emergence. We assume the estuarine portion of this stage to occur outside of the model domain. The subadult stage includes the rest of the life history up to and including the period when the approximately 18-month-old pink salmon reenter Puget Sound and move toward spawning streams, a time at which they may also be captured by fisheries.

Estimating biomass for pink salmon is difficult to do empirically, in part because both life history stages are transient. Populations from PSCB and adjacent basins reside in PSCB waters for varying amounts of time, while also spending substantial time outside the basin. We chose to use the Ecopath mass-balancing routine to estimate biomass for both life history stages. To facilitate this, we first set *EE* for juveniles at 0.2 (reasoning that a substantial component of their mortality occurs before they enter PSCB) and for subadults at 0.1 (reasoning that they experience only a small amount of mortality in PSCB, in the form of a small fishery and some predation, and that most of their mortality either occurs during their extended residence in the North Pacific or in freshwater on the spawning grounds).

We are unaware of any data on juvenile pink salmon *P/B* or natural mortality rates in Puget Sound. We assumed rates of early marine mortality similar to those observed by Parker (1968) for pink salmon juveniles from the Bella Coola River, British Columbia, in the early 1960s. Between 23% and 45% of juvenile pink salmon survived their first 40 days at sea in that study. From the midpoint of 34% survival in 40 days, we get a daily instantaneous mortality rate of 0.027, which when scaled to an annual time step yields a *P/B* of 9.844 yr⁻¹ for juvenile pink salmon. Parker (1968) also estimated mortality for subadults during the subsequent 410 days at sea; that estimate is 1.351 yr⁻¹ after rescaling to an annual time step. Fisheries add further mortality. Based on geometric mean catch data in PSCB from 1999 to 2007 (Appendix C) and geometric mean escapement data (PFMC 2008), we calculated an *F* of 0.226 yr⁻¹, resulting in a total *P/B* of 1.577 yr⁻¹ for subadults. Cumulatively, these mortality rates result in a fry-to-adult

return rate of approximately 3.25%, which is well within the range reported for many pink salmon populations (e.g., Heard 1991).

Estimates of juvenile pink salmon consumption rates are available from empirical studies. Parker and LeBrasseur (1974) estimated daily consumption rates of 7–8% body weight by juvenile pink salmon early in their marine residence. Healey (1982) used gastric evacuation rate estimates to calculate daily consumption rates of 4.6–11.2% body weight per day for juvenile pink salmon in the Strait of Georgia. Godin (1981) measured daily consumption of 6.6–13.1% body weight for juvenile pink salmon near Nanaimo, British Columbia. Simenstad et al. (1980) measured consumption of 30.2% body weight per day among pink salmon fry in Puget Sound. Because most of these estimates fell in the range of 4.6–13%, we assumed a consumption rate of 9% body weight per day, or a Q/B rate of 32.85 yr^{-1} for juvenile pink salmon. This produces a P/Q estimate for juvenile pink salmon of 0.3, which is equal to independent growth efficiency estimates made by Duffy (2003) for juvenile pink salmon in the Whidbey Basin.

For subadult Q/B , we used the pink salmon bioenergetics models of Beauchamp et al. (1989) and Moss et al. (2009). We ran a 16-month simulation, assuming monthly temperatures consistent with the upper 25 m of the water column in PSCB from WDE (no date), a prey energy density fixed at $3,500 \text{ J g}^{-1}$ (consistent with a diet of copepods, euphausiids, larvaceans, and macrozooplankton, Moss et al. 2009), and a consumer energy density of $4,534 \text{ J g}^{-1}$ (Moss et al. 2009). The initial weight in the simulation (40 g) approximated the weight at age 60 days (the transition age from juvenile to subadult). The final weight (1,616 g) was taken from average weights of pink salmon captured in Puget Sound fisheries between 1999 and 2007 (PacFIN unpubl. data, also Appendix C). The model produced daily consumption estimates, which we divided by body weights to get daily Q/B ratios. We weighted daily Q/B ratios by daily body size and abundance in a theoretical equilibrium population with a natural mortality rate of 1.351 yr^{-1} , and arrived at an annual Q/B ratio of 13.429 yr^{-1} .

The mass-balancing routine of Ecopath arrived at biomass values of $0.00845 \text{ mt km}^{-2}$ for juvenile pink salmon and $0.0772 \text{ mt km}^{-2}$ for subadult pink salmon. These values compare favorably to rough calculations of pink salmon run size and reproductive output in the Central and South Puget Sound basins over recent decades. Pink salmon escapements to the Central and South Puget Sound basins of have been estimated back to 1983 by the Pacific Fishery Management Council (PFMC).⁹ Run sizes are highly variable, ranging from approximately 3,400 in 1997 to approximately 630,000 in 2007. The geometric mean escapement to Central Puget Sound plus South Puget Sound from 1983 to 2007 is approximately 30,400 individuals, and the geometric mean odd-year commercial harvest is approximately 3,900 individuals (PFMC 2008). On average, these values sum to about 2% of the entire pink salmon run to Puget Sound over that time period (PFMC 2008). Geometric mean recreational harvest in all of Puget Sound is approximately 55,000 pink salmon per odd year over the same time period. Assuming that approximately 2% of that catch was destined for the Central or South Puget Sound basins adds an additional 1,100 individuals per odd year. The sum of these values ($30,400 + 3,900 + 1,100$) gives an approximate odd-year run size of 35,400 individuals. Pink salmon captured in PSCB between 1999 and 2007 averaged 1.616 kg (PacFIN unpubl. data).

⁹ PFMC run reconstructions do not include the Green River pink salmon population, which has not been monitored historically but has had substantial odd-year runs since 2001 (PFMC 2008).

This leads to a total return weight of 57.206 mt or 0.076 mt km⁻². Dividing this in half (because they return only every other year) yields a biomass of 0.038 mt km⁻², which is in the same order of magnitude as our subadult estimate. We might assume that the Green River population is approximately equal to the Puyallup River population (at least in recent years), which would double the biomass estimate. Moreover, a spawning population of 60,800 adults with a 1:1 sex ratio, a fecundity of 2,000 eggs per female, and an egg-to-fry mortality rate of 87.3% (Parker 1968, Quinn 2005) would yield approximately 7.72 million fry that survive to enter the marine environment the following spring. An initial weight of 0.24 g (Heard 1991) leads to a juvenile biomass of 1.853 mt or 0.0024 mt km⁻². Dividing by 2 for odd years results in a biomass of 0.0012 mt km⁻², which is well below the Ecopath estimate for juveniles, although rapid early marine growth may make up some of the difference between the emergent fry biomass estimate and the Ecopath biomass estimate.

The values described above do not reflect the recent sharp increases in adult pink salmon returns to the Puyallup and Green rivers: They now number in the hundreds of thousands, which is two orders of magnitude greater than typical runs of the 1990s and early 2000s (PFMC 2008). This likely means that values for biomass, *P/B*, and *EE* would be different in a model calibrated for 2009. We may explore the consequences of this change in later Ecosim simulations.

Juvenile pink salmon diets in Puget Sound and nearby systems have been summarized by Simenstad et al. (1982), Heard (1991), and Rice (unpubl. data). We arbitrarily input 40% of their diet as Import to account for time spent outside the model domain, and also to account for prey not tracked explicitly in the model (e.g., insect larvae and fish eggs). The remainder of the diet was mostly copepods, euphausiids, and small gelatinous zooplankton, with minor contributions from macrozooplankton and small crustaceans (Table 4). Subadult pink salmon were assumed to spend most of their time outside of the model domain; we assumed 90% of their diet was Import. The remaining component—mostly euphausiids—was based on diets of juvenile and subadult pink salmon captured in offshore pelagic habitats in Puget Sound by Rice (unpubl. data).

Juvenile pink salmon are preyed upon by harbor seals, gulls, resident diving birds, and migratory diving birds (Table 4). Other sources of predation (e.g., predatory fishes) are likely but we do not have data to quantify them. Subadults are preyed upon by harbor seals, sea lions, raptors, and spiny dogfish. A small fishery (compared to other salmon groups) comprised of several gear types takes pink salmon during odd years (Table 5, Appendix C).

We linked the juvenile and subadult pools in Ecosim using the delay-difference equations for stage-structured populations (Appendix D). We set the recruitment power parameter at 0.85, the age at transition from juvenile to subadult at 0.167 years, the weight ratio of an average subadult relative to an individual at the transition age at 100, and the von Bertalanffy growth parameter *k* at 0.14. The weight ratio and *k* parameters were approximations based on size-at-age data in Heard (1991) and the recruitment power parameter was lowered from one based on recommendations in Christensen et al. (2005). All other parameters in the delay-difference equations were set at the default values as listed in Appendix D.

Wild Salmon

This group includes juveniles and subadults from naturally reproducing populations of chum, Chinook, and coho salmon and steelhead. Although these stocks are naturally reproducing, some may be mixed stocks that originated from both native populations and naturalized hatchery releases (stock descriptions online at <http://wdfw.wa.gov/fish/sasi/>). Chum salmon are the largest component in terms of total biomass and abundance. Steelhead are a very minor component.

Our archetypal wild salmon most closely, but not entirely, reflects the life history of chum salmon because they are the most numerous representative of this group. Following an initial freshwater phase, juvenile wild fish immigrate to nearshore marine habitats, where they remain for approximately 3 months (Simenstad et al. 1982, Fresh 2006). At the end of this phase, we assume that they weigh approximately 200 g, consistent with observations that chum salmon, which enter the system weighing between 2 and 3 g, grow at an exponential rate of approximately 5% body weight per day (Salo 1991). After leaving the nearshore area, subadults spend the majority of their time outside of the PSCB model domain, although a fraction remain resident for part or perhaps all of that period (O'Neill and West 2009).

We assume a subadult marine phase lasting 3 years, which is the longer end of the typical range for chum and is also a reasonable marine life history duration for Chinook salmon (e.g., Myers et al. 1998). We assume that they grow to approximately 5 kg in size, that is, slightly larger than a typical adult chum salmon returning to Central or South Puget Sound, but smaller than a typical returning adult Chinook salmon (PacFIN unpubl. data). Returning subadults are subject to intense commercial and recreational fisheries, unless regulations protect them from fishing. Maturing adults eventually reach their natal creeks, spawn, and die (except for small numbers of iteroparous steelhead, Busby et al. 1996).

Estimating the biomass of juvenile and subadult stages of wild salmon is difficult due to several factors. For one thing, the biomass of this group might include transient populations moving through PSCB to or from other basins. Variable, population-specific migration timing, residency, and size add further complexity (e.g., Duffy et al. 2005). Moreover, our decision to pool many species and populations together in this functional group introduces another problem: Individual weights vary considerably, both at the juvenile and subadult stage.

Because of these issues, we allowed Ecopath to estimate biomass for juvenile and adult wild salmon. To facilitate this, we arbitrarily set *EE* for both juveniles and subadults at 0.2. Our rationale for the juvenile wild salmon *EE* is that much of this group's biomass spends weeks or months outside of the model domain (e.g., in freshwater or in South Puget Sound) before entering PSCB, and thus their *EE* should not be set too high. For subadults, we reasoned that most spend the vast majority of their time at sea, outside of PSCB (i.e., that the resident populations are of minor importance, but see O'Neill and West 2009). Thus their *EE* must be relatively low, but it must be greater than zero because they are targeted by fishing inside and outside of the model domain, and the developers of the EwE software recommend accounting for all fishing pressure directed at a modeled functional group, whether or not that fishing pressure occurs within the bounds of the modeled ecosystem (Christensen et al. 2005).

We examined the available literature for wild salmon P/B rates. The only empirical data for Puget Sound of which we are aware are estimates for juvenile chum salmon mortality rates in the Hood Canal Basin (Bax 1983, Whitmus 1985). These rates were unsustainably high when extrapolated beyond a few days: daily rates of mortality ranged between 31% and 46%. Instead, we used information on long-term survival rates of wild or naturally rearing chum, coho, and Chinook populations, summarized by Quinn (2005, his Table 15-1). That summary includes smolt-to-adult survival rates based on a large number of empirical studies. The proportion of smolts surviving to adulthood were 0.014, 0.031, and 0.104 for chum, Chinook, and coho, respectively (Quinn 2005). Assuming 36-month subadult phases, these values scale to instantaneous annual mortality rates of 0.949 yr^{-1} , 0.772 yr^{-1} , and 0.503 yr^{-1} for the three species. We assumed that mortality rates for juveniles were sixfold higher than for subadults (an arbitrary approximation based on the P/B ratios we calculated for pink salmon, see previous subsection), which yielded juvenile P/B of 5.692 yr^{-1} for chum salmon, 4.632 yr^{-1} for Chinook salmon, and 3.018 yr^{-1} for coho salmon. We then weighted the mortality rates (at monthly intervals) by the projected abundances and weights of the three species to come up with the final weighted estimates of 5.591 yr^{-1} for juveniles and 0.989 yr^{-1} for subadults.

We estimated juvenile wild salmon Q/B based on several indirect measures taken from the literature. Duffy (2003) estimated growth efficiency of juvenile chum, Chinook, and coho salmon in the Whidbey and South Puget Sound basins, using salmonid bioenergetics models and empirically derived diet and growth estimates. Spring and summer growth efficiencies of juvenile chum salmon were quite high (40%) in the Whidbey Basin, but were lower in the South Puget Sound Basin (26–34%). Growth efficiencies of Chinook and coho salmon juveniles were much lower (Chinook = 12–22%, coho = 17–25%). If the most conservative juvenile chum salmon growth efficiency (26%, i.e., $P/Q = 0.26$) serves as a reasonable compromise, then dividing P/B by P/Q yields a Q/B estimate of 19.662 yr^{-1} .

However, the above Q/B estimate implies a ration of approximately 5.4% body weight per day on an annual basis. That ration is at the low end of the range of estimated springtime daily rations for juvenile chum salmon in the Nanaimo Estuary (4.4–18% body weight per day, Healey 1979), and is far lower than daily ration estimates made by Simenstad and Salo (1982) for juvenile chum salmon in Hood Canal. Simenstad and Salo's estimated daily rations (15–25% body weight) would produce extraordinary Q/B ratios (54.75 to 91.25 yr^{-1}) over the course of a full year; those ratios may, in fact, be reasonable, because chum salmon grow very rapidly during the nearshore phase (Healey 1979, Salo 1991, Quinn 2005). For now, however, we assumed a relatively conservative Q/B of 30 yr^{-1} for this group.

For subadult wild salmon, we used in situ daily ration estimates derived from a study of chum salmon feeding in continental shelf areas of the North Pacific Ocean (Kosenok and Naidenko 2008). They found seasonal daily rations of 2.6–2.8% body weight (summer) and 1.2–2.5% body weight (fall). We took seasonal midpoints (2.7% and 1.85%, respectively) and also the lowest observed ration (1.2%), and assumed that the average of those three values (1.917%) was a reasonable mean overall daily ration; that equates to a Q/B of 7.00 yr^{-1} . The resulting P/Q (0.141) is greater than that of subadult pink salmon (0.117).

Given these parameters and the top-down requirements of predators and fisheries, Ecopath calculated biomass of $0.0951 \text{ mt km}^{-2}$ for juvenile wild salmon and $11.918 \text{ mt km}^{-2}$ for

subadult wild salmon. As noted above, it is very difficult to empirically verify these biomass estimates. The subadult value can be compared to a rough approximation of returning chum salmon biomass in recent spawning runs. Naturally produced chum salmon run sizes (i.e., harvest plus escapement) to Central and South Puget Sound in recent years have been close to 500,000 fish (WDFW no date). We can further assume tens of thousands more returning wild Chinook, coho, and steelhead (PFMC 2008).

Assuming a mean weight of 5 kg for these fish, a run of 600,000 wild salmon would yield 3,000 mt of biomass, or approximately 4 mt km⁻² moving through the PSCB model domain. Although that number is substantially less than our biomass estimate, we note that the subadult pool spends a considerable amount of time outside of PSCB, and in any given year only a portion of all of the subadult biomass will actually be maturing and reentering Puget Sound. Thus the biomass estimate should realistically exceed the biomass of the total run, and our biomass estimate may be plausible. This issue highlights the desirability of finer age structure of the salmon pools, so that different phases of salmon life history could be modeled more discretely.

Wild salmon diets are difficult to characterize because they can vary markedly by species, size, habitat type, season, and location (e.g., Levy and Levings 1978, Groot and Margolis 1991, Quinn 2005). We largely relied on diet data for juvenile chum, Chinook, and coho salmon in Washington estuaries, as summarized by Simenstad et al. (1982, their Table 5). We gleaned additional diet information from a report on nearshore habitat use by juvenile salmon in PSCB by Brennan et al. (2004).

In calculating a grand mean diet for juvenile wild salmon, we weighted the mean diet data from Simenstad et al. (1982) according to the proportional abundances of juveniles, as derived from the *P/B* estimation exercise outlined previously. We also assumed that 33% of their diet was Import: 25% of the diet was assumed to have been consumed outside the model domain, and an additional 8% were prey items that were eaten in the PSCB model domain but are not functional groups in the model (e.g., insects). Besides Import, diets consisted mostly of mobile invertebrates—small crustaceans, copepods, macrozooplankton, euphausiids, small gelatinous zooplankton, soft infauna, shrimp, and microzooplankton (Table 4). Approximately 5% was assigned to fish groups, which is consistent with Simenstad et al. (1982) although they did not specify the taxonomy of consumed fishes. We expect some predation to be on juvenile Pacific herring, sand lance, surfperch, and demersal fish, based on recent stomach samples from juvenile salmon captured in the Whidbey Basin (Rice unpubl. data).

Subadult wild salmon diets are dominated by prey eaten outside of the model domain, where most subadult wild salmon growth occurs. Import accounts for 90% of their diet. For the remainder, we used stomach content data from salmon captured in pelagic habitats in the adjacent Whidbey Basin (Rice unpubl. data). Principal prey items were macrozooplankton and small gelatinous zooplankton, along with euphausiids, forage fish, and Pacific herring (Table 4).

Predation on juvenile wild salmon is poorly characterized in this model. Currently, we only include juvenile lingcod, harbor seals, and certain seabirds as predators on juvenile wild salmon. It seems likely that other fishes and possibly some large invertebrates feed on them as well. We include harbor seals, sea lions, raptors, spiny dogfish, and adult lingcod as predators on subadult wild salmon.

Several fisheries target subadult wild salmon passing through PSCB. In terms of biomass landed, this functional group supports a larger fishery than any other in the model (Table 5). Estimates of commercial catches come from PFMC run reconstructions of wild Chinook and coho salmon (2008) and from WDFW for chum salmon (no date). We used geometric mean landings from 1996 to 2002 (Table 5); catches were allocated among different gear types according to data from PacFIN (Appendix C).

In addition, recreational anglers take many wild subadults each year. PFMC estimates total recreational catches of Chinook and coho salmon in Puget Sound, but the data are not broken down by basin nor are they separated into wild and hatchery stocks (PFMC 2008). Thus we made some assumptions with respect to recreational harvest. Because wild salmon (particularly Chinook and coho salmon) are protected from recreational harvest for much of the year in marine waters of Puget Sound (WDFW 2009), we arbitrarily assumed that only 20% of recreationally caught Chinook and coho salmon were wild fish. We also assumed that recreational landings were proportional to the reconstructed run sizes to the different regions of Puget Sound (PFMC 2008).

During 1996–2002, geometric mean recreational harvests were 34,646 Chinook salmon and 74,352 coho salmon in all of Puget Sound. During that same time period, approximately 79% of the total wild Chinook salmon and 16% of the total wild coho salmon returning to Puget Sound passed through PSCB (PFMC 2008). At those proportions and assuming 20% of the recreationally harvested fish were wild, the average recreational harvest would be 5,489 Chinook and 2,401 coho subadults. For chum salmon, we assumed that recreational chum salmon landings were approximately 90% wild (i.e., proportional to wild and hatchery run sizes). Based on this, we assumed approximately 1,800 wild chum salmon were taken annually in the recreational harvest (i.e., 90% of the long-term average of recreational chum salmon catches near the Nisqually River and Kennedy Creek, WDFW no date). Assuming mean weights of 6 kg, 2.5 kg, and 4 kg for returning adult Chinook, coho, and chum salmon, respectively, total recreational harvest equals 0.061 mt km^{-2} .

We linked the juvenile and subadult pools in Ecosim using the delay-difference equations for stage-structured populations (Appendix D). We set the recruitment power parameter at 0.85, the age at transition from juvenile to subadult at 0.25 year, the weight ratio of an average subadult relative to an individual at the transition age at 25, and the von Bertalanffy growth parameter k at 0.15. The weight ratio and k parameters were approximations based on size-at-age data in Salo (1991) and Healey (1991), and the recruitment power parameter was lowered from one based on recommendations in Christensen et al. (2005). All other parameters in the delay-difference equations were set at the default values as listed in Appendix D.

Hatchery Salmon

Hatchery salmon are produced by state, federal, and tribal hatcheries throughout the Pacific Northwest, mainly for the purpose of supporting salmon fisheries and more recently in a variety of efforts to help restore declining wild stocks. More than 20 state and tribal hatcheries produce salmon in tributaries to PSCB or in the South Puget Sound Basin (map of these hatcheries online at http://wdfw.wa.gov/hat/graphics/hat_map.jpg). Hatcheries release juvenile

salmon at different ages and sizes, including many that are at the smolting stage and are physiologically ready to migrate to sea.

