Exxon Valdez Oil Spill
Restoration Project Final Report

Trophic Mass-Balance Model of Alaska's Prince William Sound Ecosystem, for the Post-Spill Period 1994-1996

Restoration Project 99330-1
Final Report

edited by
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Study History: This collaborative modeling study of Prince William Sound was initiated in 1998 under the category Ecosystem Synthesis, and the lead agency for administering the contract is the National Oceanic and Atmospheric Administration (NOAA). The FY98 funding request included research groups form two institutions: the Fisheries Centre of the University of British Columbia, and the Department of Ecology and Evolutionary Biology of the University of Tennessee. The NOAA contract included an additional year option period for which we submitted an additional full proposal for FY99 including both institutions and was accepted.

Abstract: The food web of Prince William Sound (PWS) was characterized with a mass-balanced model of trophic flows (Ecopath), constructed by a broad collaboration of experts using data from 1994-1996. This was the post-spill period with the best available data. This model of the PWS food web was then analyzed using the dynamic simulation routines Ecosim and Ecospace, now included in the Ecopath modeling software. The PWS model is a cohesive synthesis of the PWS biotic community, with a focus on its structure, and how it might respond to natural and anthropogenic perturbations. This volume includes written contributions from over thirty-five experts on the 48 biotic components of the PWS ecosystem defined by the collaborative group. Biotic components range from particular life stages of a species to species aggregations. In this way, all species in the ecosystem are included explicitly or implicitly. Groups are described in terms of biomass, production and consumption rates, diet compositions, migration rates, and fishery catches. These estimates were the main input parameters. Synthesis, refinement, and "new knowledge" was attained during the iterative balancing process, resulting in thermodynamically possible scenarios of biomass flows (=energy flows). Seasonal variability, spatial distributions, habitat associations, interannual trends, and basic biological information were also described, resulting in a useful compendium of the PWS ecosystem. The model can be used to simulate indirect trophic effects of a particular human activity, such as fishing or oil spills. Spatially explicit questions can also be addressed using the new Ecospace routine. Functional responses of ecosystem components to simulated disturbances can indicate the relative importance of interactions. This model will be useful for ecological research and ecosystem-based resource planning in Prince William Sound, including fisheries management and land use planning. With the accompanying CD ROM, the model is useful to students and local communities.

Key Words: Alutiiq dictionary, bird, benthic, collaborate, disturbance, Ecopath with Ecosim, Ecospace, *Exxon Valdez* Oil Spill, fish, food web, impact assessment, invertebrate, mammal, marine algae, mass-balance model, plankton, production, trophic interaction, simulation, synthesis

Project Data: All data used for this project can be found in this report, on the CD ROM, in the electronic file of the model (available from the Fisheries Centre), or from individual contributors.

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Trophic Mass-Balance Model of Alaska's Prince William Sound Ecosystem, for the Post-Spill Period 1994-1996

2nd Edition

Fisheries Centre, University of British Columbia, Canada

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2nd Edition

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Abstract

Information about the ecological components of Alaska's Prince William Sound (PWS) has increased considerably since the 1989 *Exxon Valdez* oil spill (EVOS), but the structure and functional characteristics of the overall food web are still not well understood. A better understanding of the whole PWS food web and its dynamics was achieved by constructing a balanced trophic model using the Ecopath approach. This was the best available framework to summarize available ecosystem information in a trophic context, as it explicitly accounts for multi-species interactions. The PWS model is a cohesive synthesis of the overall biotic community with a focus on energy flow structure, and response to perturbations--both natural and anthropogenic. Flows of biomass among the various components of the food web were quantified using estimates provided by a collaborative group of over 35 experts on PWS ecosystem components.

Forty-eight biotic components were included in the PWS model ranging from life stages of individual species to aggregated functional groups. These groups were organized into primary producers, zooplankton, benthic invertebrates, planktivorous 'forage fishes', larger fishes, birds, mammals, and detritus, for the purpose of model documentation. Estimates of biomass flows related to fisheries landings and discards in Prince William Sound are also incorporated.

Biomass, production rates, consumption rates, and diet compositions were specified as (empirically-based) inputs for each defined biotic component, as were migration rates, biomass accumulation rates, and fishery catches and discards. Outputs of the Ecopath model included biomass and flux estimates for individual groups that were refined through the collaborative mass-balancing approach, and useful characterizations of the whole food web. The outputs of Ecosim and Ecospace are also featured. These include simulations of population trajectories through time, and habitat-based re-distributions of organisms in space.

The dynamic modelling routines Ecosim and Ecospace can be used to simulate the ecosystem-level effects of disturbances and management actions, and to provide insights into ecosystem-level changes and dynamics that may occur in Prince William Sound. The Ecopath model of PWS can be used to help guide future research programs in the region, to help assess impacts of the EVOS, and to help resource agencies and local communities achieve ecosystem-based conservation and management in the face of increasing human activities in the region. This approach can also be used to help distinguish the relative importance of physical forces and tropic forces in marine ecosystems.

An annotated list of Alutiik words was included in this volume to facilitate cross-cultural flows of ecosystem knowledge. This list might serve as one step in helping to promote a more community-based approach to management of the wild living resources of Prince William Sound.

Director's Foreword

For many years single species stock assessment of fisheries has reigned supreme and separate from mainstream marine ecology, but, for marine conservation, this approach and lack of integration has been conspicuously unable to answer the crucial questions of our time. Such questions include the how human fisheries impact the interplay of predators, competitors and prey in natural systems, the impact, both acute and chronic, of marine pollution, and the effects of progressive shoreline development on the stability and value to human society of coastal ecosystems.

The first mass-balance models of marine ecosystems in the North-eastern Pacific, covering the Alaska Gyre, the shelf of southern British Columbia, and the Strait of Georgia, were constructed in November of 1996 at a workshop held at the UBC Fisheries Centre (*see* Fisheries Centre Research Report 1996, Vol. 4, No 1). That work was extended to a preliminary ecosystem model of Prince William Sound, Alaska, prior to the 1989 *Exxon Valdez* oil spill (*see* Fisheries Centre Report 5(2), Dalsgaard and Pauly 1997), in its most likely form between 1980-1985, based on data from published literature. Ecopath models are forgiving in that they can be improved and enhanced using new information without having to be completely reconstructed.

Ecopath is a straightforward trophic modelling approach to ecosystems, which balances the budget of biomass production and loss for each component in the system by solving a set of simultaneous linear equations. The Ecopath approach is the only ecosystem model to obey the laws of thermodynamics. It is based on pioneering work by Dr J. J. Polovina from Hawai'i in the early 1980s, and was developed by Dr Daniel Pauly when he was at ICLARM, Manila, and by Dr Villy Christensen from Denmark and now at the Fisheries Centre. Dr Carl Walters at the Fisheries Centre recently developed Ecosim and Ecospace, dynamic versions of Ecopath.

A Trophic Mass-Balance Model of Alaska's Prince William Sound Ecosystem, for the Post-Spill Period 1994-1996 was published in 1998 as Fisheries Centre Research Report Vol 6 No4. This report, describing the post-spill ecosystem, builds on this earlier work by harnessing the immense body of data and information gathered during the EVOS research program. The 2^{nd} *Edition* of this report improves on the previous work after feedback from the EVOS team. The model structure and parameter values have been refined after workshops and consultations. These include explicit new components for salmon carcasses, orcas, detritus, fishery sectors and discards; improved assimilation coefficients and parameters for sharks, herring, orcas and others. This work represent one of the most complex mass-balance models constructed to date, and moreover is supported by the largest synthesis of validated ecosystem data and research effort ever assembled. Simulations using ECOSIM simulations presented here, together with their uncertainties, are intended to receive serious consideration in the evaluation of policy options for Prince William Sound.