The hatchery salmon group contains the same four species as the wild salmon group (Chinook, chum, coho, and steelhead), but in different relative amounts compared to the wild group, which was dominated by chum salmon. Between 1995 and 2001, state-run hatcheries alone released between 10 million and 18 million hatchery-reared juvenile Chinook, chum, coho, and steelhead annually into rivers feeding PSCB (WDFW unpubl. data). They released an additional 15 million to 22 million into South Puget Sound streams (WDFW unpubl. data), the survivors of which would presumably have moved through PSCB as they migrated seaward. These releases tended to be approximately 60% Chinook salmon, 28% coho salmon, 9% chum salmon, and less than 3% steelhead.

Annual releases from tribal hatcheries during the same time period ranged from approximately 8 million to 12 million juveniles in PSCB tributaries and 3 million to 6 million juveniles in South Puget Sound tributaries. These releases were approximately 53% Chinook salmon, 28.5% chum salmon, 17% coho salmon, and just over 1% steelhead (RMPC unpubl. data). Returns were also substantial and reflected a greater importance of Chinook and coho salmon. From 1996 to 2002, geometric mean escapements of hatchery adults to Central and South Puget Sound catchments were approximately 39,900 Chinook, 73,800 coho, and 27,100 chum adults (PFMC 2008, WDFW no date).

Modeling hatchery salmon as a distinct group is necessary for several reasons. First, because they are artificially propagated, they are relatively disconnected from the ecology of the system. The number of juveniles in the system is a function of human decisions as much as it is a function of environmental conditions. Second, they are subject to certain fisheries that wild salmon are not; for example, some wild stocks of Chinook salmon are protected and must be released when caught, whereas anglers can retain hatchery-produced Chinook salmon, identifiable by the clipped adipose fin. Third, hatchery production is a controversial practice, due to the potential impacts of hatchery salmon competing with or interbreeding with wild salmon (e.g., Ruckelshaus et al. 2002). Having distinct hatchery salmon pools in the model allows us to explore scenarios in which hatchery production is changed with the intent of obtaining a management or conservation objective.

Our archetypal hatchery salmon is an attempt to approximate the life histories of chum, coho, and ocean-type Chinook salmon, that is, Chinook salmon whose juveniles migrate from freshwater to sea within months of becoming free-swimming fry and being released from the hatchery. They represent the majority of hatchery-produced Chinook salmon in Puget Sound (e.g., PFMC 2008). Chum salmon juveniles similarly enter the marine environment during their first spring, soon after release from the hatchery. By contrast, juvenile coho salmon and stream-type Chinook salmon are reared to be much larger and typically go to sea after rearing for more than a year in the hatchery and stream environments. We presume that the juvenile hatchery salmon stage, during which the salmon lives in nearshore marine habitats, lasts approximately 3 months (e.g., Simenstad et al. 1982). We assume a subadult marine phase lasting 2.5 years. This is a compromise between Puget Sound coho, which typically spend 18 months at sea (Weitkamp et al. 1995); chum, which typically spend 2 to 3 years at sea (Salo 1991); and Chinook, which typically spend at least 3 years at sea (Myers et al. 1998).

As with other salmon groups, we used the Ecopath mass-balancing algorithm to estimate biomass for both juvenile and subadult hatchery salmon. Of all salmon groups, juvenile hatchery salmon would perhaps be the most feasible for which to empirically derive biomass, because total annual releases are recorded by hatcheries. However, because variable levels of mortality occur before the released juveniles arrive in PSCB waters, and because hatchery releases from other basins including the Whidbey Basin and Hood Canal may spend a part of their time in PSCB,¹⁰ even the release data are not absolute measures of initial juvenile hatchery salmon biomass for PSCB. We set juvenile *EE* at 0.2, which partly accounts for the time they spend outside of PSCB. For subadults, we also assumed an *EE* of 0.2, reflecting that most of this phase is spent outside of PSCB, but also reflecting that an important portion of their annual production is lost to fisheries each year.

To estimate hatchery salmon *P/B*, we used data on postrelease mortality rates of hatchery stocks, and then parsed that mortality into the juvenile and subadult phases. Quinn et al. (2005) examined release-to-adult survival rates of Chinook and coho salmon from two hatcheries in Puget Sound from 1969 to 1998. The data they compiled from the Soos Creek hatchery probably best represent the majority of Puget Sound hatcheries, in terms of the size of salmon at the time of release (mean Chinook weight = 5.17 g, mean coho weight = 25.25 g). Differences were stark: estimated marine survival for Soos Creek hatchery Chinook salmon averaged 0.77%, while Soos Creek hatchery coho salmon averaged 7.35% (Quinn et al. 2005). Subyearling Chinook survival may have been lowered during even-numbered years by the presence of large numbers of juvenile pink salmon in Puget Sound, a conclusion also reached by Ruggerone and Goetz (2004).

Contemporary data on fry-to-adult survival of hatchery chum salmon from Puget Sound were not readily available in the literature. Survival reported by Salo (1991) for Hood Canal hatchery chum salmon ranged from 0.25 to 3.0%, although those data were from 1916 to 1971. For now, we assume that hatchery chum salmon have the same mean survival (1.4%) as reported by Quinn (2005) for naturally rearing chum salmon populations. We applied these species-specific survival rates to geometric means of estimated run sizes of hatchery salmon to Central and South Puget Sound from 1996 to 2002 (Chinook and coho salmon data from PFMC 2008, chum salmon data from WDFW no date) and back calculated the number of smolts required to produce the adult run sizes. We then solved for the necessary instantaneous annual mortality rates, assuming durations of 3 and 30 months for the juvenile and subadult phases, and also assuming (as with pink salmon and wild salmon, above) that juvenile mortality was sixfold greater than subadult mortality. Juvenile and adult mortality rates, respectively, were 7.300 yr⁻¹ and 1.217 yr⁻¹ for Chinook salmon, 3.916 yr⁻¹ and 0.653 yr⁻¹ for coho salmon, and 6.403 yr⁻¹ and 1.067 yr⁻¹ for chum salmon. We then weighted the mortality rates (at monthly intervals) by the projected abundances of the three species to come up with the final weighted estimates of 6.492 yr⁻¹ for juveniles and 1.017 yr⁻¹ for subadults.

In the absence of data to demonstrate otherwise, we opted to use the same *Q/B* estimates and justifications as were used for juvenile and subadult wild salmon (30 yr⁻¹ and 7 yr⁻¹, respectively). Strictly speaking, the two groups likely have different *Q/B* ratios because the relative abundances of Chinook, coho, and chum salmon within the two groups are different, but

¹⁰ K. Fresh, NWFSC, Seattle, WA. Pers. commun., 23 March 2009.

we assume that capturing the differences between the two salmon groups is not as important as capturing the relative differences between salmon, collectively, and nonsalmonid functional groups (i.e., intraguild differences are less important than interguild differences).

With the above parameters and the top-down demands of predators and fisheries on hatchery salmon (see below), Ecopath's mass-balancing procedure produced biomass estimates of 0.0819 mt km⁻² for juvenile hatchery salmon and 6.071 mt km⁻² for subadult hatchery salmon. By comparison, from 1996 to 2002, Central plus South Puget Sound run sizes averaged 56,000 hatchery Chinook salmon and 132,000 coho salmon (geometric means, PFMC 2008). Run sizes of hatchery-produced chum salmon at the same time had a geometric mean of approximately 51,500 (WDFW no date). Assuming individual body weights of 6 kg, 2.5 kg, and 4 kg for returning adult Chinook, coho, and chum salmon, respectively, these run sizes would have approximately 872 mt of salmon biomass, or 1.151 mt km⁻² moving through PSCB, which is much lower than the Ecopath biomass estimate. However, as with wild salmon (see Wild Salmon subsection above), we would expect the run-size biomass to be smaller than the Ecopath biomass estimate because a large amount of standing subadult biomass is at sea.

For juvenile hatchery salmon diets, we relied primarily on the nearshore juvenile salmon diet data provided in Simenstad et al. (1982) with further information from Brennan et al. (2004), and weighted the species-specific diets according to the juvenile abundance estimates generated during the *P/B* derivation exercise described above. We assume that 25% of their diet was consumed outside the model domain, and add a further 11% to account for prey that are consumed in PSCB but that are not part of the model (e.g., insects). This produces a total Import component of 36% of their diet. The remainder of the diet is dominated by zooplankton groups, small crustaceans, and small fishes (Table 4). Simenstad et al. (1982) did not specify which fishes appeared in juvenile salmon diets; we assume that it is mostly juvenile Pacific herring and forage fish, along with surfperches and demersal fish.

For subadults, we assume that 90% of their diet is Import, prey consumed outside the model domain. The remaining 10% was allocated among prey observed in subadult Chinook, coho, and chum salmon stomachs following capture in offshore pelagic habitats in the adjacent Whidbey Basin (Rice unpubl. data). Species-specific diets were weighted according to relative run-size estimates as alluded to in the *P/B* calculation section, described above. Key prey included macrozooplankton, forage fish, juvenile and adult Pacific herring, small gelatinous zooplankton, and euphausiids (Table 4).

As with other salmon groups, predation on hatchery salmon is poorly parameterized in this model. Currently, we include only juvenile lingcod, harbor seals, and certain seabirds as predators on juvenile hatchery salmon; however, it seems likely that other fishes and possibly some large invertebrates feed on them as well. We include harbor seals, sea lions, raptors, spiny dogfish, and adult lingcod as predators on subadult hatchery salmon.

Commercial fisheries use several gear types to catch subadult hatchery salmon. In total, these fisheries make subadult hatchery salmon the second most important source of landed biomass in the system, behind only subadult wild salmon (Table 5). Estimates of the commercial catch are available from the PFMC run reconstructions of hatchery Chinook and coho salmon (PFMC 2008) and from the WDFW for hatchery chum salmon (WDFW no date). We used

geometric mean landings from 1996 to 2002; catches were allocated among different gear types according to data from PacFIN (Appendix C).

In addition, recreational anglers take many hatchery-produced subadults each year. PFMC estimates total recreational catches of Chinook and coho salmon for the entirety of Puget Sound, but these catches are not broken down by basin nor are they separated into hatchery stocks and naturally reproducing stocks (PFMC 2008). Thus we made some assumptions with respect to recreational landings of subadult hatchery salmon. We arbitrarily assumed that 80% of recreational landings of Chinook and coho salmon are of hatchery fish, whereas recreational chum salmon landings were proportional to wild and hatchery chum salmon run sizes. Because PFMC's counts of recreational Chinook and coho landings in Puget Sound are not broken down by basin, we also assumed that recreational landings are proportional to the reconstructed total run sizes to each major basin or drainage in the PFMC analysis (PFMC 2008).

During the years 1996–2002 in all of Puget Sound, geometric mean recreational harvests were 34,646 Chinook salmon and 74,352 coho salmon. During that time period, approximately 67% of the total hatchery-produced Chinook salmon and 41% of the total hatchery-produced coho salmon that returned to Puget Sound passed through PSCB, according to the run reconstruction model (PFMC 2008). These assumptions lead to an average recreational harvest of 18,570 Chinook and 24,387 coho subadults. We further assume approximately 200 hatchery-produced chum salmon taken in the recreational harvest (i.e., 10% of the long-term average of recreational chum salmon catches near the Nisqually River and Kennedy Creek (WDFW no date). Assuming mean body weights of 6 kg, 2.5 kg, and 4 kg for returning adult Chinook, coho, and chum salmon, respectively, we are left with a recreational harvest of 0.229 mt km⁻².

We linked the juvenile and subadult pools in Ecosim using the delay-difference equations for stage-structured populations (Appendix D). We set the recruitment power parameter at 0.01, the age at transition from juvenile to subadult at 0.25 years, the weight ratio of an average subadult relative to an individual at the transition age at 25, and the von Bertalanffy growth parameter k at 0.15. The weight ratio and k parameters were approximations based on size-at-age data in Salo (1991) and Healey (1991). The recruitment power parameter was lowered drastically from the default of one because these are hatchery fish and thus their recruitment is essentially disconnected from adult run size, necessitating a low recruitment power parameter (Christensen et al. 2005). All other parameters in the delay-difference equations were set at the default values as listed in Appendix D.

Gadiforms

Gadiform fishes have undergone dramatic declines in biomass in Puget Sound in recent decades and are a focus of fisheries management concern in the ecosystem. The larger species are protected from fishing, in hopes of rebuilding local populations. We have divided representatives of this order into three monospecific functional groups, based on differences in their feeding ecology and status. A fourth gadiform, Pacific tomcod (*Microgadus proximus*), is included in an aggregated group of small groundfish (see Demersal Fish subsection below) because it is much smaller and has little commercial or recreational importance.

Pacific Hake

Pacific hake (*Merluccius productus*) are of great importance to the ecology and the fisheries of the west coast of North America. In particular, a massive stock of hake makes annual migrations between winter spawning grounds in southerly waters of the California Current ecosystem and summer feeding grounds off the coasts of British Columbia, Washington, and Oregon. That stock supports the largest fishery (in terms of biomass landed) on the U.S. West Coast. By contrast, two much smaller stocks with limited ranges of migration dwell year-round near the northern extent of their range, one in Puget Sound and the other in the Strait of Georgia (Gustafson et al. 2000). The three stocks are genetically discrete (Iwamoto et al. 2004). The Puget Sound stock was once far more abundant than now, but was badly depleted in the 1980s, most likely by heavy fishing pressure or possibly by ecological effects such as predation by pinnipeds (Gustafson et al. 2000).

Following a petition to list Puget Sound Pacific hake under the Endangered Species Act (Wright 1999), a federally appointed biological review team (BRT) concluded that the two Pacific hake stocks in the Puget Sound–Georgia Basin represent a distinct population segment (DPS) of the species as a whole (Gustafson et al. 2000). That DPS was judged by the BRT not to be worthy of listing as endangered, although the BRT did conclude that the DPS could possibly risk extinction in the near future. NOAA considers this DPS a Species of Concern (NOAA 2009), and WDFW considers it a Candidate Species, one whose status “may meet the listing criteria defined for State Endangered, Threatened, or Sensitive” (<http://wdfw.wa.gov/wlm/diversty/soc/candidat.htm>).

There are two major spawning areas in Puget Sound: Port Susan, located in the Whidbey Basin, and Dabob Bay, located in Hood Canal. Pacific hake gather in these areas to spawn during winter months and then disperse to feeding areas throughout the sound (Gustafson et al. 2000). Adults are primarily midwater feeders that prey on euphausiids and other crustaceans, cephalopods, and small fishes. They are preyed upon by many piscivorous fishes and pinnipeds. Fisheries targeting Pacific hake in Puget Sound ended in 1991 (Gustafson et al. 2000).

We used the Ecopath mass-balancing routine to estimate Pacific hake biomass. Hydroacoustic surveys from earlier decades indicated an 88% decline in the population biomass between 1983 and 1999, although much of this decline is due to a marked decrease in mean individual mass (Gustafson et al. 2000). There have also been declines in length at maturity. Because the population was obviously in a state of dramatic change, we felt it unwise to simply default to the most recent biomass estimate (2,365 mt in 1999, Gustafson et al. 2000) as our initial estimate for biomass. We assumed a very high *EE* (0.9) for Pacific hake, implying that predation by other model groups currently consumes 90% of production. This is consistent with the notion that Pacific hake numbers have continued to dwindle even though fishing was halted in 1991.

For Pacific hake *P/B*, we opted to use the mean production estimate from the status review of Puget Sound Pacific hake by Gustafson et al. (2000). Their instantaneous annual production estimates ranged from 0.30 to 0.51 yr⁻¹; we used the average, 0.405 yr⁻¹. This value exceeds the natural mortality estimate of 0.23 yr⁻¹ for the outer coast stock of Pacific hake, as estimated by Dorn et al. (1999). However, as Gustafson et al. (2000) note, a natural mortality of

0.23 yr⁻¹ coupled with a production rate of 0.30 to 0.51 yr⁻¹ would result in an increase of population biomass, not the precipitous decline described above. Thus we conservatively assume that total mortality (P/B) must at least equal the production estimate developed by Gustafson et al. (2000). This parameter merits further research.

We based the Pacific hake Q/B parameter on the bioenergetics analysis by Francis (1983) for Pacific hake on the outer coast. Francis estimated that Pacific hake consumption, in terms of percent body weight eaten each day, ranged from 0.713 (for large, age-8 individuals) to 1.094 (for small, age-2 individuals). Although we could apply the rate for small individuals to the Puget Sound stock, owing to the much smaller size-at-age of the Puget Sound stock compared to the outer coast stock (Gustafson et al. 2000), we opted instead to apply the rate for large individuals, reasoning that consumption rates for Pacific hake in Puget Sound must be relatively low in recent decades, as evidenced by the steep decline in individual growth rate. When 0.713% is multiplied by 365 days, the Q/B ratio for Pacific hake in PSCB is equal to 2.602 yr⁻¹. This estimate, combined with the P/B estimate, produces a reasonable P/Q estimate of 0.156.

Ecopath's mass-balancing routine estimated Pacific hake biomass at 3.405 mt km⁻², based on all other parameter inputs.

Pacific hake diet composition was based on the stomach analyses by Reum (2006, unpubl. data). As described in Appendix C, we seasonally weighted the raw stomach content data collected by Reum (unpubl. data), assuming a Q_{10} of 2.6 for food consumption based on bioenergetics modeling for a related species (walleye pollock) by Ciannelli et al. (1998). Approximately half of their diet is euphausiids; other key prey are macrozooplankton, shrimp, small crustaceans, juvenile Pacific herring, smaller Pacific hake, and soft infauna (Table 4).

Pacific hake in PSCB are eaten by harbor seals, sea lions, migratory diving birds, raptors, spiny dogfish, walleye pollock, lingcod, piscivorous flatfish, and demersal fish (Table 4). As noted in the preceding paragraph, Pacific hake are also mildly cannibalistic.

Pacific Cod

Pacific cod (*Gadus macrocephalus*) are large gadoids of great importance to the ecology and fisheries of the North Pacific. Puget Sound is close to the southeastern limit of this species' spatial range (Pedersen and DiDonato 1982). Once abundant and sought by recreational and commercial fisheries, Pacific cod have declined sharply since the 1980s and are now protected from commercial and recreational fishing throughout Puget Sound. A status review in the late 1990s concluded that this decline did not constitute an extinction threat to a distinct population segment (DPS) of the species as a whole, although the authors of the review acknowledged difficulty in defining DPSs at the scale of the Northeast Pacific (Gustafson et al. 2000). It is unclear whether protection from fishing has led to recovery for Pacific cod. Predation by pinnipeds, seabirds, and predatory fishes may be constraining recovery (Gustafson et al. 2000). Pacific cod are considered a Candidate Species by WDFW. It is because of this special status that we include them in this model: An ecosystem model may prove useful in exploring the feasibility (and ecological consequences) of restoring Pacific cod in Puget Sound.

For a biomass estimate, we used the most recent published information, derived from Gustafson et al. (2000), who cite data collected by W. Palsson (WDFW) in the 1990s. Palsson's trawl survey data indicated a total biomass of 252.25 mt of Pacific cod in PSCB, Admiralty Inlet, and Whidbey Basin combined. The PSCB makes up approximately two-thirds of this spatial area, so if we assume even spatial distribution, then the PSCB portion of that biomass is 169.01 mt, or 0.223 mt km⁻². More recent trawl surveys in PSCB conducted by Reum (2006, unpubl. data) suggest similar biomass; based on the methods detailed in Appendix C, Reum's data indicated a Pacific cod density of 0.181 mt km⁻². We used a value of 0.200 mt km⁻², which is roughly the average of the two empirical measures.

For our *P/B* estimate, we considered several sources. Natural mortality of Pacific cod in Washington and British Columbia waters has been reported as 0.65 yr⁻¹ (Fournier 1983, Gunderson 1997). More recent EwE studies from British Columbia waters imply lower rates. Ainsworth et al. (2002) used 0.258 yr⁻¹ for juveniles and 0.174 yr⁻¹ for adults, values derived from the method described in Appendix C. Priekshot (2007) used much greater natural mortalities for adults (0.37 yr⁻¹, derived from studies in Alaska by Thompson et al. (2003) and juveniles (0.8 yr⁻¹, source unknown). We elected to use 0.260 yr⁻¹, which is similar to the Ainsworth et al. (2002) estimate for juveniles and is in between the adult estimates by Ainsworth et al. and Priekshot (2007). It is much lower than the natural mortality estimate from Fournier (1983) and Gunderson (1997), but a low productivity rate may be appropriate for a species that has remained at low numbers despite more than a decade of protection from fishing.

We derived Pacific cod *Q/B* from Ainsworth et al. (2002), who estimated their values using methods described in Appendix C. They calculated juvenile and adult *Q/B* of 3.429 yr⁻¹ and 2.286 yr⁻¹, respectively, but their calculations assume temperatures of 4°C, which is considerably cooler than Puget Sound waters are likely to be in most seasons and at most depths (WDE no date). Using the same methods but assuming a mean temperature of 10.3°C, the juvenile and adult *Q/B* estimates are 4.540 yr⁻¹ and 3.027 yr⁻¹, respectively; we used the average of these two values, 3.784 yr⁻¹.

The Ecopath mass-balancing algorithm estimated Pacific cod *EE* to be 0.52, based on the above parameters and the top-down demands of predators plus a trace of fishing mortality (Table 5, Appendix C).

Pacific cod are predators and become increasingly piscivorous as they grow (Yang 2004). Our diet estimates are an attempt to represent both juvenile and adult feeding patterns, as described in nearby systems (Ainsworth et al. 2002, Priekshot 2007). Initial Pacific cod diets consist mostly of demersal fish, adult Pacific herring, small crustaceans, and forage fish (Table 4). Lesser contributions come from walleye pollock, small-mouthed flatfish, shrimp, adult *Cancer* crabs, deposit feeders, macrozooplankton, euphausiids, copepods, infaunal bivalves, squid, and other Pacific cod.

Besides cannibalism, the only explicit sources of predation mortality on Pacific cod are harbor seals, sea lions, and raptors (Table 4). We assume trace fishery removals (Table 5).

Walleye Pollock

Puget Sound is near the southeastern limit of the range of walleye pollock around the North Pacific Rim (Pedersen and DiDonato 1982). They are thought to have multiple spawning stocks in Puget Sound, although it is likely that only one stock is represented in PSCB (Gustafson et al. 2000). As with other large gadiforms, walleye pollock were formerly more abundant in Puget Sound, and were once targets of commercial and recreational fisheries; in PSCB, recreational fisheries were the main source of harvest. However, they have declined sharply since the 1980s and are now protected from commercial and recreational fishing. There is no clear evidence that this decline represents an extinction threat to walleye pollock as a whole (Gustafson et al. 2000). It remains unclear whether protection from fishing has led to recovery in Puget Sound. Predation by pinnipeds, seabirds, and predatory fishes may be constraining recovery (Gustafson et al. 2000).

Because no formal assessments of walleye pollock biomass have been conducted in the PSCB since the mid-1990s (Gustafson et al. 2000), we opted to allow the model to estimate walleye pollock biomass via the mass-balancing routine. We did attempt to estimate biomass based on recent research trawl data in PSCB (Reum 2006, unpubl. data), using the analytical methods described in Appendix C. However, the biomass estimates we calculated with that method (0.798 mt km^{-2}) were insufficient to balance the model: Walleye pollock EE was greater than one unless P/B was increased to greater than 2 yr^{-1} , which is nearly double the empirically derived rates for juvenile Alaska walleye pollock (Hollowed et al. 2000). The bottom-trawl gear used by Reum may have been inefficient at capturing walleye pollock, which spend some time off the bottom (Gustafson et al. 2000). For the purposes of mass balancing, we assumed a very high EE (0.9), implying an initial condition in which 90% of walleye pollock production is preyed upon by other model groups. We did so because there is speculation that pinniped predation is keeping gadiform populations from rebuilding in Puget Sound (e.g., Gustafson et al. 2000).

Our P/B estimates for walleye pollock stem from EwE models of two nearby systems (Beattie 2001, Priekshot 2007). In his model of the north and central coasts of British Columbia, Beattie (2001) estimated P/B of juvenile walleye pollock based on daily mortality estimates of age-1 and age-2 individuals that expand to an annual natural mortality rate of 1.061 yr^{-1} . For adults, Beattie (2001) cited a natural mortality rate of 0.15 yr^{-1} , estimated by Saunders and Andrews (1996). In his EwE model of the Strait of Georgia ecosystem, Priekshot (2007) cited several assessments of walleye pollock biology in Alaska waters, finding age-specific natural mortalities that ranged from 0.9 yr^{-1} for age-1 pollock (Ianelli et al. 2003) to 0.1 for fishable pollock in the Gulf of Alaska (Dorn et al. 2003). By contrast, Beamish et al. (1976) estimated a natural mortality rate of 0.84 yr^{-1} for Strait of Georgia walleye pollock. Priekshot (2007) settled on P/B estimates of 0.8 yr^{-1} and 0.4 yr^{-1} for juvenile and adult walleye pollock, respectively; again, those estimates include some fishing mortality. From this assortment of possibilities, we assumed a P/B of 0.8 yr^{-1} , which is similar to the Beamish et al. (1976) estimate for walleye pollock in the Strait of Georgia, and which falls between the juvenile and adult walleye pollock estimates used by Beattie (2001), but is skewed toward juveniles.

Our Q/B estimate draws from a simple assumption that walleye pollock $P/Q = 0.2$, as was assumed by Beattie (2001) and Ainsworth et al. (2002) in their EwE models of nearby systems. This assumption, coupled with our P/B estimate of 0.8 yr^{-1} , yielded a Q/B of 4.0 yr^{-1} .

With our parameter estimates plus the top-down demand of predators, Ecopath's mass-balancing function generated a biomass estimate of 3.704 mt km^{-2} for walleye pollock. This estimate clearly exceeds the estimate calculated from the trawl data of Reum (2006, but see caveats above), and should be treated with caution in the absence of an updated, comprehensive assessment of walleye pollock biomass.

Walleye pollock diets were estimated according to stomach contents of individuals captured in Central Puget Sound (Reum 2006, unpubl. data) and weighted by season to account for temperature effects on consumption rate (see methods in Appendix C). The resulting diet proportions were dominated by small crustaceans, euphausiids, shrimp, and macrozooplankton (Table 4). Lesser amounts came from Pacific hake, copepods, demersal fish, infaunal bivalves, soft infauna, and algal/plant material.

At different points of their life history, walleye pollock are fed upon by harbor seals, sea lions, resident diving birds, raptors, spiny dogfish, skates, ratfish, lingcod, piscivorous flatfish, small-mouthed flatfish, and demersal fish.

Other Demersal Roundfish

Rockfish

The rockfish group contains many species of *Sebastes* and, for the time being, also some large cottids (Table A-2). We made this grouping for two reasons: first, only a few of the *Sebastes* species are actually common in PSCB; second, we believe that the differences within this group (in terms of individual species' production and consumption rates, diets, predators, and importance to fisheries) are less important than the differences between this group and other functional groups. Given its broad range of sizes, ages, ecological roles, conservation status, and importance to fisheries, it is possible that this group may be split more finely in future model iterations.

Rockfish are a source of significant and growing conservation concern. Several *Sebastes* species in Table A-2, including relatively numerous ones like copper and quillback rockfish, are species of concern at the state and federal levels that may warrant listing as Sensitive, Threatened, or Endangered species (<http://wdfw.wa.gov/wlm/diversty/soc/candidat.htm>). Moreover, NOAA recently recommended listing the Puget Sound population of bocaccio as endangered and the Puget Sound populations of canary and yelloweye rockfish as threatened (<http://www.nwr.noaa.gov/Publications/FR-Notices/2009/upload/74FR18516.pdf>). These findings are consistent with broad, coast-wide concern for *Sebastes* populations, which have been shown to be vulnerable to fishing pressure and extended regimes of environmental conditions that do not support recruitment (Parker et al. 2000).

We elected to split the rockfish functional group into two life history stages, linked by a delay-difference equation (Appendix D). Rockfish populations typically consist of long-lived

Table A-2. Key representatives of the rockfish functional group in the PSCB EwE model. The order of appearance in this table does not necessarily indicate the order of abundance. Maximum lengths are also listed.

Common name	Scientific name	Maximum fork length (cm)
Copper rockfish	<i>Sebastes caurinus</i>	66 ^a
Quillback rockfish	<i>S. maliger</i>	61 ^a
Brown rockfish	<i>S. auriculatus</i>	56 ^a
Black rockfish	<i>S. melanops</i>	69 ^a
Bocaccio	<i>S. paucispinis</i>	91 ^a
Canary rockfish	<i>S. pinniger</i>	76 ^a
Yelloweye rockfish	<i>S. ruberrimus</i>	91 ^a
Vermilion rockfish	<i>S. miniatus</i>	76 ^a
Yellowtail rockfish	<i>S. flavidus</i>	66 ^a
Greenstriped rockfish	<i>S. elongatus</i>	43 ^a
Redstripe rockfish	<i>S. proriger</i>	51 ^a
Red Irish lord	<i>Hemilepidotus hemilepidotus</i>	51 ^b
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>	90 ^c
Cabezon	<i>Scorpaenichthys marmoratus</i>	99 ^c

^a Love et al. (2002)

^b Love (1996)

^c FishBase (<http://www.fishbase.org>)

individuals that spend most of their lives as reproductively active adults, producing large numbers of offspring that rarely survive to maturity (King and McFarlane 2003). Year-class strength is often stochastic, likely driven by circulation and production patterns that promote both pelagic larval growth and retention of larvae near suitable postlarval settlement habitat (e.g., Tolimieri and Levin 2005). To aid in capturing this dynamic, we divided the biomass pool into a mature adult stage and an immature juvenile stage. Assuming that rockfish in Puget Sound are best represented by relatively abundant species such as copper, quillback, brown, and yellowtail rockfish, we settled on a transition from juvenile to adult at approximately age 7 (e.g., Love et al. 2002).

We used Ecopath's mass-balancing routine to determine juvenile and adult rockfish biomass. We did so because we lack adequate survey data for virtually all of the species in Table A-2, and acquiring such data is not likely in the near term because these species generally live near high-relief, rocky habitat that is difficult to sample. We set *EE* for juveniles at 0.8 in the initial model state, implying that 80% of their production is lost to predation each year. We assumed *EE* for adults to be 0.5. This is lower than many of the other fish groups considered so far. Our rationale for the low *EE* is that fishing on rockfish in PSCB is minor, compared to fishing on rockfish in systems such as the California Current (Field 2004). In addition, adults of these species are large, spiny, and tend to live in complex habitats rich in refugia, providing some defense against all but the largest piscivores (e.g., lingcod, spiny dogfish, marine mammals). Also, they have low natural mortalities once mature (King and McFarlane 2003).

We assumed adult rockfish $P/B = 0.240 \text{ yr}^{-1}$. We derived this from Gowan (1983), who estimated the annual total mortality rates of three of the most common rockfish species in PSCB (copper, quillback, and brown rockfish) to be 0.233 yr^{-1} , 0.227 yr^{-1} , and 0.274 yr^{-1} , respectively.

We note that this estimate is greater, typically by a factor of 1.5 to 2, than the P/B estimates made by Field (2004) for several shelf rockfish species in the California Current in the 1990s. By contrast, we assumed a much lower P/B ratio for juvenile rockfish (0.36 yr^{-1}) than did Field (1.5 yr^{-1}). Our estimate follows the convention of Beattie (2001) and Ainsworth et al. (2002), where juvenile P/B is assumed to be 50% greater than adult P/B for split-pool groups for which juvenile mortality data are not available. The very high mortality experienced by larvae can be accounted for in functions used in Ecosim to alter the shape of the stock-recruitment function or the stochasticity of year-class strength, as described in Christensen et al. (2005).

The Q/B estimates for rockfish were calculated via bioenergetics modeling, based on the generic rockfish bioenergetics model of Harvey (2005). We simulated the energetic needs of equilibrium populations of copper, quillback, and brown rockfish, assuming von Bertalanffy growth, length-weight, maturation, fecundity, and natural mortality patterns as summarized in Love et al. (2002). We developed ontogenetic diet histories based on data on copper rockfish and quillback rockfish diets (Moulton 1977, Reilly et al. 1992, Murie 1995), diet accounts for brown rockfish summarized by Stein and Hassler (1989), and anecdotal rockfish diet information in Love et al. (2002). Bioenergetics model outputs included monthly estimates of total consumption required to reach the size-at-age predicted by the von Bertalanffy growth models, which enabled us to estimate consumption per unit biomass at monthly increments. These monthly Q/B estimates were then weighted by year-class abundance, as inferred from the mortality rates described by Gowan (1983), and averaged across the three species for juveniles (<age 7) and adults. Juvenile Q/B was 2.672 yr^{-1} , while adult Q/B was 1.437 yr^{-1} .

Based on the above parameters, the demands of predators, and some fishing mortality, Ecopath calculated biomass of 0.454 mt km^{-2} for juvenile rockfish and 0.327 mt km^{-2} for adult rockfish.

The diet of rockfish was compiled from the sources noted above in the Q/B description, again assuming that copper, quillback, and brown rockfish are the most representative species in this functional group. For our diet estimates, we used the bioenergetics outputs from the Q/B estimation. For each species, we estimated the consumption of each prey type by an equilibrium population of the rockfish (i.e., consumption was weighted by body weight and abundance as a function of the estimated mortality rate). Once prey-specific consumption estimates were made, we averaged across species for both the juvenile and the adult stages. In this way, we accounted for changes in size, abundance, and dietary ontogeny across the three representative species. Diets span a range of pelagic fishes, zooplankton, benthic invertebrates, and some demersal fishes, as shown in Table 4; juvenile Pacific herring, shrimp, and small crustaceans are the most important groups.

Rockfish are eaten by juvenile and adult lingcod, spiny dogfish, harbor seals, sea lions, resident diving birds, and raptors (Table 4). Some adult rockfish are lost to fisheries, though likely more to recreational fishing than any commercial gear (Table 5). Unfortunately, we lack empirical data on recreational catches and thus made an arbitrary assumption on recreational harvest rates of rockfish.

The parameters for the delay-difference equation (Appendix D) that dynamically links the biomasses of the juvenile and adult pools in Ecosim are: 7 years for the age at transition,

0.125 for the k parameter from the von Bertalanffy growth function (based on data provided in Love et al. 2002), and 3.25 for the ratio of the weight of an average adult to the weight of an individual at the transition age (derived from the bioenergetics modeling efforts).

Lingcod

Lingcod are one of the Puget Sound ecosystem's top predators. They reach considerably larger sizes than most other teleosts in the system, including their taxonomic cousins the greenlings; the L_{∞} of female lingcod in this area can exceed 1 m (Smith and McFarlane 1990). Their maximum life span in this area is between 15 and 20 years, with maturity occurring between the ages of 2 and 5 (Shaw and Hassler 1989, Smith and McFarlane 1990). Lingcod are generally solitary predators, feeding voraciously on other fishes and macroinvertebrates around complex habitats such as rocky reefs and outcroppings and typically staying within home ranges of several hundred square meters (Tolimieri et al. 2009). Their role as predators on rockfish is of particular interest because rockfish conservation and population rebuilding has become a major goal of West Coast fisheries management. Some research has suggested that marine protected areas designed to protect rockfish may actually fall short of their goals because lingcod may benefit from the fishing closures and consume rockfish in large numbers (e.g., Mangel and Levin 2005, Beaudreau and Essington 2007). Lingcod are a prized target of recreational hook-and-line anglers and spearfishers, and limited seasons for both gear types occur in Puget Sound each year.

We chose to split this functional group into two life history stages, juvenile and adult, with biomass dynamics linked through the delay-difference function described in Appendix D. We split them into these stages primarily so that we could develop scenarios in Ecosim where juvenile lingcod biomass is supplemented by hatchery releases. Hatchery production of juvenile lingcod has been proposed as a means of enhancing lingcod populations in Puget Sound and adjacent waters (Wespestad et al. 1994, Cook et al. 2005, Rust et al. 2005).

Lingcod biomass has not been assessed in Central Puget Sound to our knowledge. The trawl surveys of Central Puget Sound conducted by Reum (2006) are not reasonable for estimates of lingcod biomass, because the trawl locations likely did not correspond to preferred habitat for juvenile or adult lingcod. We instead considered estimates from nearby inland waters with similar community structure. Beattie (2001) derived estimates of lingcod biomass (adults and juveniles, total biomass = 0.065 mt km⁻²) from virtual population analysis conducted by Martell (1999) on lingcod in Hecate Strait. Martell (1999) conducted a similar analysis on Strait of Georgia lingcod and estimated population biomass of approximately 1.3 mt km⁻² in 1999; additionally, the biomass trend was on a steadily increasing trajectory (see also Priekshot 2007).

These are quite disparate estimates. We set our initial adult lingcod biomass between these two values, but we were conservative, assuming that there may not be as much lingcod habitat in PSCB as there is in the Strait of Georgia. Our starting adult lingcod biomass was arbitrarily set at 0.3 mt km⁻². For juvenile lingcod biomass, we initially assumed that the ratio of juvenile:adult biomass was approximately 0.3, based on a simulated equilibrium population of lingcod that follow sex-specific weight-at-age estimates and age-specific mortality estimates as described by Jagielo and Wallace (2005). However, we were unable to achieve mass balance for juvenile lingcod; their EE was consistently greater than one because of high predation mortality. We thus set juvenile lingcod EE at 0.9 and allowed the model to estimate juvenile lingcod

biomass. Both adult and juvenile lingcod biomass values should be interpreted with caution, pending quantitative monitoring work.

Our estimate of P/B again drew from research on lingcod in British Columbia waters. We considered the EwE modeling work done by Beattie (2001), Ainsworth et al. (2002), and Priekshot (2007). Beattie (2001) used a P/B of 0.8 yr^{-1} for adults, based on tagging-based mortality estimates of lingcod in the Strait of Georgia by Smith et al. (1990), although lingcod in the Strait of Georgia experienced high fishing mortality in that time (Smith et al. 1990, Martell 1999, Priekshot 2007). Ainsworth et al. (2002) assigned prefishing P/B ratios of 0.389 yr^{-1} and 0.26 yr^{-1} , respectively, to juvenile and adult lingcod along northern Vancouver Island; these estimates were made using the Pauly method (1980) (Appendix C). Priekshot's (2007) model of the Strait of Georgia in 1950 (prior to the period of intense exploitation) arrived at a lingcod P/B of 0.35 yr^{-1} based on the Ecopath mass-balancing routine. Assuming that lingcod in the PSCB model experience natural mortalities similar to those estimated by Ainsworth et al. (2002) and Priekshot (2007), and assuming a low level of recreational fishing mortality on adults, we arrived at P/B ratios of 0.389 yr^{-1} for juveniles and 0.28 yr^{-1} for adults.

We derived estimates of lingcod Q/B from bioenergetics modeling done by Beaudreau and Essington (2009) for several size classes of lingcod from northern waters of Puget Sound. We used their bioenergetics model parameters to simulate consumption for an equilibrium population of male and female lingcod, where von Bertalanffy growth functions, length-weight relationships, and mortality rates were sex-specific (from Jagielo and Wallace 2005), initial sex ratio was 1:1 but changed with age owing to sex-specific mortality rates, and maturity occurred at 4.5 yr. Models were run in monthly time steps, with monthly temperature estimates taken from WDE data (no date) for the upper 25 m of the water column and prey energy density fixed at $5,000 \text{ J g}^{-1}$. The proportion of maximum consumption (the p value in fish bioenergetics models, Kitchell et al. 1977) was adjusted to fit the growth curves from Jagielo and Wallace (2005). Monthly Q/B estimates were weighted by age-specific biomasses and summed, juvenile Q/B equaled 3.070 yr^{-1} , and adult Q/B equaled 1.932 yr^{-1} . These values are conservative relative to values used in Ecopath models from nearby systems (Beattie 2001, Ainsworth et al. 2002; juvenile range 3.3 yr^{-1} to 3.9 yr^{-1} , adult range 2.8 yr^{-1} to 3.3 yr^{-1}), but are consistent with the value (2.4 yr^{-1}) used by Priekshot (2007) for all lingcod.

Given the parameters outlined above and the demands of predators and fisheries, Ecopath's mass-balancing routine estimated an EE of 0.141 for adult lingcod and a biomass of 0.124 mt km^{-2} for juvenile lingcod.

Lingcod are highly predatory fish that feed primarily on other fishes (Shaw and Hassler 1989, Beaudreau and Essington 2007). We mainly based our lingcod diet on studies done by Beaudreau (2009) on lingcod in the San Juan Islands of Puget Sound. Her research indicates a size-based transition from strong dependence on pelagic fishes (sand lance, Pacific herring, small gadiforms) and shrimp to increasing dependence on demersal fishes (rockfish, sculpins, greenlings, flatfishes, and others). Beaudreau (2009) also documented cannibalism by juvenile and adult lingcod. For juvenile lingcod, we assume a diet comprised mostly of pelagic fishes, along with various demersal fish groups, shrimp, planktonic invertebrates, and cephalopods; a small amount of cannibalism is also included (Table 4). For adults, we assume a diet comprised mostly of demersal and semipelagic fishes, along with pelagic fishes, benthic invertebrates,

cephalopods, and small numbers of euphausiids and salmon. Cannibalism is directed at juvenile lingcod.

Juvenile lingcod are preyed upon by very few groups, mainly other lingcod and in trace amounts by raptors, demersal fish, and age 1+ *Cancer* crabs (Table 4). Adult lingcod are preyed upon in small amounts by harbor seals and sea lions. We arbitrarily allocated annual landings of 0.01 mt km⁻² adult lingcod biomass to the recreational fishery (Table 5).

The parameter values used in the Ecosim delay-difference equation to dynamically link the juvenile and adult biomass pools (Appendix D) include a von Bertalanffy k of 0.125 (Jagiello and Wallace 2005), a transition age of 4.5 years (Jagiello and Wallace 2005), and a ratio of 3.0 for the weight of an average adult relative to the weight of a fish at the transition age, as derived from growth curves used in the bioenergetics modeling described previously. Ecosim default values were used for all other delay-difference parameters (Appendix D).

Demersal Fish

This functional group is a catch-all pool of relatively small, round-bodied teleosts that spend most of their lives associated with benthic habitats throughout the system. In general, these fish can be found over a wide range of substrate types, mostly feeding on invertebrates while providing an important prey resource for higher trophic levels. Many families are represented, including but not limited to those listed in Table A-3.

As a whole, these species have not been monitored in a way that would allow empirical biomass estimation. Some species in Table A-3, such as plainfin midshipmen, poachers, and eelpouts, were captured in the bottom trawl survey work by Reum (2006). Using Reum's data and the methods outlined in Appendix C, for example, we estimated season-weighted and depth-weighted biomass densities of 0.124 mt km⁻², 0.023 mt km⁻², and 0.023 mt km⁻² for midshipmen, poachers, and eelpouts, respectively. However, that represents a partial component of this assemblage. Also, the bottom trawl survey sampled only soft sediments, not the complex substrates (e.g., rocky reefs, macrophytes beds) inhabited by many demersal fish species. Moreover, many of these fishes are small-bodied and could conceivably pass through or burrow under bottom trawl gear. We therefore estimated demersal fish biomass with the Ecopath mass balance routine. We set EE at 0.8 to facilitate this.