The report is the latest in a series of research reports published by the UBC Fisheries Centre. A list is shown on our web site at http:/fisheries.com. The series aims to focus on broad multidisciplinary problems in fisheries management, to provide a synoptic overview of the foundations and themes of current research, to report on work-in-progress, and to identify the next steps and ways that research may be improved. Edited reports of the workshops and research in progress are published in *Fisheries Centre Research Reports* and are distributed to all project or workshop participants. Further copies are available on request for a modest cost-recovery charge. Please contact the Fisheries Centre by mail, fax or email to 'office@fisheries.com'.

Tony J. Pitcher
Professor of Fisheries
Director, UBC Fisheries Centre

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Preface to the 2nd Edition

Scientists and other humans must make generalizations about nature because of its infinite complexity. It follows that any 'understanding' of an ecosystem, or a food web, is the result of a generalization, or a rule. Such rules assume there are properties of nature that can be characterized accurately, or at least to a useful degree. Continual support of, and participation in, science and exploration is necessary because the limitations of our understanding result in imperfect characterizations of nature, which are then used to make decisions about human-ecosystem interactions. The need for understanding ecosystems increases in parallel with our ability to modify them, but our *ability* to understand them invariably lags behind.

In keeping with this, *A balanced trophic model of Alaska's Prince William Sound ecosystem for the period 1994-1996* was constructed almost ten years after the *Exxon Valdez* oil spill (EVOS) catastrophe. The main aspect of this retrospective analysis is its potential for enabling ecosystem-based resource planning for the future through analyses that explicitly account for multispecies interactions, as pointed out by Pauly et al. (1998). Its purpose, which has been achieved, was to synthesize much of the information collected since EVOS into a cohesive picture of the food web in Prince William Sound (PWS). A broad collaboration of experts from the region met this goal during an iterative model construction process. In many respects, this collaborative approach gave the PWS model an aspect of self-organizing refinement that was wholly unexpected.

The initial expectations of this project were surpassed in several ways. First, virtually anyone can analyze the Prince William Sound model using the easy-to-use, windows-based software *Ecopath with Ecosim,* freely distributed on the world wide web (www.ecopath.org); Second, users can conduct both temporal and spatial dynamic simulations of fishing or other disturbances; Third, natural resource management agencies, local community groups, and regional school districts are incorporating this model into their programs; and finally, models of four other aquatic ecosystems of Alaska are included along with the PWS model on a CD ROM containing useful resources relating to Alaska's aquatic ecosystems, including a database of Alaska's fishes, a dictionary of Alutiiq terms, videos and pictures of animals and plants, and links to additional information.

The popularity of the PWS model and the positive feedback we received throughout this project almost completely drowned out the few criticisms. However, it was consideration of these criticisms that led us most directly to refinement of the PWS model. Subsequent improvements are reflected in this 2nd edition.

Although the collaborators' independently-derived contributions resulted in an initial model with relatively good internal consistency, it was inevitable that the input parameters would be subject to further refinement. Refinements reflected in this 2nd edition include PWS-specific estimations of the mass of nearshore and offshore detritus pools; explicit treatment of fishery discards and salmon carcasses using the detritus category "nekton falls"; adjustment of assimilation efficiencies for benthic and planktonic organisms; explicit treatment of subsistence, recreational, and commercial fishery sectors; adjustment of herring catch information, adjustment of shark consumption rates; splitting orcas into resident and transient groups, adding sea otters to the transient orca diet, discussions of detritus pools, the dynamic nature of nearshore benthos, and the stabilizing effects of complex behaviors. These refinements are discussed in the sections corresponding to the groups referred to above.

The Ecopath model of Prince William Sound is considered 'final,' only for the purposes of defining a common stopping point that can be utilized by interested parties in a format documented by this 2nd edition. However, we expect that future application of this model will result in continued refinement of its parameters and structure, and our general understanding of this dynamic ecosystem.

- The editors

INTRODUCTION

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The 1989 *Exxon Valdez* Oil Spill (EVOS) in Prince William Sound (PWS) Alaska was perceived by the media and the global public as an ecological catastrophe in light of the quantity of oil spilled (~36,000 tonnes) and the extent of its spread throughout a relatively pristine area of Alaskan coastal wilderness. In scientific terms, the scale of the disturbance was indeed catastrophic, and the impacts on biota were severe, but the full extent of the impacts remain uncertain (see Spies et al. 1996). Beyond its ecological impacts, the EVOS adversely affected native communities, other local communities, fishing people, and the wider Alaskan and American public.

Determining the ecological impacts of this spill was considered necessary by resource trustee agencies and the public in order to guide cleanup and determine natural resource damages. From a scientific perspective, the EVOS was an excellent, though unfortunate, opportunity to study the ecological impacts of a large oil spill in a high-latitude marine environment. In particular, it was an opportunity to elucidate marine ecological processes related to the effects of large perturbations, thereby providing insight into the structure and resilience of marine ecosystems (*see* Paine et al. 1996). Ideally, science programs for determining ecological impacts would quantify the ecological state before and after a perturbation at exposed and un-exposed areas (or provide experimental perturbations at realistic scales). A number of studies incorporated such spatial comparisons, but research on the effects of the oil spill rarely had optimal (ideal) designs because pre-spill ecological information was scarce (*see* Hilborn 1996).

Despite these constraints, a great deal of information has been collected about PWS, its ecological processes and inter-relationships, and the effects of the EVOS (Spies et al. 1996). Research programs of various scopes have collected information about particular components and segments of the PWS ecosystem revealing some mechanisms of exposure, effects, and ecological processes. Some segments of the ecosystem have been characterized at a detailed resolution, while other components and processes are more elusive, or are simply less studied. Although our knowledge of the Prince William Sound system has deepened considerably, and our knowledge of the interrelationships among ecosystem components has increased (see McRoy and Echeverria, 1990, Cooney 1997, Duffy 1997, Holland-Bartels et al. 1997), our understanding of whole-ecosystem processes can be enhanced through synthesis of existing ecosystem information. Such a synthesis was undertaken during the present project through the construction of a whole ecosystem model by a broad collaboration of experts (Appendix A).

The purpose of the Ecopath modelling approach is to provide a cohesive picture of the PWS ecosystem by constructing a mass-balanced model of food-web interactions and trophic flows using information collected since the EVOS. This refined model was initially built upon the basic PWS trophic structure identified in a preliminary model of PWS (Dalsgaard and Pauly 1997). The Ecopath model includes all biotic components of the ecosystem, implicitly or explicitly, and provides a quantitative description of food-web interactions and relationships, as well as energy flows among components. This model not only functions as a tool for learning more about individual components, but it can help facilitate our understanding of how the system as a whole might respond to perturbations. To fully achieve these types of analysis and learning, Ecopath files can be used in the Ecosim and Ecospace simulations, which are temporally and spatially dynamic modelling routines that can be used to simulate indirect and whole-ecosystem effects of disturbances or management actions in both time and space (discussed later).

Prince William Sound

The Physical Setting

Prince William Sound (PWS) is a nearly enclosed embayment at the northern apex of the gulf of Alaska. At over 9,000 km^2, it covers 15 times the area of San Francisco Bay and twice the area of Chesapeake Bay (Figure 1; Wheelwright 1994). PWS is a submerged section of the surrounding Chugach Mountains, the highest coastal range in the world, which towers up to 4 km over the waters of the sound. The depths of PWS are highly variable, to a maximum approaching 800 m, with a mean depth of 300 m (Cooney 1993, Loughlin 1994). The coastline is highly structured (Figure 1). Much of this convoluted shoreline plunges steeply to considerable depths just beyond a narrow beach shelf, or even more precipitously as vertical walls in the fjords of the western and northern sound.