Given this group's taxonomic diversity (Table A-3) and large number of relatively poorly studied species, we were not confident about how to characterize P/B or Q/B ratios. We opted to set Q/B at 6.0 yr⁻¹, which is greater than Q/B estimates from comparable groups in other Northeast Pacific Ecopath models (e.g., 2.5 yr⁻¹ for benthic fish in Field [2004], 5.256 yr⁻¹ for Priekshot [2007]). It is similar, however, to species-specific estimates for plainfin midshipmen (5.703 yr⁻¹) and sturgeon poachers (6.934 yr⁻¹), which we calculated using the Q/B estimation methods described in Appendix C. If we assume a growth efficiency (P/Q) of 0.2, which is a fairly standard value for fishes, then P/B must be 1.2 yr⁻¹.

With the parameter estimates provided above, and the top-down pressure from predators, Ecopath estimated an initial biomass of 4.565 mt km⁻² for demersal fish. This is comparable to biomass estimates for small demersals in the Strait of Georgia Ecopath model (5.5 mt km⁻²,

Table A-3. Key families and representatives in the demersal fish functional group in the PSCB EWE model. The order of appearance in this table does not necessarily indicate the order of abundance.

Family	Representative species	Scientific name
Cottidae	Roughback sculpin	<i>Chitonotus pugetensis</i>
	Sailfin sculpin	<i>Nautichthys oculofasciatus</i>
	Scalyhead sculpin	<i>Artedius harringtoni</i>
	Slim sculpin	<i>Radulinus asprellus</i>
	Spinyhead sculpin	<i>Dasycottus setiger</i>
	Spotfin sculpin	<i>Icelinus tenuis</i>
	Staghorn sculpin	<i>Leptocottus armatus</i>
	Threadfin sculpin	<i>I. filamentosus</i>
Hexagrammidae	Whitespotted greenling	<i>Hexagrammos stelleri</i>
	Kelp greenling	<i>H. decagrammus</i>
	Rock greenling	<i>H. lagocephalus</i>
	Painted greenling	<i>Oxylebius pictus</i>
Batrachoididae	Plainfin midshipmen	<i>Porichthys notatus</i>
Agonidae	Bigeye poacher	<i>Bathyagonus pentacanthus</i>
	Blacktip poacher	<i>Xeneretmus latifrons</i>
	Bluespotted poacher	<i>X. triacanthus</i>
	Pygmy poacher	<i>Odontopyxis trispinosa</i>
	Smootheye poacher	<i>X. leiops</i>
	Sturgeon poacher	<i>Podothecus accipenserinus</i>
Zoarcidae	Bigfin eelpout	<i>Lycodes cortezianus</i>
	Black eelpout	<i>L. diapterus</i>
	Blackbelly eelpout	<i>L. pacificus</i>
	Shortfin eelpout	<i>L. brevipes</i>
	Snakehead eelpout	<i>Lycenchelys crotalinus</i>
Bathymasteridae	Northern ronquil	<i>Ronquilus jordani</i>
Pholidae	Various gunnels	<i>Pholis</i> spp., <i>Apodichthys</i> spp.
Stichaeidae	Various pricklebacks	<i>Anoplarchus</i> spp., <i>Chirolophis</i> spp., etc.
Gadidae	Pacific tomcod	<i>Microgadus proximus</i>
Gobiidae	Blackeye goby	<i>Rhinogobiops nicholsii</i>
Syngnathidae	Bay pipefish	<i>Syngnathus leptorhynchus</i>
Aulorhynchidae	Tube-snout	<i>Aulorhynchus flavidus</i>

Priekshot 2007) and benthic fish in the California Current Ecopath model (4.1 mt km⁻², Field 2004).

The diet proportions of this group represent an amalgamation of stomach content data from representative species captured in recent trawl surveys of PSCB conducted by Reum (2006, unpubl. data). From several representative species groups captured in the survey (Pacific tomcod, plainfin midshipmen, various poachers, various eelpouts, and various small sculpins), diets were weighted by season and depth to account for temperature changes and bathymetric effects (see methods in Appendix C) and averaged across all taxa. The resulting diet was a highly diverse mix of both planktonic and benthic invertebrates, plus small amounts of fish, squid, and microalgae (Table 4). To a small extent, they are intraguild cannibals.

Demersal fish are preyed upon by virtually every other vertebrate group, except for some of the pelagic fishes (Table 4). In addition, octopus and *Cancer* crab feed on this group.

Flatfish

We identified two separate functional groups of flatfish in the PSCB model. The main criterion by which we separated flatfish into groups was diet: one group clearly had higher amounts of fish in their diets, while the other fed almost exclusively on benthic invertebrates. The key representatives are listed in Table A-4 and are described in greater detail below.

Piscivorous Flatfish

This group is comprised of at least two species, Pacific sanddab and sand sole, that had notably higher amounts of fish in their diets than the other common, small flatfish examined by Reum (2006) and Reum and Essington (2008). There are two other species of piscivorous flatfish that we considered for this group: arrowtooth flounder (*Atheresthes stomias*) and petrale sole (*Eopsetta jordani*). Both species are found in PSCB and are known piscivores (e.g., Love 1996), but we currently lack data on their relative abundance or diets in PSCB. How this affects the role of this functional group in the model is unknown, but it is reassuring to note that in their recent trawl surveys in PSCB, Reum (2006) and Reum and Essington (2008) caught Pacific sanddabs and sand sole, but no arrowtooth flounder or petrale sole.

Our estimate of piscivorous flatfish biomass is based on Pacific sanddab and sand sole biomass per unit area data derived from trawl casts in PSCB (Reum unpubl. data, see estimation methods in Appendix C). We weighted the data according to season and depth-area data for PSCB, then summed the data for both species. The final estimated biomass was 1.155 mt km⁻², the vast majority (>97%) of which was Pacific sanddabs. However, there was high variability around the biomass estimate (coefficient of variation = 85%) due to seasonally variable catches of Pacific sanddab. On average, Pacific sanddab biomass in summer and fall was 4 to 10 times greater than in winter.

Table A-4. Key representatives of the flatfish functional groups in the PSCB EwE model. The order of appearance in this table does not necessarily indicate the order of abundance.

Functional group	Common name	Scientific name
Piscivorous flatfish	Pacific sanddab	<i>Citharichthys sordidus</i>
	Sand sole	<i>Psettichthys melanostictus</i>
Small-mouthed flatfish	English sole	<i>Parophrys vetulus</i>
	Dover sole	<i>Microstomus pacificus</i>
	C-O sole	<i>Pleuronichthys coenosus</i>
	Starry flounder	<i>Platichthys stellatus</i>
	Speckled sanddab	<i>Citharichthys stigmaeus</i>
	Rock sole	<i>Lepidopsetta bilineata</i>
	Rex sole	<i>Glyptocephalus zachirus</i>
	Flathead sole	<i>Hippoglossoides elassodon</i>
	Butter sole	<i>Isopsetta isolepis</i>
Slender sole	<i>Lyopsetta exilis</i>	

We used the estimation method described in Appendix C to derive a P/B estimate for piscivorous flatfish; the method calculates P/B as a function of von Bertalanffy growth parameters and temperature. Unfortunately, von Bertalanffy growth parameters are not available for either Pacific sanddab or sand sole from the Puget Sound area; in fact, we could only derive estimates of k and L_∞ from length-at-age data for Pacific sanddab captured in central California waters in the middle of the last century (Arora 1951). Based on data in Arora's tables, we calculated von Bertalanffy $k = 0.251$ and $L_\infty = 31.7$ (both sexes combined). These values and a mean annual temperature estimate of 10.68°C for PSCB waters at depths between 0 and 25 m (WDE no date) yield an estimated P/B of 0.467 yr^{-1} . This may be an overestimate, as we might expect Pacific sanddabs in Puget Sound to have lower k and larger L_∞ than Pacific sanddabs off central California.

We are unaware of bioenergetics models for Pacific sanddabs or sand sole (or, in fact, for any flatfishes common to the west coast of North America). Thus to quantify piscivorous flatfish Q/B , we used the Christensen and Pauly (1992) estimation method, described in Appendix C. We again applied an annual average temperature of 10.68°C (see previous paragraph) and we calculated maximum weight with the von Bertalanffy growth parameters and length-weight conversions that we derived from Arora (1951). These values produced a Q/B estimate of 6.007 yr^{-1} using the equation described in Appendix C. The P/B and Q/B estimates yield a P/Q of 0.08, which is plausible but lower than expected.

The mass-balancing routine in Ecopath calculated an EE of 0.686 for piscivorous flatfish, implying that in the initial model state, two-thirds of the group's annual production is lost to predation by other functional groups or to fisheries.

We used stomach content data collected by Reum (2006, unpubl. data) and Reum and Essington (2008) to describe piscivorous flatfish diets. Raw diet data were weighted by depth and season (Appendix C) and by species, with the vastly more abundant Pacific sanddab weighted more than sand sole. Their diets were quite diverse; approximately 35% were fish groups, primarily surfperches, juvenile Pacific herring, and demersal fish (Table 4). Planktonic and benthic invertebrates comprised most of the remainder of their diet.

Piscivorous flatfish are preyed upon by harbor seals, sea lions, resident diving birds, spiny dogfish, adult lingcod, and age 1+ *Cancer* crabs (Table 4). They are captured at very low rates by commercial longline gear (Table 5, Appendix C), and although they are certainly captured by recreational anglers, we do not have empirical estimates for recreational landings.

Small-mouthed Flatfish

This group is comprised of several species of small- to medium-sized flatfish (Table A-4). English sole is probably the most abundant single species, while substantial numbers of rock sole and C-O sole are also present (Reum 2006). Starry flounder are relatively abundant in shallow waters while Dover and rex sole occur in the deeper waters of Puget Sound. This group is highly abundant and forms (along with ratfish and spiny dogfish) the bulk of demersal fish biomass in PSCB (Reum 2006). Small-mouthed flatfish species are grouped primarily due to their trophic similarity, as they all feed on infaunal organisms (e.g., polychaetes, clams) and small benthopelagic crustaceans (Reum and Essington 2008).

Our estimate of biomass is based on trawl casts in PSCB (Reum unpubl. data, see biomass estimation methods described in Appendix C). We weighted the catch data according to season and depth-area data for PSCB, then summed the data for all small-mouthed flatfish species. The final estimated biomass was 7.962 mt km^{-2} , which was mostly English sole (4.571 mt km^{-2}), followed by rock sole (1.500 mt km^{-2}), and C-O sole (1.215 mt km^{-2}).

Given the relative importance of English sole in this functional group, we used an estimate of natural mortality for English sole as our initial value for P/B . An instantaneous annual mortality estimate of 0.26 yr^{-1} comes from work by Forrester and Ketchen (1963), who examined characteristics of bottomfish in nearby Strait of Georgia. That value was also used in a recent stock assessment of English sole along the U.S. West Coast (Stewart 2007). Holland (1969) estimated much higher English sole mortality rates in Central Puget Sound in the 1950s; an unexploited population dominated by age 3–5 individuals had an instantaneous annual mortality of approximately 0.43 yr^{-1} . We assumed the average of these two regional estimates, that is, $P/B = 0.345 \text{ yr}^{-1}$. This value is much lower than that of piscivorous flatfish (0.467 yr^{-1}), which is consistent with the fact that English sole are longer-lived than Pacific sanddabs. According to FishBase (<http://www.fishbase.org>), English sole have been aged at 17 years, whereas Pacific sanddabs have been aged at 9 years. The two species grow to relatively similar sizes, implying that English sole productivity must be somewhat lower. In equating P/B to natural mortality, we assume that fishing mortality on this group is minor.

We found no bioenergetics modeling information on small-mouthed flatfish species, and thus used the Christensen and Pauly method (1992) described in Appendix C to estimate small-mouthed flatfish Q/B . This method requires estimates of theoretical maximum size, as derived from von Bertalanffy growth relationships and length-weight conversions. Of the three abundant species in this functional group, the only one for which we could find growth and length-weight relationships was English sole. Based on von Bertalanffy growth parameters and length-weight conversions described by Stewart (2007), the theoretical maximum weight of an English sole is 580.11 g.

The Christensen and Pauly (1992) method also requires a temperature estimate. As English sole were ubiquitous and abundant at all depths sampled by Reum (2006), we used the average bottom temperature (10.48°C) of all offshore stations in PSCB that are monitored monthly by WDE (no date). When these values were applied to the equation discussed in Appendix C, the resulting Q/B was 5.512 yr^{-1} . This value along with the P/B estimate yields a P/Q of 0.047, which is quite low but potentially in keeping with the slow growth and long life of English sole.

The Ecopath mass-balancing routine produced an EE of 0.654 for small-mouthed flatfish, indicative of a moderately high degree of predation pressure on annual production.

We characterized diet based on stomach content data for the majority of the small-mouthed flatfish listed in Table A-4 (English sole, rock sole, C-O sole, slender sole, speckled sanddab, Dover sole, and rex sole). Stomach contents were analyzed by Reum (2006) and Reum and Essington (2008). We aggregated the raw data from these studies (Reum unpubl. data) and weighted them by season as described in Appendix C. The resulting diet was dominated by soft

infauna, infaunal bivalves, and small crustaceans (Table 4). Also present were a variety of pelagic and benthic invertebrates and traces of benthic primary producers and fish.

Small-mouthed flatfish are eaten by age 1+ *Cancer* crabs, demersal fish, adult rockfish, juvenile and adult lingcod, Pacific cod, spiny dogfish, ratfish, skates, raptors, resident diving birds, harbor seals, and sea lions. There is no viable commercial fishery for them in PSCB, although some recreational harvest occurs for nearshore species. Unfortunately, we lack data on recreational harvest and thus input an arbitrary placeholder level of recreational catch (Table 5).

Chondrichthyans

Chondrichthyans are very abundant in Puget Sound. The spotted ratfish (*Hydrolagus colliei*) and the spiny dogfish may account for most of the demersal fish biomass in deeper waters of the system (Reum 2006). Collectively, the sharks, skates, and ratfish in Puget Sound span multiple trophic levels and are common at nearly all depths.

Spiny Dogfish

The spiny dogfish is an abundant shark found throughout the world's temperate and subarctic oceans, from nearshore habitats to shelf and slope waters (Love 1996). They rarely achieve lengths greater than 1.5 m, but can live beyond 75 years. They are notably slow to mature, with many females reaching first maturity at more than 20 years of age. Once mature, they produce litters of 1 to 20 pups every 2 years. Their ecological importance in Puget Sound is clear, based on their abundance, high trophic position, diverse diet, and direct trophic links to several high-profile functional groups (e.g., Pacific herring, salmon, marine mammals). They are also targeted in fisheries, although not to the extent that they were historically. During World War II, millions of spiny dogfish were harvested in Puget Sound because of the high nutritional value of their livers. This market diminished quickly when laboratory synthesis of vitamin A became feasible, and their main value is now as a food fish (Bonham et al. 1949, Taylor and Gallucci 2009). Some hypothesize that spiny dogfish abundance in Puget Sound has declined relative to historic levels (e.g., Palsson 2009), and that major demographic shifts have occurred between the 1940s and the present day (Taylor and Gallucci 2009).

Spiny dogfish biomass estimates were derived from depth-stratified seasonal trawl surveys conducted in PSCB by Reum (2006, unpubl. data). The estimation methods are described in Appendix C. We averaged the summer and fall biomass estimates to produce the final biomass of 5.254 mt km². The variability around the biomass estimates for given depths and seasons was high; coefficients of variation ranged from 45% to 100% (data not shown). We omitted the winter samples from this calculation because spiny dogfish were nearly absent from Reum's winter data, suggesting that most spiny dogfish were not present in the system for at least one-third of the year (Reum 2006). We handled this in Ecopath by assuming that their diet is 30% Import.

Spiny dogfish *P/B* was approximated from natural and fishing mortality estimates in Puget Sound and adjacent waters. Wood et al. (1979) estimated instantaneous annual natural mortality of 0.094 yr⁻¹ for all age groups of spiny dogfish in waters around Vancouver Island, and we assumed the same rate of natural mortality for spiny dogfish in PSCB. Based on the total

biomass estimate and total commercial landings in PSCB (Table 5, Appendix C), the instantaneous annual fishing mortality (F) of spiny dogfish is 0.009 yr^{-1} . The sum of natural and fishing mortality, 0.103 yr^{-1} , is our P/B estimate.

We generated the Q/B ratio using a spiny dogfish bioenergetics model (Harvey 2009). A bioenergetics simulation was run for an equilibrium population of sharks, ages 0 to 75, with von Bertalanffy growth parameters and maturation schedules consistent with spiny dogfish in coastal Washington waters (Ketchen 1972, 1975) and an instantaneous mortality of 0.103 yr^{-1} . The model used a monthly time step and temperatures consistent with monthly mean Puget Sound water temperatures at depths of 50–75 m (WDE no date) and size-dependent diets based on Jones and Geen (1977). The model generated annual estimates of total prey biomass consumed per unit of dogfish biomass, which were then weighted by the abundance of the age class relative to the overall population. The sum of the weighted age-specific estimates was the overall Q/B estimate of 2.692 yr^{-1} .

The above parameters plus the top-down demands of predators and fisheries led to an EE of 0.175 following mass-balancing in Ecopath.

Spiny dogfish diets were estimated based on stomach contents examined by Reum (2006, unpubl. data) as described in Appendix C. We assumed a Q_{10} of 2.3 when making temperature-dependent corrections to prey contributions (Harvey 2009). As noted above, we attributed 30% of spiny dogfish diet to Import, because Reum (2006) captured almost no spiny dogfish during the winter. We assumed that most spiny dogfish emigrated from the system in winter, although that assumption is tenuous.¹¹ The remainder of their diet is remarkably diverse, with principal dependence on fish (Table 4). Important prey categories include Pacific herring, walleye pollock, ratfish, flatfish, octopuses, salmon, and *Cancer* crabs.

Spiny dogfish are preyed upon in small amounts by harbor seals, sea lions, raptors, and adult lingcod (Table 4). Spiny dogfish are captured in gill net, longline, set net, and recreational fisheries (Table 5, Appendix C).

Skates

Two species of skate are common in Puget Sound: the longnose skate (*Raja rhina*) and the big skate (*Raja binoculata*) (Reum 2006). Like most skates, these species live on or over soft sediments, feeding on a variety of invertebrates and small fishes. Little is known about their ecological role in Puget Sound, and they are not particularly targeted by fisheries in this region. Skates have been implicated as important components of groundfish communities in other systems, such as the continental shelf off the northeastern United States (Fogarty and Murawski 1998, Frisk et al. 2008, Link and Sosebee 2008). On the west coast of North America, longnose skate populations have declined 30–40% over the last century, possibly because their life history traits (slow growth, late maturation, low fecundity) leave them vulnerable to fishing mortality (Gertseva 2009). The present modeling effort may help shed light on the potential community role of skates in PSCB.

¹¹ W. Palsson, WDFW, Mill Creek, WA. Pers. commun., 25 March 2009.

We estimated skate biomass using seasonal trawl survey data collected in PSCB in 2004 and 2005 (Reum 2006, unpubl. data). Trawl data were converted to biomass density estimates weighted by depth and season, as described in Appendix C. Estimated biomass was 0.680 mt km^{-2} ; based on catch data, approximately 96% of the biomass was longnose skate (Reum 2006, unpubl. data).

We do not have empirical estimates of P/B for skates in Puget Sound. Gertseva (2009) assumed that natural mortality of longnose skates on the outer U.S. West Coast was 0.2 yr^{-1} , and previous Ecopath models from the Northeast Pacific Ocean have used P/B ratios ranging from 0.15 yr^{-1} (Ainsworth et al. 2002) to 0.31 yr^{-1} (Beattie 2001, Preikshot 2007). Ainsworth et al. (2002) calculated their value by applying the Pauly (1980) method, described in Appendix C, to an unfished skate population. As skates in PSCB likely receive little fishing pressure, we used the Pauly (1980) method as well, drawing longnose skate von Bertalanffy growth equation parameter estimates from McFarlane and King (2006) and using annual average temperature data for PSCB provided by WDE (no date). We used a temperature of 10.3°C , taken from 50 to 75 m waters, the deepest water for which data were available from all months. Most skate biomass was captured in deeper waters by the survey (Reum 2006), thus the mean annual temperature we used may be a slight overestimate. When these values were entered into the P/B estimation equation, the resulting value was 0.127 yr^{-1} .

We derived our Q/B estimates using the Christensen and Pauly (1992) method, outlined in Appendix C, where Q/B is a function of temperature and maximum weight. We again set temperature at 10.3°C , and determined maximum weight using von Bertalanffy parameters from McFarlane and King (2006) and the length-weight conversion equation of Gertseva (2009). The resulting Q/B estimate was 3.201 yr^{-1} . Dividing P/B by Q/B yields a P/Q of 0.04, a low growth efficiency that is consistent with a long-lived, slow-growing fish.

The above parameter estimates, coupled with predatory and fishery demands, produced an EE of 0.084 for skates after mass-balancing. This implies a low degree of top-down control on skates in Puget Sound, as the model is currently structured.