PWS is located at the Northeastern corner of the Aleutian trench where the Pacific plate subducts under a bend in the North American plate making it one of the most seismically active regions in the world (Jacob 1986, Brown et al. 1989; p. 25). Ice sheets retreated from PWS 12,000 to 15,000 years ago, but the region is still shaped by its 150 glaciers. Some have begun rapid retreats, though a few advancing glaciers reflect local increases in precipitation. Some 20 of the 150 glaciers calve directly into PWS waters (Michelson 1989). The perimeter of PWS is dominated by glacially carved fjords, some with prominent lateral gradients of glacial sedimentation in the water column.

Much of the waters of PWS are characteristically estuarine. Warm moist air arriving from the south becomes trapped, uplifted, and cooled by the surrounding Chugach Mountains, releasing considerable precipitation over the region. Annual precipitation ranges from 160 to 440 cm in the coastal towns of PWS, though snowfall alone can reach 2290 cm in parts of the nearby Chugach Mountains (Michelson 1989). Rain runoff and snowmelt enter from myriad streams, but icebergs and glacial melt also contribute fresh water. Even greater amounts of fresh water enter PWS as a stratified lens aloft an incurrent of marine water at the Hinchenbrook entrance. This substantial freshwater input comes from the alongshore freshwater system associated with the northwest-trending Alaska coastal current, fed by numerous rivers and glaciers from as far south as British Columbia (Wheelwright 1994). PWS thus contains complex gradients among its fresh water, estuarine, and marine settings.

Prince William Sound, as defined in Figure 2 by the PWS Ecopath working group (Appendix 1), includes a variety of deep and shallow habitats from extensive intertidal mudflats to pinnacle islands, deep basins, fjords, and holes. The annually averaged depth of the euphotic zone is approximately 25 m (D. Eslinger, UAF Institute of Marine Sciences, pers. comm.).

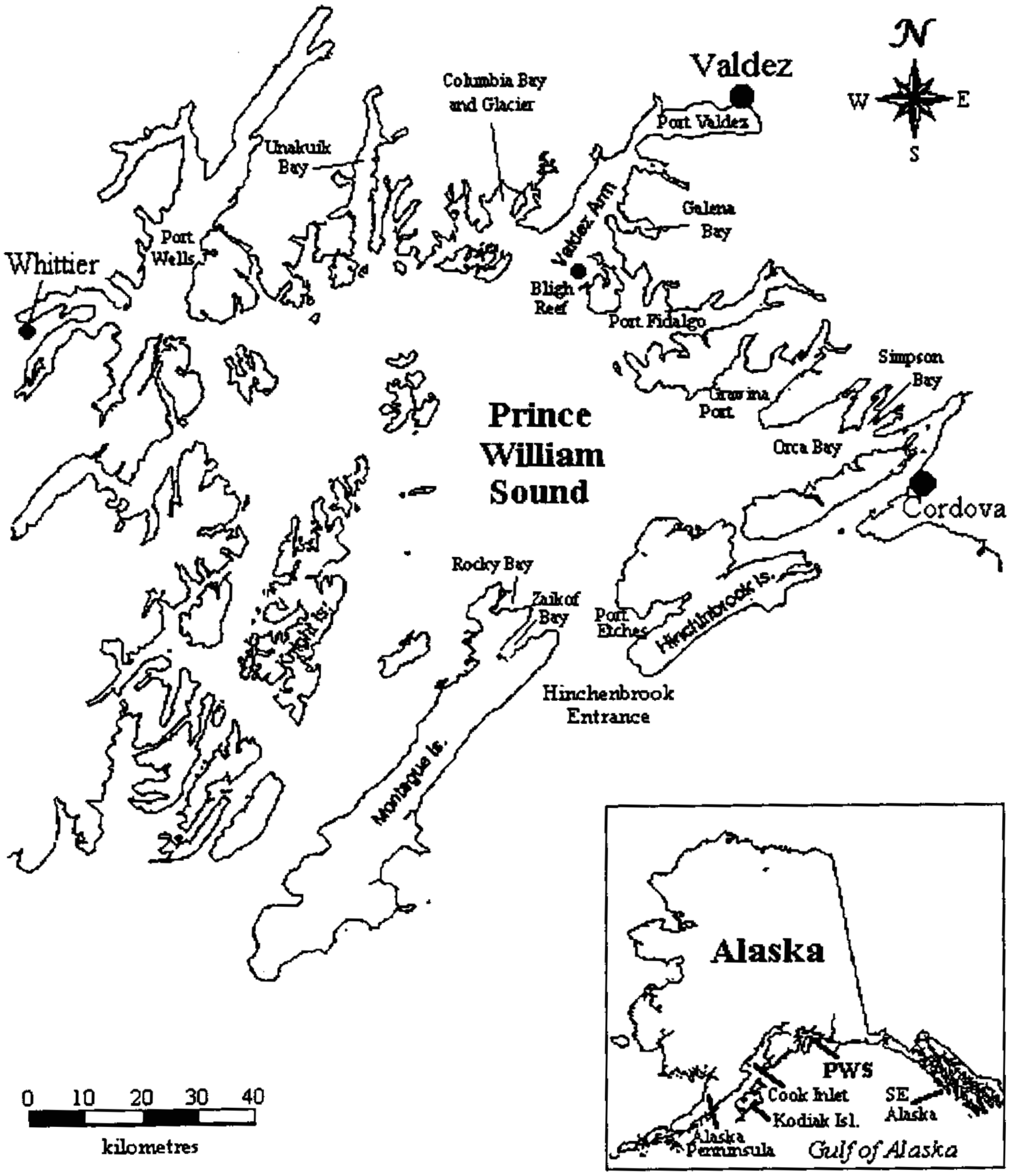

Figure 1. Map of Prince William Sound (PWS), Alaska, (modified from Braddock et al. 1996).

The physical flux of Prince William Sound carries over into the biological regime. The profusion of its wildlife--the aggregations of seabirds, sea otters, salmon, herring, killer whales, periwinkles, jellyfish, eagles--tends to obscure the variability of the numbers within the species.

Jeff Wheelwright, Degrees of Disaster, 1994

Biological Inhabitants

Prince William Sound, like other marine ecosystems, is characterized by a wide variety of plants and animals distributed unevenly in space and whose populations fluctuate in response to physical and oceanographic changes, occurring over a range of scales. Some organisms are adapted to undergo considerable fluctuations over time, like krill whose populations can vary by a factor of 50, while other organisms have developed more stable life histories through mechanisms such as prey switching, food storage, and mobility. The input of solar and imported energy into the system is mediated by independently varying physical cycles and disturbances, but the flow of that energy through the biotic components of the system is stabilized not only by the species-level mechanisms mentioned above, but also by community-level mechanisms such as opportunistic and competitive compensations within the ecosystem's food web. In this way, variability and shifts in populations can effectively 'even out' the energy flow through the system in the face of environmental disturbances and physical fluctuations.

Thus, ecosystems contain both highly variable and less variable components as well as a tendency for dampening of energy throughflow, through individual, population, and community level compensations. Notwithstanding such biotic 'stabilizing' mechanisms, or the importance of physical changes and disturbances, constraints in energy flow (feeding) exist throughout the system such that organisms in the food web must eat enough of the appropriate foods to sustain themselves, and the population levels of prey are somewhat controlled by their predators. Alternatively, these feeding constraints are lifted by the extent of feeding plasticity—the organism's proclivity for prey switching.

The static Ecopath modelling approach enables a description of the possible scenarios of relationships, flows, and interactions based on the known conditions in an ecosystem during a particular time period. The dynamic Ecosim approach, which then follows, enables simulation of particular disturbances or agents of physical forcing on the system or on particular biotic components within the context of an interactive ecosystem, based on the known interactions and energy flow constraints. Moreover, Ecosim can be re-expressed in a spatial context, leading to a spatially-explicit routine called Ecospace.