Skate diets were estimated based on stomach contents examined by Reum (2006, unpubl. data). Skates were captured by bottom trawl in PSCB from 2004 to 2005. Raw diet data were weighted by depth and season, as described in Appendix C; we assumed a Q_{10} of 2.3 when making temperature-dependent corrections to prey contributions. Benthic and benthopelagic crustaceans were the major source of prey (Table 4). Minor prey items included various fish groups, infaunal bivalves, and other grazers.

Skates form a minor part of the diets of harbor seals and sea lions (Table 4). A small amount of skate biomass is taken by longline fisheries (Table 5, Appendix C).

Ratfish

The spotted ratfish may be the most abundant demersal fish species in Puget Sound, in terms of biomass per unit area. This is especially true in deeper waters of the sound (Reum 2006), although at night some part of the population spreads into shallower waters (Love 1996). Their numbers in Central Puget Sound remain high in all seasons, unlike many other species that

experience seasonal shifts in abundance (Reum 2006). They primarily feed on infaunal and epifaunal benthic invertebrates; a small amount of their diet is fishes. Although they are frequently caught in groundfish capture gears on the U.S. West Coast, ratfish are not targeted by sport or commercial fisheries, and the closure of groundfish trawling in PSCB affords them protection from incidental fishing mortality.

Ratfish biomass estimates were derived from depth-stratified seasonal trawl surveys conducted in PSCB during 2004 and 2005 (Reum 2006, unpubl. data), according to the methods described in Appendix C. The final biomass calculation was done by unweighted averaging across all seasons, because ratfish showed no evidence of moving into or out of the system on a seasonal basis. The initial estimate of biomass was 36.1 mt km^{-2} . Ratfish biomass is noteworthy not only because it is considerably greater than that of most other fish groups (Table 3), but also for its seasonal consistency. The estimates derived from Reum's raw data for summer, fall, and winter were 38.329, 35.495, and $34.474 \text{ mt km}^{-2}$, respectively.

Direct measures of ratfish P/B are not available from Puget Sound. Therefore, we used the Pauly (1980) method, as described in Appendix C, where P/B is a function of water temperatures and the growth rate (k) and theoretical maximum length (L_{∞}) in the von Bertalanffy growth equation. We assumed a temperature of 10.3°C , the annual mean at 50–75 m in PSCB (WDE no date), and von Bertalanffy parameters reported by Ainsworth et al. (2002). This yielded a P/B estimate of 0.305 yr^{-1} .

Ratfish Q/B has not been quantified directly. Beattie (2001) and Ainsworth et al. (2002) estimated that Q/B is 1.4 yr^{-1} for ratfish in waters around British Columbia. However, that calculation assumed an average temperature of 6°C , whereas an average temperature of 10.3°C is more reasonable for ratfish living near the bottom of Puget Sound (WDE no date). We rescaled the previous Q/B estimate to a temperature of 10.3°C by applying a consumption Q_{10} of 2.3 (Appendix C), which is similar to Q_{10} values used for other small chondrichthyans (e.g., Brett and Blackburn 1978). Using this method yielded a Q/B of 1.653 yr^{-1} for PSCB ratfish.

In the mass-balancing step, Ecopath calculated ratfish $EE = 0.105$, implying that relatively little ratfish production is lost to predation by other functional groups.

Ratfish diet composition was estimated based on stomach content analysis on ratfish captured in the depth-stratified and season-stratified bottom trawl surveys (Reum and Essington 2008, Reum unpubl. data). Raw stomach content data were converted to diet proportions weighted by season, using methods described in Appendix C; we again assumed a consumption Q_{10} of 2.3. The resulting diet composition for ratfish was dominated by three highly aggregated groups: infaunal bivalves, small crustaceans, and soft infauna (Table 4). The balance of their diet included a wide variety of primary producers, pelagic and benthic invertebrates, and a small amount of fish; however, the sheer biomass of ratfish may make even these small diet allotments important sources of mortality to the prey groups.

Ratfish are preyed upon by spiny dogfish (Table 4).

Seabirds

Seabirds are a special class of organisms in the context of a marine ecosystem model and the Puget Sound model in particular. Relatively speaking, they are a small component of community biomass. However, their high activity levels and endothermic nature result in very high consumption rates, which increase their ecological footprint. They can more or less be regarded as apex predators, as very few species (apart from other birds or terrestrial nest predators) feed on them. Many species are protected to at least some extent by general legislation and treaties (e.g., the Migratory Bird Treaty Act), and a small number of species are covered by state or federal endangered species legislation. They are also regarded as leading indicators of marine ecosystem change (e.g., Cairns 1987, Piatt et al. 2007, Mallory et al. 2010). They interact with a wide range of marine species in many habitats, ranging from nearshore to pelagic zones. Finally, the Puget Sound area is recognized as important nesting or feeding grounds for marine birds, many of which appear to have experienced marked declines in recent decades (Nysewander et al. 2005, Bower 2009). For these reasons, ecosystem models must account for the functional diversity of seabirds. We represent them in six functional groups, based on their trophic position, their primary foraging habitat, and whether they are primarily Puget Sound residents or migratory species that spend one or more seasons outside of Puget Sound for either feeding or breeding purposes. Groups and representative species are listed in Table A-5.

Gulls

This group consists mainly of gulls (*Larus* spp.), representing a range of sizes, but also includes surface feeders such as the Caspian tern (*Hydroprogne caspia*). Some are year-round residents while others are seasonal migrants (Table A-5). These birds are familiar due to their gregarious nature and close associations with humans. They are important consumers of near-surface or shoreline animals, carrion, refuse, and even other seabirds.

We used the Ecopath model to estimate gull biomass, due to problems in mass balancing. Estimates of gull biomass were available from winter aerial surveys of Puget Sound, as described in Appendix C. The survey counts were adjusted with a bias-correction factor of 1.33 (Evenson unpubl. data), and assumed individual weights of 0.95 kg (based on average weights in Hunt et al. 2000). This yielded a biomass estimate of 0.036 mt km⁻². However, early attempts to balance the model resulted in $EE \gg 1$ for gulls, due to predation by raptors (see Raptors subsection below). We therefore chose to make EE , rather than biomass, an input variable and set it at 0.6, assuming that raptor predation was a moderate source of total gull mortality.

The P/B ratio for gulls was taken from the Ecopath model of the northern California Current developed by Field (2004). Field set the P/B of gulls at 0.12 yr⁻¹, based on Schreiber and Burger's (2002) suggestion of a taxonomic order-level survival rate for gulls of approximately 74–97% per year.

Consumption rates for gulls were estimated using relationships between body size and energy requirements (Hunt et al. 2000, see methods in our Appendix C). We estimated energy intake for 10 gull species common to Puget Sound. To convert energy consumed to mass of prey consumed, we assumed that gull diets have an energy density of 5,000 J g⁻¹, consistent with a

Table A-5. Key representatives of the marine bird functional groups included in the PSCB EwE model. Season indicates the season in which they are most abundant in Puget Sound, according to the Seattle Audubon Society (<http://www.birdweb.org/birdweb/index.aspx>) and WDFW.¹² The order of appearance does not necessarily indicate the order of abundance.

Functional group	Common name	Scientific name	Season(s)
Gulls	Glaucous-winged gull	<i>Larus glaucescens</i>	Year-round
	Thayer's gull	<i>L. thayeri</i>	Fall, winter, spring
	Heermann's gull	<i>L. heermanni</i>	Summer, fall
	California gull	<i>L. californicus</i>	Summer, fall
	Ring-billed gull	<i>L. delawarensis</i>	Fall, winter, spring
	Mew gull	<i>L. canus</i>	Fall, winter, spring
	Bonaparte's gull	<i>L. philadelphia</i>	Fall, winter, spring
	Caspian tern	<i>Hydroprogne caspia</i>	Spring, summer
Migratory divers	Western grebe	<i>Aechmophorus occidentalis</i>	Fall, winter, spring
	Red-necked grebe	<i>Podiceps grisegena</i>	Fall, winter, spring
	Horned grebe	<i>P. auritus</i>	Fall, winter, spring
	Eared grebe	<i>P. nigricollis</i>	Fall, winter, spring
	Common merganser	<i>Mergus merganser</i>	Fall, winter, spring
	Hooded merganser	<i>Lophodytes cucullatus</i>	Fall, winter, spring
	Red-breasted merganser	<i>M. serrator</i>	Fall, winter, spring
	Common loon	<i>Gavia immer</i>	Fall, winter, spring
	Pacific loon	<i>G. pacifica</i>	Fall, winter, spring
	Red-throated loon	<i>G. stellata</i>	Fall, winter, spring
	Common murre	<i>Uria aalga</i>	Fall, winter, spring
Resident divers	Rhinoceros auklet	<i>Cerorhinca monocerata</i>	Year-round
	Pigeon guillemot	<i>Cephus columba</i>	Year-round
	Double-crested cormorant	<i>Phalacrocorax auritus</i>	Year-round
	Pelagic cormorant	<i>P. pelagicus</i>	Year-round
	Brandt's cormorant	<i>P. penicillatus</i>	Year-round
	Marbled murrelet	<i>Brachyramphus marmoratus</i>	Year-round
Nearshore divers	Surf scoter	<i>Melanitta perspicillata</i>	Fall, winter, spring
	Black scoter	<i>M. nigra</i>	Fall, winter, spring
	White-winged scoter	<i>M. fusca</i>	Fall, winter, spring
	Greater scaup	<i>Aythya marila</i>	Fall, winter, spring
	Lesser scaup	<i>A. affinis</i>	Fall, winter, spring
	Canvasback	<i>A. valisineria</i>	Fall, winter, spring
	Common goldeneye	<i>Bucephala clangula</i>	Fall, winter, spring
	Barrow's goldeneye	<i>B. islandica</i>	Fall, winter, spring
	Bufflehead	<i>B. albeola</i>	Fall, winter, spring
	Harlequin duck	<i>Histrionicus histrionicus</i>	Fall, winter, spring
	Ruddy duck	<i>Oxyura jamaicensis</i>	Fall, winter, spring
	Long-tailed duck	<i>Clangula hyemalis</i>	Fall, winter, spring
	Herbivorous birds	Tundra swan	<i>Cygnus columbianus</i>
Canada goose		<i>Branta canadensis</i>	Year-round
Black brant		<i>B. bernicla</i>	Fall, winter, spring
Cackling goose		<i>B. hutchinsii</i>	Fall, winter, spring
Mallard		<i>Anas platyrhynchos</i>	Year-round
Gadwell		<i>A. strepera</i>	Year-round

¹² S. Pearson, WDFW, Olympia, WA. Pers. commun., 5 May 2009.

Table A-5 continued. Key representatives of the marine bird functional groups included in the PSCB EwE model. Season indicates the season in which they are most abundant in Puget Sound, according to the Seattle Audubon Society (<http://www.birdweb.org/birdweb/index.aspx>) and WDFW.¹³ The order of appearance does not necessarily indicate the order of abundance.

Functional group	Common name	Scientific name	Season(s)
Herbivorous birds (continued)	American wigeon	<i>A. americana</i>	Fall, winter, spring
	Northern shoveler	<i>A. clypeata</i>	Year-round
	Northern pintail	<i>A. acuta</i>	Fall, winter, spring
	Green-winged teal	<i>A. crecca</i>	Fall, winter, spring
Raptors	Bald eagle	<i>Haliaeetus leucocephalus</i>	Year-round

diet of planktonic and benthic invertebrates, fish, and scavenged items. Daily prey consumption was multiplied by 365 days and divided by the body mass of an average individual (0.95 kg, see above) to yield an annual Q/B ratio of 172.533 yr^{-1} .

In the mass-balancing step of Ecopath, the biomass of gulls was calculated at $0.0622 \text{ mt km}^{-2}$, which is almost double our empirical estimate (see above). This may be reasonable, as gull densities in Puget Sound are as much as three times greater in summer than in winter, when the survey data we used were collected (Nysewander et al. 2005).

Quantitative diet studies for gulls in PSCB generally do not exist, nor are there data on seasonal differences in diet. Summer diet data for glaucous-winged gull chicks on Vancouver Island (Vermeer 1982a) suggest strong reliance ($\approx 70\%$) on planktivorous fishes such as Pacific herring, sand lance, and saury (*Cololabis saira*), whereas adults fed more on human refuse. Vermeer et al. (1987) examined seasonal diets of mew and Bonaparte's gulls at Active Pass (Strait of Georgia) and found much heavier reliance on euphausiids and macrozooplankton in upwelling areas and nearshore and intertidal organisms outside of upwelling areas. Gulls may also raid nests of other seabirds during the breeding season (e.g., Parrish 1995, Good 2002). While this may be a minor component of gull diets, it may be an important source of mortality for the depredated species.

We attempted to represent this functional group diversity as follows. We assumed 40% of their diet was Import, which lessens the ecological footprint of gulls by accounting for external food resources (seasonal migration outside of the model domain, plus feeding on refuse or terrestrial food sources). The balance of the initial diet is dominated by pelagic groups (juvenile Pacific herring, euphausiids, macrozooplankton, forage fish, surfperches, and juvenile salmon) and further supplemented by benthic invertebrates, demersal fishes, and detrital groups (Table 4). Trace levels of their diet are attributed to gulls and resident divers, to represent nest predation.

In addition to the intraguild nest predation, gulls are preyed upon by raptors (Table 4). We are assuming no loss of gulls to incidental mortality in active or derelict fishing gear.

¹³ See footnote 12.

In the 1990s gull densities measured in Puget Sound surveys were highly variable (Nysewander et al. 2005). Although they appeared to decline overall, it is difficult to quantify an actual trend existed that would translate to a *BA* term. It does appear that their numbers declined by more than 40% between the 1970s and the 1990s (Nysewander et al. 2005, Bower 2009). The cause of the long-term decline is unknown.

Migratory Divers

Migratory divers are diving birds that mostly forage in waters deeper than the subtidal zone and that nest in the summer outside of the model domain. Major representatives are grebes, mergansers, loons, and common murre (Table A-5). Distinguishing migratory divers from other diving birds is important: they experience distinct, external sources of mortality during their breeding seasons outside of the model compared to resident divers; also, they tend to feed in different habitats of Puget Sound compared to nearshore divers.

Estimates of biomass relied on the methods described in Appendix C. Aerial density estimates were made separately for western grebes, red-necked grebes, small grebes (i.e., horned and eared grebes), mergansers, loons, and murre. Each density estimate was multiplied by a bias correction factor (ranging from 1.16 to 1.54, Evenson unpubl. data) and a mean individual mass appropriate for the region, obtained from Poole (2005). These corrected biomass densities were then summed to yield an overall biomass estimate of 0.0414 mt km⁻² for migratory divers. Western grebes were the dominant species, comprising more than 60% of the functional group biomass, while mergansers and loons each comprised 15–20% of the group.

P/B estimates come from survival rates (*S*), summarized in Poole (2005); we set *P/B* equal to $-\ln(S)$. Species for which no data could be found were assigned the average *S* of congeners. *P/B* ratios were weighted by the density estimates and summed to generate the final *P/B* estimate of 0.195 yr⁻¹.

Consumption rates were based on allometric functions of daily energy requirements (Hunt et al. 2000, see methods in Appendix C). Estimates of daily prey intake were converted from units of joules to grams of prey by assuming a prey energy density of 6,500 J g⁻¹, consistent with a rich diet of pelagic fish and some pelagic invertebrates. Mass-specific daily prey intakes were multiplied by 365 days, weighted by the relative aerial biomass density estimates, and summed to produce a *Q/B* of 118.965 yr⁻¹.

Ecopath calculated the *EE* via the mass-balancing routine. *EE* = 0.123, which implies a relatively low level of predation mortality in the initial model state.

With a few exceptions, quantitative diet studies for migratory divers in Central Puget Sound do not exist, nor are there data on seasonal differences in diet. We characterized their initial diets based on a variety of reports on diets of grebes, mergansers, and loons in marine waters of British Columbia (Wetmore 1924, Cottam and Knappen 1939, Munro 1941, Reimchen and Douglas 1984, Pauly and Christensen 1996, Gillespie and Westrheim 1997, McIntyre and Barr 1997, Mallory and Metz 1999, Barr et al. 2000). We characterized common murre diets from studies of incidentally taken murre from gill net fisheries in Central Puget Sound (Lance and Thompson 2005). These reports include some quantitative estimates of adult diets and prey

delivered to chicks. These species are primarily piscivores with a small amount of feeding on invertebrates and vegetation. The initial diet, compiled from the reports above and weighted according to the relative biomasses of the bird species, is dominated by juvenile Pacific herring, forage fish, demersal fish, and surfperch. Minor contributors include benthic primary producers, shrimp, small crustaceans, other grazers, soft infauna, squid, and several fish groups including juvenile salmon. An additional 33% comes from the Import pool to account for food consumed when these birds seasonally migrate outside of the model domain.

Migratory divers are preyed upon by raptors. They also experience incidental loss to fishing gear, but as data are not yet available, we will assume no fishing mortality rate (F) at present.

In the 1990s numbers of some of these species appeared to decline in southern Puget Sound (Nysewander et al. 2005), although those authors were cautious in interpreting the apparent decline in western grebes, one of the most numerous species in this functional group. Their caution owes to the highly aggregated nature of western grebes, and the possibility that lower numbers in later years might simply have been due to large aggregations of grebes being out of the area when the surveys occurred, not to a drop in actual population. Loon biomass appeared to increase during the 1990s, while common murrelets and mergansers were highly variable (Nysewander et al. 2005). Given the unclear nature of these trends, we did not assign a *BA* term to this group.

Resident Divers

Resident divers are diving birds that mostly forage in waters deeper than the subtidal zone and that may nest in the PSCB. Major representatives are pigeon guillemots, cormorants, and rhinoceros auklets (Table A-5). We also included the marbled murrelet, a special case because it is an endangered species under the U.S. Endangered Species Act. We say that they may nest in the PSCB because many cormorants, guillemots, and auklets actually nest outside of the PSCB during summer months, but then immigrate to the Central Basin to feed for many months of the year (i.e., only a subset of the mature biomass is resident year-round). For example, seasonal bird counts by WDFW in the 1990s indicated that cormorant numbers were 500% more abundant in winter than summer (Nysewander et al. 2005). Further complicating this functional grouping is the difficulty of identifying cormorant species from aerial surveys. The WDFW aerial surveys identify cormorants in aggregate rather than at the species level, and two of the species (Brandt's cormorant and the pelagic cormorant) nest primarily along the outer coast (species profiles online at <http://www.birdweb.org/birdweb/index.aspx>). We treat all cormorants in aggregate as members of this functional group.

Estimating biomass for resident divers follows the seabird biomass methodology described in Appendix C. Surveyors recorded pigeon guillemots, rhinoceros auklets, and cormorants in aggregate. Marbled murrelets were aggregated with ancient murrelets (*Synthliboramphus antiquus*). Because the latter are very rare in PSCB, we assumed that all murrelets in PSCB are marbled murrelets. Species or aggregate counts were multiplied by a bias correction factor of 1.33 (Evenson unpubl. data), then by the mean individual weights of the species (from Poole 2005) to produce biomass densities. The sum of those densities equaled the

initial biomass for resident divers, $0.0112 \text{ mt km}^{-2}$. Cormorants comprised nearly 97% of the biomass.

We used published annual survival rates (S) to calculate P/B for resident divers. Estimates of S for most of the resident divers were available in a number of studies, albeit from systems other than Puget Sound (Bertram et al. 2000, Wires et al. 2001, Schreiber and Burger 2002, Peery et al. 2006); $-\ln(S)$ was assumed to equal P/B . Using the relative biomass densities from the aerial surveys, we calculated a weighted average P/B of 0.164 yr^{-1} , which seems appropriate for birds with maximum ages ranging from 10 to 18 years (Schreiber and Burger 2002).

We again used the Hunt et al. (2000) allometric scaling function to estimate the Q/B ratio for resident divers (Appendix C). Daily energy intake was converted from joules to grams by assuming a diet energy density of $6,500 \text{ J g}^{-1}$, consistent with a high-quality diet rich in pelagic fish. Multiplying daily intake by 365 days and dividing by average individual mass yielded annual Q/B estimates, which were then weighted by relative abundance and summed to produce a weighted mean Q/B of 118.379 yr^{-1} .

Ecopath's mass-balancing algorithm provided the estimate of EE , based on rates of predation relative to the P/B rate. The $EE = 0.37$.

Several published and unpublished reports have described diets of resident divers in Puget Sound or in nearby waters. The high proportion of cormorants in the functional group's biomass drives the diet patterns of the group (Table 4). Cormorant diets reported by Robertson (1974), Wiens and Scott (1975), and Couch and Lance (2004) reflect a diet dominated by nearshore demersal fishes, surfperch, and some pelagic fishes. Other resident divers are also overwhelmingly piscivorous, with pigeon guillemots feeding most heavily on nearshore demersal fishes while auklets and murrelets feed more on Pacific herring, sand lance, and other pelagic species. We assigned 33.3% to the Import box for food eaten outside of the model domain, in order to account for the summer emigration of most of the cormorants.

Resident divers are preyed upon by raptors and gulls. Resident divers suffer incidental mortality in fishing gear, but as data are not yet available, we will assume no F at present.

We did not assign a BA term to this group, as there was no clear density trend in the 1990s for the most dominant species, the cormorants (Nysewander et al. 2005).

Nearshore Divers

The nearshore divers are primarily comprised of scoters (*Melanitta* spp.) and goldeneyes (*Bucephala* spp.), as well as ruddy ducks, harlequin ducks, long-tailed ducks, and scaups (Table A-5). Birds in this group are diving ducks that spend much of the year in Puget Sound; breeders depart for the summer to nest elsewhere. They mostly feed on benthic invertebrates in nearshore waters, and many of them eat Pacific herring roe off submerged vegetation during the springtime herring spawning period (e.g., Lewis et al. 2007).

We estimated biomass for nearshore divers based on the aerial survey methods described in Appendix C. Surveyors recorded species aggregates (scoters, goldeneyes, scaups) and readily

identifiable individual species (harlequin ducks, buffleheads). Counts were multiplied by species-specific or aggregate-specific bias correction factors ranging from 1.28 to 1.61 (Evenson unpubl. data) and converted to biomass estimates by multiplying by estimated mean individual weights (range: 0.42 kg for buffleheads to 1.115 kg for scoters, Poole 2005). The sum of these biomasses, averaged across the area surveyed, was 0.0846 mt km⁻².

Nearshore diver P/B comes from several studies of annual survival rates for the representative species (e.g., Savard et al. 1991, Kremenz et al. 1997, Ludwichowski et al. 2002, Mowbray 2002, Rotella et al. 2003, Flint et al. 2006, Rodway 2007); most of these studies were for migratory North American populations. Annual survival rates (S) were converted to P/B ratios according to the relationship $P/B = -\ln(S)$, then weighted according to the empirical estimates of biomass densities described above. The weighted average P/B of all species and aggregates was 0.291 yr⁻¹.

We estimated nearshore diver Q/B using the same methodology described for other birds, where daily energetic requirements are a function of body size (Hunt et al. 2000, see methods in our Appendix C). Nearshore diver body sizes, on average, range from 0.4 kg (bufflehead) to 1.7 kg (white-winged scoter) (Hunt et al. 2000). We weighted the daily energy demands according to the relative abundances and body sizes of each species or aggregate, and assumed dietary energy density of 4,200 J g⁻¹, consistent with a diet of bivalves. The final weighted average Q/B for this functional group was 205.235 yr⁻¹.

We allowed Ecopath to estimate EE in the mass-balancing step. The estimated value (0.076) reflects low pressure applied by predators and human causes in the model domain.

Information on nearshore diver diets comes from several sources. Henny et al. (1991) studied surf scoter diets in Commencement and Elliott bays, both of which are in PSCB. Vermeer and Bourne (1984) described white-winged scoter diets in the Strait of Georgia from the 1960s and 1970s. Scoters are known to feed on Pacific herring roe during herring spawning events (Lewis et al. 2007). Scaup diets in southern British Columbia have been described by Munro (1941) and Vermeer and Levings (1977). Vermeer and Levings (1977) measured diets of common goldeneye, while Vermeer (1982b) measured diets of Barrow's goldeneyes and buffleheads. Harlequin duck diets have been measured in Puget Sound (Gaines and Fitzner 1987) and coastal British Columbia (Vermeer 1983, Rodway et al. 2003). The latter authors noted feeding by harlequin ducks on herring roe. From this variety of sources, we derived biomass-weighted estimates of the functional group's overall diet. To account for feeding outside of PSCB and opportunistic scavenging of nonmarine food sources while in PSCB, we assigned just over 38% of nearshore diver diets to the Import category. For dynamic prey pools, the most important groups are infaunal bivalves, small crustaceans, mussels, and other grazers (Table 4). Minor contributions come from juvenile Pacific herring, predatory gastropods, soft infauna, shrimp, barnacles, benthic macroalgae, and algal/plant material.

Nearshore divers are preyed upon by raptors. We assume no incidental fishing mortality.

According to analysis of winter aerial counts, densities of surf scoter, goldeneyes, and scaups—all important representatives of this group—declined by 20–40% in the Puget Sound region between the winters of 1993–1994 and 1999–2000 (Nysewander et al. 2005). No

mechanism for the decline was given by Nysewander et al. (2005), and we do not know if the decline results from processes occurring within Puget Sound or in other areas of the birds' geographic ranges. When we attempted to input a proportional BA term (-0.03 yr^{-1}), the model went out of balance because the nearshore diver EE declined to less than 0 (i.e., the compensatory production related to the BA terms was greater than the predation mortality imposed by raptors). Because of this, we did not input a BA term that might affect mass-balancing results in Ecopath; we instead recommend handling this decline using forcing functions in Ecosim.

Herbivorous Birds

The herbivorous bird functional group includes species for which plant or algal material is the major food source. This group is primarily comprised of dabbling ducks, geese, and brants, many of which are migratory birds that are most abundant in PSCB during the fall, winter, and spring months (Table A-5).

We estimated biomass for herbivorous birds using the aerial survey data and methods described in Appendix C. Surveyors recorded counts of aggregate groups for the most part (e.g., dabbling ducks, geese). Counts were corrected for the bias associated with aerial counts, using aggregate-specific bias correction multipliers ranging from 1.33 to 1.47 (Evenson unpubl. data). The corrected counts were multiplied by aggregate-specific estimates of mean individual biomass (from Poole 2005) and summed, yielding an estimated biomass of 0.055 mt km^{-2} .

As with other bird functional groups, we estimated P/B using published data on annual survival rates, mostly from Hestbeck (1993), Poole (2005), Eichholz and Sedinger (2007), and Hines and Brook (2008). Annual survival probabilities (S) were converted to instantaneous annual mortality rates (i.e., estimates of P/B) by the formula $P/B = -\ln(S)$ and weighted by the relative biomasses of the species and aggregates. Although geese typically have higher annual survival rates than dabbling ducks, the latter made up 85–90% of the total biomass of the group based on the aerial survey data. The weighted average P/B for herbivorous birds was 0.427 yr^{-1} .

For the Q/B ratio, we again used the allometric method for estimating daily energy requirements of seabirds as developed by Hunt et al. (2000) and described in Appendix C. We calculated daily energy intake for the average individual body weights of representative herbivorous birds listed by Hunt et al. (2000), and converted the food requirements from units of joules to grams by assuming a dietary energy density of $2,500 \text{ J g}^{-1}$, consistent with a diet dominated by plant material. These daily requirements were then expanded to annual requirements and weighted according to the relative biomass of dabbling ducks and geese, based on the bias-corrected aerial survey counts. The weighted average Q/B was 329.082 yr^{-1} .

We allowed Ecopath to calculate the EE for herbivorous birds as a function of predatory demand and direct or indirect mortality due to human activities. The EE was 0.080, reflecting the relatively low amount of top-down pressure currently imposed on this group.

Diets of herbivorous birds in Puget Sound are poorly studied. These birds likely forage both in nearshore marine habitats and inland or highly disturbed habitats while they reside in the Puget Sound area. For example, geese and swans that overwinter in the area primarily forage

terrestrially, in fallow fields. Some dabbling ducks may also feed heavily on larvae of terrestrial insects, which are not model components. In addition, we assume that they spend approximately one-third of the year outside the model domain. Thus we have assumed 60% of their diet to be Import (Table 4). The remaining diet is mostly benthic macroalgae, eelgrass, and algal/plant material, with a small amount of other grazers and small crustaceans.

Herbivorous birds are eaten by raptors. We assume no losses due to hunting, and no incidental losses to fishing gear.

We assume no *BA* term for this group. According to Nysewander et al. (2005), the density of these birds has changed for a variety of reasons in recent decades. Populations of dabbling ducks increased by 100–200% in the late 1980s as a result of feeding programs and management actions; however, their densities in the 1990s were variable and may have declined, as measured in aerial surveys (Nysewander et al. 2005, see methods in Appendix C). Geese and brants were far more abundant in the 1990s than in the 1970s (Bower 2009). However, we do not have conclusive evidence of a contemporary trend that would justify a *BA* input.

Raptors

Raptors are birds of prey, nondiving birds whose principal prey items are vertebrates, including fish, other birds, and land mammals. In this model, the major representative of the raptor group is the bald eagle. Other raptors such as the osprey (*Pandion haliaetus*) occur in the area, but we assume their roles to be minor relative to the bald eagle. Bald eagles are iconic birds of high social value. Throughout much of their North American range, bald eagle populations declined to dangerously low levels in the twentieth century, due to habitat loss, illegal poaching, and high contaminant loads in their prey. They were declared federally endangered in 1976. Since then, state and federal protection and improvements in environmental quality have promoted increases in nearly all populations throughout North America, including the Pacific Northwest (Stinson et al. 2007). Their status was upgraded to threatened in 1995, and they were delisted altogether in 2007. Despite delisting, bald eagles remain protected by federal legislation, including the Bald and Golden Eagle Protection Act and the Migratory Bird Treaty Act, and by state rules (WAC-232-12-292).

As of 2000, an estimated 4,500 eagles spend part of the year in Washington, up from less than 1,500 in 1983. Most of these eagles overwinter in Washington and spend the balance of the year in Canada and Alaska, while the remainder are year-round residents that nest in the summer months. Based on available nesting habitat, the current carrying capacity of bald eagles in Washington state is likely closer to 6,000 (Stinson et al. 2007).

To estimate biomass of raptors, we used recent data from bald eagle counts in the study area (Blatz unpubl. data). Between 1998 and 2002, an annual average of 73.75 nesting adults were observed along Puget Sound shorelines (i.e., within ≈ 0.8 km of the shoreline). At an average of 4.5 kg per adult bird (Stalmaster and Gessaman 1984), that would imply a resident adult population biomass of 0.332 mt, or a biomass density of $0.00044 \text{ mt km}^{-2}$. The statewide bald eagle population increases by threefold to fourfold during the winter (Stinson et al. 2007). Assuming a conservative threefold increase for purposes of estimation, we get an estimated biomass of $0.00131 \text{ mt km}^{-2}$. This result ignores some potential sources of bias. For example,

we assume only pairs of adult birds in the nests, but no juveniles. Also, we do not know whether the winter increase noted by Stinson et al. (2007) is similar in all areas.

Raptor P/B estimates stem from annual survival rate data on bald eagles in Washington, as reported by Stinson et al. (2007), citing unpublished data by J. W. Watson (WDFW). Those data suggest very high survival (93–100%) of hatchlings through age 2, followed by lower annual survival (70–73%) of subadults and adults. By fitting an exponential curve to the survival data, we calculated an instantaneous annual mortality rate of 0.314 yr^{-1} , which we used for P/B .

Raptor Q/B estimates were taken from a bioenergetics model developed for overwintering bald eagles in the Nooksack River area of Puget Sound by Stalmaster and Gessaman (1984). They used their model to estimate daily food requirements of bald eagles as a function of temperature, activity level, rainfall, and prey quality. Daily energy intake during winter months was approximately $2,068 \text{ kJ bird}^{-1} \text{ day}^{-1}$, or $490 \text{ g bird}^{-1} \text{ day}^{-1}$ if chum salmon carcasses were the main food source. We simply extrapolated this daily food intake rate over the course of a year for a 4.5 kg eagle and found a Q/B rate of 39.744 yr^{-1} . This may represent an overestimate for year-round residents, whose consumption rates may drop during the warmer, drier months of summer and fall. Alternatively, resident birds have the added costs of parental care during the summer.

There are no predators on raptors in the model, and we assume no losses due to accidental entanglement in gear or to illegal activities (e.g., shooting or poaching). However, we have included a BA rate, reflecting the steady population increase that bald eagles have experienced in recent decades. We assumed a BA of $0.000118 \text{ mt km}^{-2} \text{ yr}^{-1}$, that is, an annual biomass increase of 9%, consistent with observations by Stinson et al. (2007). That represents 28.7% of the P/B rate; by virtue of mass balance, the EE for raptors thus is 0.287.

In compiling their diets (Table 4), we first assumed that raptors acquire nearly 60% of their diet from the Import category, following the assumptions that 1) approximately 75% of the total biomass spends 75% of the year outside of the system, and 2) while in the system, eagle diets include at least some items that are not model groups (e.g., terrestrial mammals, freshwater fishes, birds not associated with marine habitats). Beyond the Import category, bald eagles eat a variety of birds, invertebrates, and fish. They feed heavily on salmon carcasses after salmon spawning occurs in fall and winter.

A survey of Puget Sound area nests ($n = 17$) during breeding season in June and July 1980 found their diet to include grebes, common murrelets, glaucous-winged gulls, scoters, ducks, auklets, pigeon guillemots, loons, herons, pheasants, rockfish, lingcod, Pacific hake, sculpins, Pacific cod, flatfish, plainfin midshipmen, freshwater fish, terrestrial mammals, and bivalves (Knight et al. 1990). A 1986–1997 study of bald eagles nesting in 78 territories in tidally influenced marine and estuarine ecosystems and along freshwater lakes and rivers of Puget Sound and Hood Canal revealed dependence on (in descending order of importance) surface-feeding birds, piscivorous birds, waterfowl, small mammals, bivalves, flatfish, lingcod, spiny dogfish, rockfish, sculpins, salmonids, and crabs (Watson 2002). We summarized available data (Table 4) to the best of our ability and weighted the relative importance of certain groups based on seasons; for example, migratory diving birds are most abundant in the winter, when eagles are also most abundant, and thus have a different relative importance than resident diving birds.

Marine Mammals

Twelve species of marine mammals (six cetaceans, five pinnipeds, and one mustelid) occur in the waters of Puget Sound. Of these, three pinnipeds (harbor seal, California sea lion [*Zalophus californianus*], and Steller sea lion [*Eumetopias jubatus*]) are relatively common in the Central Basin and are included in the model. The remaining marine mammals, including killer whales, aka orcas (*Orcinus orca*), are quite rare or occur seasonally in low numbers in the PSCB. We chose to exclude them from this model (Appendix B).

Harbor Seals

Harbor seals are the most common pinniped in the Puget Sound–Georgia Basin, with a population in the late 1990s numbering close to 13,000 (Jeffries et al. 2003). This followed a substantial increase from a population of 3,000 seals in the late 1970s, and the relatively stable population since the late 1990s may indicate that the population is at carrying capacity. Harbor seals are year-round residents, generally displaying high haul-out site fidelity and localized home ranges (Suryan 1995, Hardee 2008). They are widespread throughout all basins of Puget Sound, but the majority of the population is found among and around the San Juan Islands and in the Strait of Juan de Fuca. More than 1,000 individuals are believed to reside in the Central and South Puget Sound basins (Jeffries et al. 2003), but most (>700) are close to Gertrude Island, a haul-out site in the South Puget Sound Basin (Lambourn et al. 2001). Breeding sites in the Central Basin include Commencement Bay, Liberty Bay, and Sinclair Inlet.

Absent an accurate count of harbor seals in PSCB, we estimated biomass by first arbitrarily assuming a total resident population of 300 individuals. Following Hunt et al. (2000), we assumed an average mass of 0.06 mt per seal, which expands to a total population biomass of 18 mt or 0.024 mt km⁻².

We set the P/B estimate equal to the maximum observed rate of population increase (R_{\max}) for harbor seals in inland waters of Washington State. Between 1978 and 1999, the harbor seal population increased dramatically and eventually stabilized; R_{\max} during that period equaled 12.6% (Jeffries et al. 2003). We thus set P/B at 0.126 yr⁻¹. This exceeds P/B estimates in other models. For example, Field (2004) set harbor seal P/B at 0.084 yr⁻¹ in his model of the northern California Current, based on results from a life history model and corroborated by regional population growth rates of 7% yr⁻¹. Similarly, Ainsworth et al. (2002) estimated P/B for pinnipeds to be 0.06 yr⁻¹, half of the maximum theoretical rate of population increase of 12%.

We estimated Q/B based on allometric relationships summarized by Hunt et al. (2000, see methods in our Appendix C) for a 0.06 mt individual. The relationship estimated daily energy intake, which we converted to prey consumption by assuming a prey energy density of 5.935 kJ g⁻¹ (see harbor seal diet composition description below). Rescaling to annual prey intake produced an annual consumption estimate of 1.476 mt of prey or a Q/B ratio of 24.594 yr⁻¹.

We allowed the model to estimate EE based on mass balance. The EE for harbor seals derives not from predation but from anthropogenic sources of mortality (bycatch and gunshot, see below). The initial EE estimate for harbor seals is 0.397.

Harbor seal diets are comprised primarily of fish, although there is seasonal- and site-specific variation. In the Strait of Georgia, Pacific hake and Pacific herring comprised 70% of their diet, with nine other fish and one squid species making up the rest (Olesiuk 1993). In Hood Canal, Pacific hake, Pacific herring, and salmon were the most important species (London et al. 2001). In South Puget Sound, harbor seals consumed mostly Pacific tomcod, Pacific herring, English sole, plainfin midshipmen, Pacific hake, and a variety of other fish and cephalopods (Cullon et al. 2005). Around the San Juan Islands, the most frequently occurring prey were Pacific herring, walleye pollock, salmon, and sand lance (Lance and Jeffries 2007). Adding further complexity, harbor seal diets are reported in terms of frequency of occurrence of prey in scat samples, rather than in terms of proportion of total gut content mass or volume, and Ecopath diets must be expressed in proportions. The initial diets we input, which are dominated by Pacific herring, walleye pollock, forage fish, salmon, and assorted other fish (Table 4), must therefore be considered assumptions. Harbor seal diets in PSCB are clearly an area where more research is desired.

Harbor seals are not preyed upon by any other species in this model, but some mortality occurs as a result of human activities. Harbor seal mortality has been documented in the nontreaty chum salmon gill net fishery in PSCB and Hood Canal, but the most recent observer data from that fishery are from 1994 (Carretta et al. 2008). Although losses likely occur in contemporary salmon fisheries, they cannot be quantified accurately because no observer program exists.¹⁴ Occasionally, dead harbor seals are found in PSCB, either entangled in derelict gear or with wounds suggestive of entanglement (Wilkinson unpubl. data). Additional mortality occurs when seals are illegally shot, probably to prevent them from damaging gear or stealing fish. At least three harbor seals were reported with gunshot wounds in PSCB waters between 2001 and 2005; all were found dead or died soon thereafter (Wilkinson unpubl. data). It is unlikely that all harbor seals killed by entanglement or gunshot are recorded. As a first approximation, we will assume that 10 harbor seals are killed in PSCB each year due to bycatch or gunshot. If each individual is an average of 0.06 mt, total bycatch and gunshot mortality amounts to 0.0008 mt km⁻² each year.

Sea Lions

California sea lions and Steller sea lions are common in Central Puget Sound. Although their overall numbers are relatively low, they are included in the model due to their large individual size, trophic position, and role as predators on salmon and gadoids.

California sea lions were first observed in Puget Sound in the mid-1970s and their peak springtime abundance increased to more than 1,000 animals throughout the sound. Recent counts number in the low hundreds despite the sharp increase of this population along the North American west coast since the 1970s (Carretta et al. 2008). Puget Sound animals are primarily adult and subadult males that migrate north from breeding islands off Southern California; they arrive in September and remain through May. California sea lions are known to aggregate for opportunistic foraging. For example, small groups in Shilshole Bay nearly decimated spawning runs of steelhead that concentrated below the Hiram M. Chittenden Locks (NMFS 1997). Other California sea lion aggregations near Port Gardner fed primarily on Pacific hake (Everitt et al.

¹⁴ M. Lance, WDFW, Lakewood, WA. Pers. commun., 12 March 2009.

1981). The continued presence of sea lions has been implicated in the failure of the Puget Sound hake stock to recover from overfishing (Schmitt et al. 1995).

Sightings of adult male Steller sea lions have increased in Puget Sound in recent years (Lance and Jeffries 2007). These are large animals with individual weights in excess of 450 kg. Sightings occur in late winter to early spring, after the males have dispersed from northern breeding grounds. They appear to be using areas of Puget Sound, as well as waters around Vancouver Island and the outer coast of Washington, to forage for elasmobranchs, small- to medium-sized schooling fishes, and cephalopods (Lance and Jeffries 2007).

We estimated biomass of sea lions by first arbitrarily assuming that only 50 individuals are regular occupants of PSCB. We further assumed that 60% of these are California sea lions and 40% are Steller sea lions.¹⁵ We assumed the average mass of an individual subadult/adult male California sea lion to be 0.225 mt (Heath 2002) and an individual adult male Steller sea lion to be 0.566 mt (Loughlin 2002); this results in a biomass density of 0.024 mt km⁻².

Sea lion P/B was assumed to be between the P/B ratios for harbor seals (0.0826 yr⁻¹) and Steller sea lions (0.074 yr⁻¹) as estimated by Barlow and Boveng (1991). Presumably, P/B for California sea lions will lie between these estimates, owing to their intermediate size relative to harbor seals and Steller sea lions. If we assume that their P/B ratio is the average of the two estimates from Barlow and Boveng (0.0783 yr⁻¹), and weight the California and Steller sea lion P/B estimates by their biomass estimates (described in the previous paragraph), then the weighted average P/B is 0.076 yr⁻¹.

The Q/B calculation for sea lions was based on allometric relationships as described by Hunt et al. (2000) and summarized in Appendix C. The relationships provided estimates of daily energy intake for California sea lions (mean weight = 0.225 mt) and Steller sea lions (mean weight = 0.566 mt), which we converted to mass intake by assuming a dietary energy density of 6.338 kJ g⁻¹, based on data from Gearin et al. (1999). Based on these calculations, California sea lions have a daily requirement of 17.35 kg of food, which scales to a Q/B of 28.15 yr⁻¹, while Steller sea lions have a daily requirement of 34.24 kg or a Q/B of 22.08 yr⁻¹. The weighted average of these two values is 24.35 yr⁻¹.

Ecopath calculated the EE based on the above parameters and the top-down demands on sea lion production. There is no predation on sea lions in this model, because we did not include transient (mammal-eating) orcas as a functional group. Some mortality occurs as a result of human activities, however. A small number of sea lions are shot illegally each year (see final paragraph in this subsection). Ecopath estimated that sea lion $EE = 0.329$.