The overarching question of the EVOS Research program is also the most persistent question of the general public: "What are the short-term and long-term effects of the *Exxon Valdez* Oil Spill?" The state or trajectory of a biological community is controlled by cyclic and other changes in the physical world as well as trophic interactions and constraints. Based on this notion, the ecological effects of EVOS can be understood best if examined within the contexts of known physical stressors, both natural and anthropogenic, and whole inter-connected communities. But because temporal and spatial controls (comparisons) were virtually unavailable after the spill, new analytical tools are needed to describe the interrelationships, constraints, and trajectories of the PWS biotic community. An empirically based, mathematical matrix describing these interactions—the PWS Ecopath model—can be used to reveal indirect and whole ecosystem effects, to the extent that input estimates are accurate. Furthermore, the relative influence of various physical and biotic factors contributing to the state of the ecosystem can be isolated within the analysis, to the extent that effects of the various factors are understood. Factors known to influence the marine flows in the deeper subtidal (McRoy 1988), whereas the high pressure spray cleanup after EVOS re-distributed beach sediment downslope to the shallow subtidal (J.L. Ruesink, University of Washington, Zoology, pers. comm.). Long-term studies of recovery were not conducted after the earthquake (Wheelwright 1994), but quake-related ecological changes might have been ongoing when the EVOS occurred 25 years later.

Sea otters - Sea otters began expanding back into their historic range sometime after the signing of the International Fur Seal Treaty of 1911. Sea otters are known to have considerable influence on the structure of both hard and soft-bottom nearshore marine communities in Alaska (Estes et al. 1974, Estes and Duggins 1995, Kvitek and Oliver 1992, Kvitek et al. 1992), and they may have been still expanding and increasing in PWS when the EVOS occurred (*also see* McRoy 1988). Because of the broad ecological influence of this species, the studies of EVOS impacts should be interpreted in light of the changes and status of sea otter populations.

Atmospheric and Oceanographic Cycles - Atmospheric and oceanographic cycles occurring on various time scales can force, or influence, components of ecosystems in the Gulf of Alaska, and PWS. These include ENSO events (3-7 year period), 'regime shifts' in atmospheric pressure patterns and storm tracks (10~ year period), the effect of lunar declination on ocean temperatures (18.6 year period), and atmospheric changes caused by sunspots (11 years) (NRC 1996). It is possible that some ecological signals associated with these forcing mechanisms are separate from ecological changes that occurred coincident with the EVOS, but the interactions of these various forcing mechanisms could result in non-cyclic, or chaotic, physical and ecosystem trajectories (Parker et al. 1995). One notable event that had the potential of confounding ecological signals of an oil spill was unusually cold weather in the winter of 1989 (Wheelwright 1994). Such an event has the potential to cause unusual stress to intertidal communities. Although changes in the PWS ecosystem are undoubtedly influenced by these and other natural cycles and mechanisms these changes are not easily predictable given our current level of knowledge about PWS and the surrounding GoA. Elucidating the effects of a strong event such as EVOS, much less predicting the effects of such a disturbance, is challenging. Nevertheless, trophic constraints exist even in such dynamic ecosystems, and examining these constraints using tools such as Ecopath may lead to a better understanding of indirect, or ecosystem-level, responses.

Defining the PWS Ecosystem

The first necessary step to constructing an Ecopath model is to define the ecosystem to be modeled. Although no ecosystem on earth is self-contained or truly separate from other ecosystems, it is useful to define distinct ecosystems. Some ecosystems are naturally well defined or distinct based on characteristics such as geography, climate, oceanography, or biotic distributions (*see Defining the Ecosystem in* NRC 1996). The Prince William Sound ecosystem is relatively easy to define, as it is somewhat separated from the Gulf of Alaska by Hinchenbrook Island, Montague Island, and other islands and peninsulas (Figure 1 and Figure 2).