Because sea lions spend much of their year outside of PSCB, we assumed that 50% of their diet came from outside the model domain (i.e., Import = 0.5). The remainder of their diet was classified using some published data and some assumptions owing to the nature of the available data. Much of the available data are frequency of occurrence data, based on analysis of scat samples. Frequency of occurrence data must be converted into proportions of total diet mass or volume, a conversion for which there is no clear methodology. Furthermore, a major source

¹⁵ M. Lance and S. Jeffries, WDFW, Lakewood, WA. Field observation, 12 March 2009.

of data, a Gearin et al. (1999) study of California sea lion scat in the Whidbey Basin of Puget Sound, examined samples collected in the late 1980s. Those data are outdated because the prey community has changed considerably in that time, particularly the declining gadoid populations. Thus these diet estimates are best viewed with healthy caution. Local studies will be required to improve these estimates, but again those studies will likely produce frequency of occurrence data.

Concerning available data, Gearin et al. (1999) concluded that California sea lions in the late 1980s primarily fed on Pacific hake, with spiny dogfish, salmonids, walleye pollock, and Pacific herring also occurring fairly commonly. Rare prey included squid, plainfin midshipmen, surfperches, cottids, skates, and lingcod. Thus California sea lions in Puget Sound seem to prefer (primarily but not exclusively) pelagic, schooling prey. For Steller sea lions, the best available information comes from scat samples collected in 2006–2007 from 12 individuals in the nearby San Juan Islands (Lance and Jeffries 2007). Those scat samples revealed very high frequencies of occurrence of spiny dogfish and skates in wintertime Steller sea lion diets, along with notable contributions from Pacific herring and other schooling fish as well as some demersal fish. Weighted according to the size and abundance of California and Steller sea lions, our estimated initial sea lion diet is 50% Import and the rest is made up of a diversity of fish groups and cephalopods (Table 4). The major fish prey are spiny dogfish, skates, gadiforms, forage fish, and Pacific herring. As implied above, these estimates are tenuous.

Essentially no predation on sea lions occurs in the model domain. We are unaware of incidental sea lion mortality in fishing gear, and thus assume that direct fishing mortality equals zero. Some sea lions are illegally shot, however, to prevent them from foraging around fishing gear. At least 10 California sea lions were killed by gunshot in the PSCB area from 1996 to 2005 (Wilkinson unpubl. data), and it seems likely that more were killed in this manner but were not reported or discovered. There are no records of Steller sea lions shot to death in PSCB during that time period. We will assume that two California sea lions in PSCB are killed by gunshot each year; at an average mass of 0.225 mt, this corresponds to an annual biomass loss of $0.0006 \text{ mt km}^{-2}$.

Bacterial and Detrital Pools

The final groups in the model fuel the enormous amount of production in Puget Sound that is supported by recycled materials (see Throughput and Transfer Efficiency subsection of Results section). Bacteria play the critical role of recycling nutrients, decomposing detrital organic matter, and providing a food source for lower trophic level consumers. Little published literature exists for Puget Sound bacteria in either the pelagic or benthic zones, thus the information presented below is largely speculative and best viewed as placeholder information until better data are available. Detrital pools in EwE are repositories for organic material that has died within the model domain due to other mortality, that is, mortality that is not due to predation by a model group nor to being landed by a fishery. Most EwE models feature one detrital pool: a generic detritus box. We recognize three distinct detrital groups in this model, because there is evidence that two additional detrital pools (algal/plant material and salmon carcasses) each play distinct ecological roles in the food web.

As a general rule, detrital pools in Ecopath have only biomass and *EE* terms, and the actual value of the biomass term is unimportant. The more important aspects are production and fate, that is, flows of material into and out of a detrital pool (Christensen et al. 2005). Detrital production is a function of the biomass, *P/B*, and *EE* values of all primary producer and consumer groups in the model. Detrital fate is controlled by the user and indicates the detrital pool into which dead material flows. At the end of each model time step, detrital materials can be set to either accumulate or, as is more typically done, be exported from the system.

Bacteria

In the absence of available data, we made arbitrary estimates of *P/B*, *Q/B*, and *EE* for bacteria and allowed Ecopath to calculate biomass based on mass balance. For *P/B* we assumed a very high rate (150 yr^{-1}), reflecting the tendency of bacteria to rapidly turn over in response to changing conditions. Following the suggestion of Christensen et al. (2005), we assumed a growth efficiency (*P/Q*) ratio of 0.5 for bacteria, which leads to a *Q/B* of 300 yr^{-1} . We set *EE* = 0.4, implying a modest degree of consumption of annual productivity by consumers that feed on bacteria. In the mass-balancing step, Ecopath calculated bacteria biomass is 6.395 mt km^{-2} .

Compared to empirical data from other Pacific systems, these estimates seem reasonable. For example, pelagic bacterial biomass estimates from the subarctic north Pacific to the equatorial Pacific average $1.327 \text{ mt C km}^{-2}$ (range 1.142–1.500), and worldwide range between 0.5 and 2.0 mt C km^{-2} (Ducklow 2000). Applying a conversion factor for C:dry cells (0.4748, Bratbak and Dundas 1984) and a range of dry weight:wet weight of 0.22 (Watson et al. 1977) to 0.43 (Ducklow 2000), estimated wet weight biomass of bacteria could vary between 2.449 and $19.147 \text{ mt km}^{-2}$. The Ecopath-calculated biomass falls into the lower third of that range. Bacterial production from the subarctic to equatorial Pacific ranges from 100.01 to $509.2 \text{ mt km}^{-2} \text{ yr}^{-1}$ (Ducklow 2000), which given the range of weight wet biomass would lead to a *P/B* range of 5.22 to 207.92 yr^{-1} . The assigned *P/B* value of 150 is near the upper end for pelagic production alone. These estimates do not account for benthic bacterial biomass or production, however.

We assume that the bacterial diet is 100% detritus.

Many organisms feed on bacteria, either actively (e.g., microzooplankton) or passively (e.g., filter feeders or organisms feeding on particulate detritus on which bacteria occur).

Detritus

This pool represents generic detritus—dead and decaying organic matter—and it receives input from all other groups (including, ultimately, the other two detrital groups listed below). It is a critical food resource for many consumers at most trophic levels, from bacteria to scavenging vertebrates.

The detritus biomass was arbitrarily set at 1.0 mt km^{-2} . In the mass-balancing step, Ecopath calculated the *EE* of detritus to be 0.393, a result of consumption by a range of functional groups. Summary descriptions of the detritus pool, provided by Ecopath following the mass-balancing step, indicate that 69% of the detritus comes from phytoplankton. Other contributors include bacteria (8.5%), copepods (3.9%), soft infauna (3.8%), microzooplankton (3.6%), benthic microalgae (1.9%), small crustaceans (1.8%), infaunal bivalves (1.2%), and

euphausiids (1.1%). Clearly, most detritus originates in the pelagic realm via phytoplankton or consumers of phytoplankton. The major consumers of detritus, in terms of total detritus consumed per year, are soft infauna, bacteria, small crustaceans, and infaunal bivalves. Thus the phytoplankton-driven detritus pool is a major subsidy of benthic production, consistent with Strickland's (1983) description of energy flow in Puget Sound.

Algal/Plant Material

The algal/plant material group was created for the purpose of more directly linking the dynamics of large benthic primary producers (eelgrass, benthic macroalgae, and overstory kelp) to consumers that are known to graze on detached algal/plant material (e.g., sea urchins, small crustaceans). Moreover, as ecosystem models of Puget Sound are developed further, we may find that this pool represents an important inshore-offshore linkage: in demersal fish surveys conducted in PSCB during 2004–2005, large amounts of detached algal/plant material were collected in bottom trawls at several sites at depths ranging from 20 to 160 m.¹⁶ This material could be a trophic subsidy for members of the demersal community.

Algal/plant material biomass was arbitrarily set at 1.0 mt km⁻². In the mass-balancing step, Ecopath calculated the *EE* of algal/plant material is 0.626, as a result of consumption by a wide range of functional groups. According to the Ecopath summary output, most algal/plant material is generated by eelgrass, with a substantial amount produced by benthic macroalgae. Overstory kelp adds a small amount. Consumption of algal/plant material is dominated by small crustaceans and other grazers; sea urchins and herbivorous birds are also notable consumers.

Salmon Carcasses

Salmon carcasses were added as a detritus pool in order to link Pacific salmon dynamics to raptors. Overwintering bald eagles derive much of their diet from spawned out salmon carcasses, and this has some potential significance because raptors are a top predator that feeds on a variety of other groups, including many seabirds. This creates the potential for year-class strength of salmon to have indirect feedbacks to the bird community. In addition, salmon carcasses represent marine-derived food and nutrient subsidies for a wide array of freshwater and terrestrial organisms, a topic that may be of interest as ecosystem models of Puget Sound develop further.

Salmon carcass biomass was arbitrarily set at 1.0 mt km⁻². In the mass-balancing step, Ecopath calculated the *EE* of salmon carcasses is 0.002, as a result of consumption by raptors. Most input to salmon carcasses comes from subadult wild salmon and subadult pink salmon. A small amount also comes from subadult hatchery salmon, some of which will stray onto natural spawning habitat rather than returning to the hatchery from which they were produced.

¹⁶ T. Essington, Univ. Washington, School of Aquatic and Fishery Sciences, Seattle. Pers. commun., 23 May 2008.

Appendix B: Omitted Groups

Many species and functional groups were not included in the Puget Sound Central Basin (PSCB) model. Some are rare or spend only a small amount of time in the system. Some are poorly studied and lack suitable information to characterize them in food web terms. Some are thought not to be very tightly linked to other functional groups and thus would show little response to food web perturbations. Many of these groups will likely be incorporated into future models that operate on broader spatial scales or that consider a broader array of ecosystem processes.

Several notable omitted species are described briefly below, including the reasons why they were excluded from the present model.

Primary Producers

We think that the included primary producers represent the most significant sources of marine autochthonous production in the model. Species of one group that has been omitted and that may play a significant ecological and management role, however, are the phytoplankton species that produce harmful algal blooms (HABs). Several taxa, including the genera *Alexandrium*, *Pseudo-nitzschia*, *Heterosigma*, and *Chaetoceros*, are found in Puget Sound and occasionally experience blooms under the right combinations of light, temperature, nutrient levels, and stratification (Ruckelshaus and McClure 2007). Some HAB species contain toxins that can render bivalves unsafe for human consumption, due to conditions such as paralytic shellfish poisoning or amnesic shellfish poisoning; the shellfish themselves are not affected by the toxins. Other HAB species produce toxins that can lead to fish kills. HAB dynamics could clearly be important in model simulations, for example, through reducing harvest rates on bivalves or increasing mortality on vulnerable fish species. We have not included them at this point simply in the interest of streamlining the model process, but we could mimic the effects of HAB-related closures on bivalve harvest in Ecosim by reducing the fishing mortality rate on infaunal bivalves, geoducks, or mussels.

Invertebrates

Invertebrates are so diverse and abundant in Puget Sound that some groups inevitably are overlooked due to either lack of data or a presumption that the groups are less essential to the functioning of the overall system. Key examples are discussed briefly.

Sea Anemones

Numerous species of sea anemone (order Actinaria) live in Puget Sound, particularly on hard substrates. Some, such as the plumose anemone (*Metridium senile*), can achieve very high biomasses in local patches. Sea anemones feed on a variety of species, ranging from small

planktonic crustaceans to benthic invertebrates to fishes (Kozloff 1983). We chose to omit them because of a general lack of data on their biological rates and diets.

Burrowing Shrimp

Two types of burrowing shrimp (infraorder Thalassinidea) inhabit Puget Sound: blue mud shrimp (*Upogebia pugettensis*) and bay ghost shrimp (*Neotrypaea californiensis*). Both are nearshore species that build extensive tunnels in soft sediments. Blue mud shrimp form semipermanent tunnels and draw large volumes of water into the tunnel by continuous movement of their pleopods, straining out phytoplankton and detritus for food (Hornig et al. 1989). By contrast, ghost shrimp reshape their tunnels continuously, feeding on detritus sifted from the sediments and, to a lesser extent, detritus and phytoplankton filtered from the circulating water (Morris et al. 1980).

Burrowing shrimp can be considered ecosystem engineers because their burrowing and filtering activities affect sediment porosity and stability (Dumbauld et al. 1997), subsurface biogeochemistry (Waldbusser and Marinelli 2006), and habitat suitability for other species, including eelgrass (*Zostera marina*) and other invertebrates (Dumbauld and Wyllie-Echeverria 2003). They are also important prey for higher consumers, notably gray whales (*Eschrichtius robustus*) (Weitkamp et al. 1992). Biomass concentrations can be enormous; in northern Puget Sound, Weitkamp et al. (1992) estimated ghost shrimp biomass densities equivalent to 1,488 mt km⁻². However, these aggregations are highly patchy and the biomass of burrowing shrimp at the scale of the entire basin is small.

Oysters

Oysters are very important to the ecology of estuarine ecosystems where they are abundant. They filter feed tremendous volumes of water, which may have feedbacks to water quality. The large reefs that they form are used as habitat by many species. Furthermore, they are an extremely valuable fishery resource for both commercial aquacultural producers and also recreational harvesters (e.g., Emmett et al. 1991). Most oysters in Puget Sound are either the nonnative Pacific oyster (*Crassostrea gigas*) or the native Olympia oyster (*Ostrea conchaphila*). The Pacific oyster, introduced from Japan in the early 1900s for aquacultural purposes, has become abundant in some parts of Puget Sound, within areas of active culture as well as in naturalized beds in the intertidal zone (Pauley et al. 1988). The Olympic oyster has declined markedly throughout much of its range, due largely to overharvest, habitat degradation, competition with introduced oysters, and nonnative predators that were introduced with nonnative oysters. It now exists primarily as small remnant populations in lower tidal zones (Couch and Hassler 1989, Gillespie 2009). Neither species is especially abundant in the PSCB, however, and hence they are not featured in this model.

Scallops

Puget Sound is home to several scallop species. Scallops are epibenthic, free-swimming, filter-feeding bivalves. Some, like the giant rock-scallop (*Crassadoma gigantea*), are associated with rocky substrates or shell hash, while others may be found on soft sediments or around the bases of man-made structures (Morris et al. 1980, Kozloff 1983). Maximum sizes range from 6

to 8 cm in diameter for reddish scallop (*Chlamys rubida*) and spiny scallop (*C. hastata*) to more than 15 cm in diameter for the giant rock-scallop and the weathervane scallop (*Patinopecten caurinus*) (Kozloff 1983, MacDonald et al. 1991). Although all of these species are prized for their culinary value, fisheries are no longer practical owing to low populations. Commercial scallop fishing in PSCB essentially ceased in the late 1990s. The State of Washington permits a limited take of rock and weathervane scallops for broodstock purposes in Puget Sound (WAC 220-52-069). Biomasses of scallops in PSCB are lower than in other Puget Sound basins,¹⁷ and we assume that their abundances are low enough to warrant exclusion from this model.

Fishes

As with the above groups, fishes are so diverse that many species are inevitably omitted from an analysis such as this. Several relatively high-profile species deserve specific mention.

Sixgill Sharks

Bluntnose sixgill sharks (*Hexanchus griseus*) may be the largest fish that regularly inhabits Puget Sound. Their ecology and habits in Puget Sound have only recently been studied in depth. Most individuals captured in Puget Sound are believed to be juveniles, although mature, pregnant females appear to enter Puget Sound in order to pup (Andrews et al. 2007). Interest in the shark has surged in recent years, due to frequent sightings by divers, destructive interactions between sixgills and fisheries (e.g., depredation of catches from longlines, raiding of crab pots), discoveries of dead specimens on beaches, and some interest in a recreational fishery, though that fishery was closed by state fisheries managers because the ability of the population to sustain a fishery was not known. Much of the recent study on sixgill sharks has been focused on seasonal and diel movement patterns, but little is known about core aspects of biology or ecology (e.g., population size, individual growth rates, diets). Our belief is that the population is currently too small to have a major effect on the ecological function of Puget Sound, and that our lack of basic ecological knowledge prevents us from developing reasonable parameter sets that could inform us of how they respond to ecosystem changes. This could change as more information is collected.

Sockeye Salmon

Sockeye salmon (*Oncorhynchus nerka*) are an abundant species in the PSCB, primarily owing to populations that spawn in the Lake Washington watershed. Spawning runs to that system may number in the hundreds of thousands, although variability is high. In years with adequate adult escapement, they support commercial and recreational fishing, and are also important for tourism, as they are the most abundant salmonid that passes through the public viewing area at the fish ladder located at the Chittenden Locks in Seattle. We omitted them from the model on two accounts. First, their life history is most distinct compared to the other species, given their extended lacustrine residence during their juvenile freshwater stage. That made it difficult for us to include them with other wild salmon species in a generic salmon pool. Second, they pass quickly through the marine waters of Puget Sound as they go to sea and return to spawn, minimizing their interaction with other model groups.

¹⁷ W. Palsson, WDFW, Mill Creek, WA. Field observation, 25 March 2009.

Sturgeons

Sturgeons (family Acipenseridae) have two representatives in this area: the white sturgeon (*Acipenser transmontanus*) and the green sturgeon (*A. medirostris*). Both receive considerable attention due to their rather exceptional biology, large size, wide geographic ranges and dramatic anadromous migrations, value as fishery targets, conservation status, and cultural significance. Ecologically, they are of potential interest as predators of benthic invertebrates. However, due to both species' rarity in Puget Sound (e.g., Monaco et al. 1990, Emmett et al. 1991), we omitted them from the PSCB EwE model.

Halibut

Pacific halibut (*Hippoglossus stenolepis*) are the largest flatfish that occur in Puget Sound, and are another iconic species of the region. They are capable of reaching more than 100 kg in weight. They are highly predatory and prized by sport anglers. WDFW records the fishing zones in which halibut are captured, and virtually all catch in Puget Sound occurs in basins to the north of PSCB. We therefore assume essentially no halibut biomass in our model domain.

Sablefish

Sablefish (*Anoplopoma fimbria*), also called black cod, are predatory demersal fish that are abundant in the Northeast Pacific Ocean. Their diets are diverse and opportunistic, and their rapid growth and large size suggest high rates of consumption of their prey resources. They are one of the most valuable components of the west coast and Alaska groundfish fisheries (Love 1996). Sablefish also occur in Puget Sound. Currently, their numbers are low, to the point that harvests have limits under Washington state law (e.g., WAC 220-48-005). Due to their current rarity, which dates back several decades, we exclude them from this model.

Wolf Eels

Wolf eels (*Anarrhichthys ocellatus*) are large predators most often associated with rocky habitats such as subtidal, high-relief boulder fields typical of northern Puget Sound. They feed on benthic invertebrates and are occasionally piscivorous. They are a high-profile species for recreational scuba divers, owing to their distinctive physical appearance and their courtship and nest-guarding behaviors (Love 1996). Occasionally taken by commercial or recreational fisheries, they are considered quite palatable. In the absence of any quantifiable information on their abundance, production, consumption, or diet, we have chosen to omit them. We presume them to be too rare in PSCB to be of great functional significance at the community scale or of great enough management importance to drive policy.

Seabirds

Shorebirds are the most substantial group of seabirds that we omitted in the current model. Some shorebirds are year-round residents but most are present from fall through spring. Examples include the great blue heron (*Ardea herodias*), belted kingfisher (*Megaceryle alcyon*), blackbellied plover (*Pluvialis squatarola*), killdeer (*Charadrius vociferous*), dunlin (*Calidris alpina*), and sanderling (*Calidris alba*). Shorebirds are generally waders that feed very close to

shore on invertebrates and fishes. We opted not to include them at this time because there are no comprehensive surveys of their abundances and we are unsure about the nature of their direct interactions with the biomass pools in the model.

Marine Mammals

The marine mammals that were omitted are species that typically spend very little time in PSCB. We opted to omit them rather than to try to judge the validity of scenarios in which they responded strongly (or elicited strong responses in other groups) following a perturbation.

Orcas

Transient and resident killer whales, aka orcas (*Orcinus orca*), are among the most iconic of species that occur in Puget Sound, but are rarely sighted in the Central Basin. The two types of killer whale are distinct, sympatric ecotypes that are most readily distinguished in ecological terms by their feeding habits; transient whales feed primarily on other marine mammals, while resident whales feed mostly on fish.

Transient killer whales are seen regularly in the fall throughout the Salish Sea, most frequently off southeastern Vancouver Island in small groups ($\bar{n} = 3$, Baird and Dill 1995, 1996). They only occasionally enter the PSCB. However, prolonged foraging visits to Hood Canal have occurred in recent years: in 2003, 11 transient whales were present for 59 consecutive days; in 2005, 6 whales were present for 172 consecutive days (London 2006). These whales were primarily targeting harbor seals.

Three pods of the Southern Resident killer whale (SRKW) stock frequent waters of Puget Sound (Caretta et al. 2008). The SRKW population, monitored by photo identification since 1974, is believed to number 83, and is listed as endangered under the U.S. Endangered Species Act. SRKW occupy the Salish Sea most days during the summer and fall, foraging mostly on Chinook salmon runs bound for spawning rivers in the Puget Sound–Georgia Basin. They primarily inhabit major channels around the San Juan Islands in the summer, but may move all the way down to South Puget Sound in pursuit of salmon. Extended foraging in the Central Basin is quite rare.

Baleen Whales

Gray whales are the largest animals that regularly occur in Puget Sound. They are baleen whales that reach up to 15 m in length and a mass of over 30 mt. Recent studies projected their west coast population at approximately 18,000 (Rugh et al. 2005). Each year, during the springtime migration from Baja California to Alaska, a small fraction of the population enters Puget Sound south of Admiralty Inlet. The total number is variable but apparently not very large (e.g., Calambokidis et al. 2002). Unlike most baleen whales, gray whales typically feed on benthic invertebrates in soft sediments. They enter shallow waters and gouge large troughs from the bottom, expelling water and sediment through their baleen and retaining the invertebrates. Gray whales feed heavily in ghost shrimp beds in Puget Sound, as documented by Weitkamp et al. (1992). We elected to omit them from the present model, assuming their ecosystem influences to be highly localized.

Two other baleen whale species, minke whale (*Balaenoptera acutorostrata*) and humpback whale (*Megaptera novaeangliae*), make very occasional visits to Central Puget Sound.

Porpoises

Two species of porpoise live in Puget Sound: harbor porpoise (*Phocoena phocoena*), the most abundant cetacean in the system, and Dall's porpoise (*Phocoenoides dalli*). Harbor porpoises feed on squid and pelagic fishes, while Dall's porpoises are primarily piscivorous and especially target demersal and midwater species (Walker et al. 1998). Recent assessments put the Washington Inland Waters stock of harbor porpoises at 10,700 (Carretta et al. 2008); most are found in the straits of Georgia and Juan de Fuca. While recent observations of live animals and strandings suggest that harbor porpoise occurrence in PSCB is increasing, their numbers are low and far below records from the 1940s, when harbor porpoises were very common in Puget Sound (Scheffer and Slipp 1948). Survey counts in Washington Inland Waters indicated about 3,500 Dall's porpoises present in 1991, although considerably fewer (900) were seen in the most recent surveys, conducted in 1996 (Carretta et al. 2008). Dall's porpoises are found throughout the Strait of Juan de Fuca and Puget Sound, with the main concentration in the Haro Strait area. They are regularly observed in PSCB in small numbers. No current estimates of the number of Dall's porpoises present in PSCB exist. In the late 1980s, it was estimated that as many as 80 Dall's porpoises were present in this region, although 20 individuals was the more frequent count (Miller 1990).

Sea Otters

Sea otters (*Enhydra lutris*) were once far more abundant in Washington state waters than they are now, although we lack definitive information that they have ever been abundant in Puget Sound. Sea otter bones have been reported at archaeological sites within Puget Sound, but these findings are rare (Lance et al. 2004). Currently, the sea otter population on the outer coast of Washington State and in the western Strait of Juan de Fuca is increasing at an annual rate of 8.2%, and individuals are occasionally seen in Puget Sound basins, so it is possible that continued population increases will lead to expansion into PSCB (Lance et al. 2004). This may have substantial effects on ecology of nearshore communities because sea otters are widely considered keystone species that can control populations of benthic herbivorous invertebrates and release kelp from grazing pressure (Estes and Palmisano 1974).

Appendix C: Frequently Used Estimation Methods

The functional group descriptions in Appendix A provide general summaries of the methods used to develop estimates for the parameters in Equation 1. In some cases, the same basic field methods and data analyses were employed for multiple functional groups. For example, biomass and diet estimation followed a common process for many of the groundfish. Or in cases where P/B (production:biomass ratio [which is roughly equal to total mortality, Christensen et al. 2005]) or Q/B (consumption:biomass ratio of a predator) estimates were unavailable in the literature, we used estimation equations developed for a range of species and systems.

Rather than repeatedly describing frequently used methods in each functional group description where they were applied, they are summarized here.

Biomass Estimation for Bottom Fish

Much of our data on bottom fish biomass comes from the work of Reum (unpubl. data) and Reum and Essington (2008). They conducted a series of bottom trawl surveys in October 2004 (fall), March 2005 (winter), and July 2005 (summer) on the eastern side of the Puget Sound Central Basin (PSCB). Sampling was done at six stations. Trawls were conducted along bathymetric contours at 20 m, 40 m, 80 m, and 160 m depths, and total area swept was measured based on the width of the trawl mouth (which was depth dependent and empirically monitored), the vessel speed, and the time the trawl was believed to be in contact with the bottom (Reum 2006). Catches in each trawl were sorted to species and counted, and each species' total aggregate mass was determined and expressed as units of mass per unit area swept. For the purposes of demersal fish parameter development in the Ecopath with Ecosim (EwE) model, we assumed that trawl selectivity = 1, that is, that the trawl sampled all demersal fish that it encountered. (By extension, we did not use the trawl data for invertebrates or pelagic fish to perform estimations of biomass.) Mean individual mass of a species in each trawl was equal to the aggregate mass divided by the number captured.

Using the raw trawl survey data (Reum unpubl. data), we determined the species-specific mean biomass density at each depth stratum in each season using delta distribution, a modified γ -distribution that accounts for samples with many zeros and occasional, exceptionally large catches (Pennington 1996). The depth-specific biomass density estimates were then expanded to the scale of the basin according to the total area of bottom habitat of the adjacent bathymetric contours. For example, the trawl data for the 20 m bathymetric contour were assumed to be representative of the area between the 10 m and 30 m bathymetric contours, and the mass-per-area-swept estimate was multiplied by the total area of bottom between 10 m and 30 m, according to bathymetry data for PSCB (Table 1). Biomass densities at nonsampled depth strata

were estimated via linear interpolation relative to the two most proximate sampled strata, except for depths shallower than 10 m and deeper than 170 m; biomass densities at those depths were assumed to be equal to the nearest sampled stratum. The stratum-specific biomass densities were summed and divided by the total model area (757.08 km²) to generate season-specific biomass estimates for each demersal species or functional group.

This method was applied to biomass estimation for spiny dogfish (*Squalus acanthias*), ratfish (*Hydrolagus colliei*), skates (*Raja* spp.), Pacific cod (*Gadus macrocephalus*), demersal fish, piscivorous flatfish, and small-mouthed flatfish.

Biomass Estimation for Seabirds

Many of the key species or genera that are in our seabird functional groups (Appendix A, Seabirds) have been monitored by WDFW since 1992. Monitoring is conducted by summer and winter aerial surveys from a float plane, as described by Nysewander et al. (2005). In brief, the plane flies surveys at low altitude (65 m) and slow speed (approximately 150 km hr⁻¹) over two habitat strata: nearshore waters (<20 m depth) and offshore waters (>20 m depth). Nearshore surveys are flown parallel to shore, while offshore survey tracks are zigzagged. Survey tracks cover 13% to 15% of the nearshore and 3% to 5% of the offshore waters in Puget Sound up to the Canadian border and out to the entrance to the Strait of Juan de Fuca. Two onboard observers identify and count all birds seen within a 50-m wide strip on each side of the plane, and the time and GPS location of each observation is recorded. Correction factors are applied to counts, given the propensity of some birds to dive and hence be missed by the surveyors. These correction factors are based on differences between concurrent observations by aerial surveys and ship-based or land-based surveys (Nysewander et al. 2005). The corrected values provide the basis for estimating population size and error. Mean individual weights can then be used to convert abundance estimates into biomass estimates.

For our purposes, we used 2005 and 2006 winter density estimates from surveys in the Central Basin, Whidbey Basin, and Admiralty Inlet, and taxon-specific correction factors provided by Evenson (unpubl. data). Taxon-specific average individual body weights were taken from several sources, mainly Hunt et al. (2000) and Poole (2005). Mean total biomass estimates were divided by the total swept area to yield biomass estimates.

***P/B* Estimation for Benthic Invertebrates**

Because secondary production of benthic marine invertebrates is difficult to study empirically, a theoretical relationship that links benthic invertebrate *P/B* to some life history or environmental characteristic is desirable. This is particularly true in Puget Sound, where benthic invertebrates are diverse and abundant. Life span should be a good predictor of *P/B*, because longer-lived benthic invertebrates will have many larger-bodied, slower-growing individuals in their populations and these individuals lower overall mass-specific productivity. As summarized by Robertson (1979), benthic invertebrate ecologists have long recognized the general relationship between life span and *P/B*, and there have been many attempts to quantify it at both limited and broad taxonomic scope. Robertson (1979) performed a comprehensive literature review of life span and *P/B* ratios for annelids, benthic gastropods, bivalves, crustaceans, and

echinoderms. From a data set of 49 studies conducted throughout the world, he fit the following relationship between measured life span and empirically estimated P/B ratios:

$$\log_{10}(P/B) = 0.66 - 0.726 \log_{10}(\lambda) \quad (6)$$

where λ is the maximum life span in years.

We used the Robertson (1979) equation to calculate P/B for sea stars, large sea cucumbers, sea urchins, other grazers, predatory gastropods, small crustaceans, barnacles, mussels, infaunal bivalves, deposit feeders, suspension feeders, and tunicates.

***P/B* Estimation for Fish**

In some cases where P/B estimates were not available from empirical data or population assessments, we estimated P/B using a generalized fish natural mortality predictive equation. Pauly (1980) developed the relationship empirically from 175 estimates of natural mortality, distributed throughout the world and representing 40 different families of pelagic and demersal fishes. Importantly, this relationship does not predict total mortality (Z), which is the sum of mortality (M) and the rate of fishing mortality (F); Z is assumed to approximate P/B in Ecopath. Thus the Pauly (1980) method must be combined with F estimates to yield P/B (Christensen et al. 2005). However, as Pauly (1980) notes, M is very difficult to measure, and a robust theoretical predictor would be of great value.

As Pauly (1980) describes, the growth parameter k from the von Bertalanffy growth equation has long been recognized as a reasonable predictor of M . In his analysis, Pauly (1980) also found that including temperature explained substantial variation in M . His interpretation was that increasing temperature induced greater predation mortality because of higher metabolic demands of predators. According to Pauly (1980), the estimation function is:

$$M = k^{0.65} \times L_{\infty}^{-0.279} \times T^{0.463} \quad (7)$$

and k is the von Bertalanffy growth parameter, L_{∞} is the theoretical maximum length (cm), and T is the mean annual temperature at which the species lives (°C). The correlation coefficient between observed and predicted values was 0.847 (Pauly 1980).

We used this method as the basis for P/B estimation of lingcod (*Ophiodon elongatus*), ratfish (*Hydrolagus colliei*), and skates. von Bertalanffy parameters came from published estimates, and T estimates were based on monthly temperature data collected by the Washington Department of Ecology throughout Central Puget Sound (WDE no date). We used temperature data from depths corresponding to expected depth distributions of the species or group in question.

***Q/B* Estimation for Fish**

Many of the Q/B estimates for fish groups come from bioenergetics model predictions, but for many fish, credible bioenergetics models are not available. Moreover, empirical estimates of consumption rates, through field measures or laboratory studies of gastric

evacuation rates, are quite difficult to obtain. Thus theoretical predictive relationships are desirable. Two reviews by Palomares and Pauly (1989, 1998) described empirical relationships between Q/B and several variables, including body weight, temperature, aspect ratio of the caudal fin, and prey type. Christensen and Pauly (1992) developed a simplified predictive equation without the aspect ratio measure, and we used this equation for many functional groups of fishes. The equation is:

$$Q/B = 10^{6.37} \times 0.0313^{Tk} \times W_{\infty}^{-0.168} \times 1.38^{Pf} \times 1.89^{Hd} \quad (8)$$

where Tk is the mean annual temperature (expressed as $1,000/(T + 273.15)$, where T is temperature in °C, W_{∞} is the theoretical maximum weight of an individual of the functional group, Pf is a dummy variable (1 if the fish is a predator or planktivore, otherwise 0) and Hd is a dummy variable (1 if the fish is primarily an herbivore, otherwise 0). W_{∞} estimates came from published length-at-age and length-weight relationships for representative species, and T estimates were based on temperature data collected monthly by WDE at multiple depths throughout Central Puget Sound (no date); we used temperature data from depths corresponding to expected depth distributions of the species or group in question.

We used this method to estimate Q/B for surfperches, piscivorous flatfish, small-mouthed flatfish, and skates.

Use of Q_{10} for Temperature-dependent Rate Estimation

Many metabolic rates are temperature dependent, and the relationship is often not a simple linear function. In several cases described in Appendix A, we were forced to rescale a rate (e.g., consumption) as a function of temperature. Often this was because consumption rates or diet data were available seasonally and we know that temperature varies on a seasonal basis. In other instances, we had consumption rates from a nearby ecosystem where water temperatures were different (often cooler) than temperatures experienced by PSCB functional groups. To do this rescaling, we used Q_{10} , a theoretical magnitude of increase in a rate when temperature increases over a small range. Q_{10} can be calculated as:

$$Q_{10} = \left(\frac{R_2}{R_1} \right)^{\frac{10}{T_2 - T_1}} \quad (9)$$

where T_1 and T_2 are the cooler and warmer temperatures, respectively, and R_1 and R_2 are the corresponding rates at those temperatures. Typically, a taxonomy-specific Q_{10} rate is available from the general scientific literature (particularly literature relating to bioenergetics) and the equation is rearranged to solve for the unknown R . T estimates were based on temperature data collected monthly by WDE throughout Central Puget Sound (no date); we used temperature data from depths corresponding to expected depth distributions of the species or group in question.

The Q_{10} calculation was a critical part of bottom fish diet estimation (see next subsection below). It was also used in Q/B estimations for jellyfish and ratfish.

Bottom Fish Diet Estimation

Predator-prey interactions are the main way that functional groups are linked to one another in EwE. Thus reasonable diet proportions are an important part of initial model development. Reum (2006) examined the stomach contents of many bottom-dwelling fish species in several seasons, depths, and sites in PSCB between 2004 and 2005. His data represent the best set of information on contemporary feeding habits of the bottom fish community. We made extensive use of his data and developed diet proportions for a number of functional groups, weighted by season as described below.

Reum (2006) conducted a series of bottom trawl surveys in October 2004 (fall), March 2005 (winter) and July 2005 (summer) on the eastern side of PSCB. Sampling was done at six stations; trawls were conducted along bathymetric contours at 20 m, 40 m, 80 m, and 160 m depths. For each functional group, raw stomach content data (Reum unpubl. data) were sorted taxonomically, and prey items were pooled to correspond to our functional groups (Table 2). The proportion of total stomach content weight of each prey group was averaged across all sampled fish for a given season. We pooled across all depths and sites because of the considerable spatial variability of stomach contents (Reum and Essington 2008). To consolidate seasonal diet proportions into an annual diet, we took the weighted average of the seasonal proportions. Weighting was based on the temperature differences experienced from season to season. Assuming consumption rate is positively correlated with temperature, more consumption should occur during warm months, giving the diets during those months more weight than diets in cold months. We accomplished this by using taxonomy-specific consumption Q_{10} values, applied to seasonal temperature data (see previous subsection, Use of Q_{10} for Temperature-dependent Rate Estimation).

We used this method to characterize diets of surfperch, Pacific hake (*Merluccius productus*), walleye pollock (*Theragra chalcogramma*), demersal fish, piscivorous flatfish, small-mouthed flatfish, spiny dogfish, skates, and ratfish.

Q/B Estimation for Seabirds and Marine Mammals

Hunt et al. (2000) developed methods to estimate daily energy requirements for a vast range of seabirds and marine mammals that inhabit large marine ecosystems throughout the northern Pacific Ocean. The scope of their study included many of the species represented in our model's seabird and pinniped functional groups. We used their methods for our Q/B calculations, relying specifically on their parameter values for seabirds (except raptors) and marine mammals in the northern California Current.

For seabirds, Hunt et al. (2000) adopted an allometric equation developed by Birt-Friesen et al. (1989), which estimates daily energy requirements as a function of mean body mass. Body mass is an appropriate predictor because it is related to factors such as total metabolic activity (which is greater in large than in small birds) and the specific rate of metabolic heat loss (which is greater in small than large birds). The equation is equal to the function:

$$Y = 11.455 \times W^{0.727} \quad (10)$$

where Y is daily energy required (in kilojoules [kJ]) and W is body weight (in g). We used weights provided by Hunt et al. (2000) for representative species in our functional groups. Equation 10 predicts the energy needs for basic functions (growth, metabolism, activity, and reproduction). It does not account for assimilation efficiency and Hunt et al. (2000) assumed that seabirds assimilate approximately 75% of their ingested prey energy. Thus we must multiply Y by the reciprocal of 0.75 (i.e., 1.333) to calculate daily energy consumption. Dividing this value by the energy density of the aggregate diet yields the total mass consumed per day. We used energy density estimates provided by Hunt et al. (2000). They intended their estimates to represent daily energy requirements during the summer (June–September). We assumed no change in daily energy requirements in other months, and thus multiplied the daily mass consumed by 365 days and divided by body mass to generate Q/B for representative species.

The same basic method was used for marine mammals, this time drawing from allometric relationships for phocids and otariids (including California [*Zalophus californianus*] and Steller [*Eumetopias jubatus*] sea lions). These relationships were originally developed by Perez et al. (1990) and were summarized and applied by Hunt et al. (2000). The phocid equation, which was the basis for estimating Q/B in harbor seals (*Phocoena phocoena*), was equivalent to:

$$Y = 0.8411 \times W^{0.749} \quad (11)$$

while the otariid equation, which was the basis for estimating Q/B in sea lions, was equivalent to:

$$Y = 1.5266 \times W^{0.737} \quad (12)$$

In both cases, Y is daily energy required (in kJ) and W is body weight (in kg). As with seabirds, daily estimates of Y were adjusted for assimilation efficiency (again assuming 75% efficiency, Hunt et al. 2000), and were converted to daily prey intake by dividing by aggregate diet energy density. Multiplying by 365 days and dividing by body weight yielded annual Q/B .

Commercial Harvest Estimates

Unless otherwise noted, commercial harvest levels in PSCB were based on data collected by WDFW and reported by the Pacific Fisheries Information Network (PacFIN) for the years 1998–2007. PacFIN data consisted of number and weight of species caught by a particular gear type in a specific geographic region, according to commercial logbook data. Commercial harvest data included both tribal and nontribal sectors. For classifying harvest information, WDFW divides Puget Sound into individual management and catch reporting areas. Several WDFW areas are nested within the boundaries of the two Puget Sound Partnership (PSP) areas that make up PSCB, so all of the harvest in those areas is attributed to Central Puget Sound. In a few cases, the PSP boundaries split a WDFW area; in those cases, we assumed that the catch reported by PacFIN was distributed uniformly throughout the WDFW area. The proportion of the WDFW area in each PSP region was then used to allocate the catch. For example, WDFW Area 9 (Admiralty Inlet) spans four PSP regions, so the PacFIN catch is allocated using the proportion of the WDFW area in each region: Hood Canal (36.2%), Whidbey Island (41.7%), north Central Puget Sound (14.3%), and south Central Puget Sound (7.8%). For this area, then, 22.0% of the catch reported by PacFIN for WDFW Area 9 is attributed to the Central Puget Sound.

All PacFIN data were obtained in retrievals, dated 25 February 2008 and 18 March 2008, from the PacFIN Web site (http://pacfin.psmfc.org/pacfin_pub/data.php).

Catches for each year were summed by gear type, converted into units of mt km^{-2} , and allocated to the appropriate functional groups. We took the annual average for the period examined in order to fairly represent long-term fishing mortality.

Appendix D: Representing Life History

Ecopath with Ecosim (EwE) has many specialized methods for simulating biological and ecological relationships that fall outside the basic processes described by the master equations (Equation 1 and Equation 2). These include life history representation (age structure), controlling the strength of top-down and bottom-up predator-prey interactions, and mediation of trophic effects due to behavioral or habitat-related interactions. All are described in detail in the EwE support literature (Christensen et al. 2005) and a variety of EwE-related publications (e.g., Christensen and Walters 2004, Ainsworth et al. 2008a). We have run, or foresee the need to run, many simulations in which these special functions are used. The only specialized function that is extensively used in this document is the life history structuring; we briefly describe it here.

For some functional groups, incorporating life history is necessary because ontogenetic changes (e.g., in vital rates, diet, habitat use, or fishery value) lead to substantially different ecology for the life history stages. EwE handles life history in two ways: split-pool dynamics, where a taxonomic group has two dynamically linked groups, typically juveniles and adults; or multistanza dynamics, where a group has greater than two dynamically linked stages (Christensen et al. 2005). We opted to use only split-pool dynamics in this application, after attempts to use the multistanza method (which is recommended by Christensen et al. 2005) produced unsatisfactory results during mass balancing of Ecopath.

The equations used for the split-pool life history produce dynamics according to a Deriso-Schnute delay-difference model, which tracks the number of individuals in the juvenile and adult pools (Deriso 1980, Schnute 1987, Walters et al. 2000). Individuals in a cohort grow, age, and mature according to eight input parameters, plus the dynamic values of biomass, mortality rate, and consumption rate as determined in Ecosim. These terms determine the numbers of adults and juveniles according to five relevant equations, which are described by Christensen et al. (2005). Collectively, these terms enable the model to simulate changes in growth, mortality, and reproduction that derive from changes in feeding conditions (Walters et al. 2000).

The eight new input parameters mentioned above are:

- minimum relative time spent as a juvenile (default value = 1)
- maximum time spent as a juvenile (default = 1.0001)
- a recruitment power parameter (default = 1.0)
- age of transition from the juvenile to adult pool
- the weight ratio of an average adult to a newly matured adult
- the von Bertalanffy k parameter

- the base ratio of food intake used for reproduction (default = 0.8)
- the proportion of an increase in food intake that is used for growth (default = 0.3)

Typically, users only enter the von Bertalanffy k , the age at transition, and the weight ratio. The other values are generally left at their default values, unless circumstances dictate otherwise (Christensen et al. 2005).

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