Some PWS organisms spend their entire life cycles inside the Sound; others reside there for only part of their life cycles, migrating in and out of adjacent rivers, the Gulf of Alaska, or to and from distant latitudes. Still, the PWS Ecopath working group agreed on the boundaries of the PWS ecosystem presented in Figure 2, though some inevitable limitations of these boundaries were noted by some participants (e.g. some small pelagic fishes spawn on both sides of Montague Island, and the outside of Hinchenbrook Entrance is particularly unique and productive; E. Brown, UAF Institute of Marine Sciences, pers. comm.).

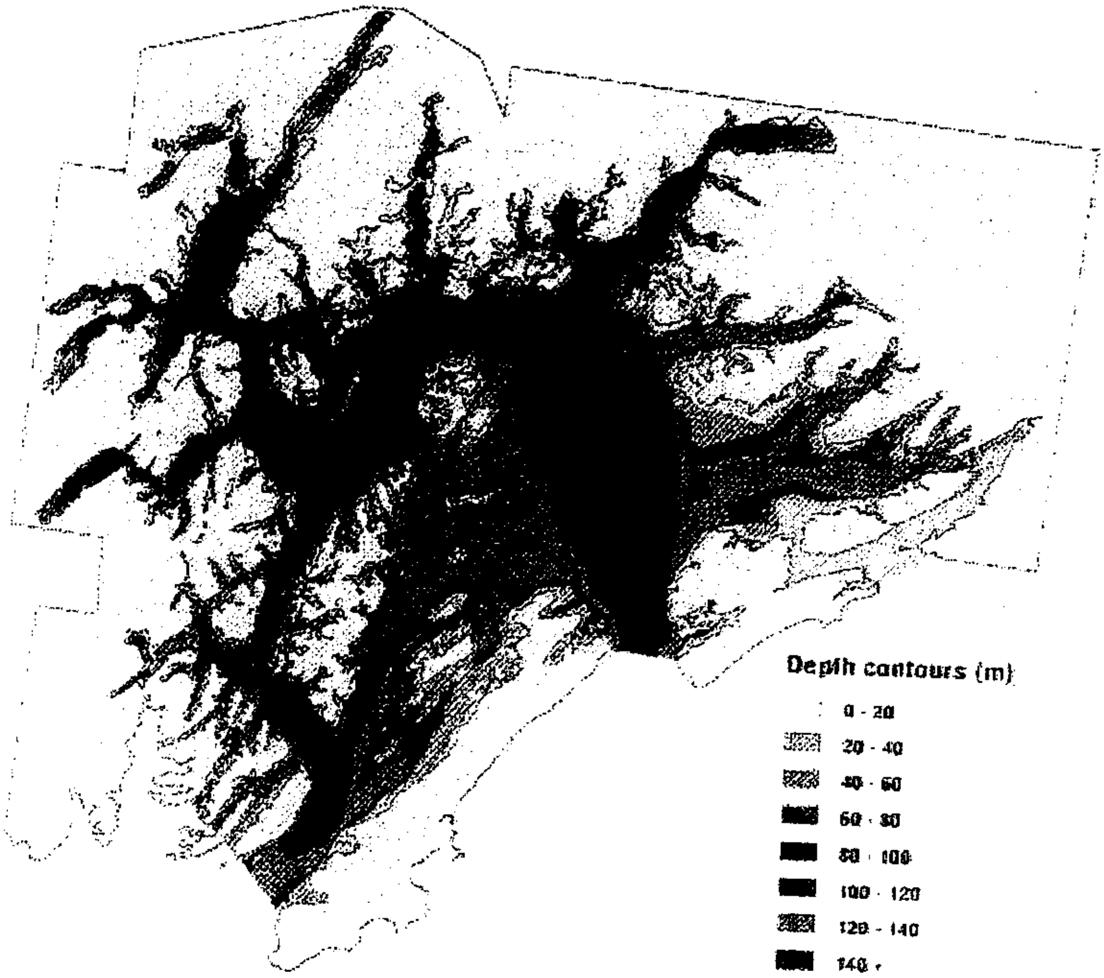

Figure 2. Depth contours and defined boundaries of PWS ecosystem (GIS analysis and mapping provided by G. Esslinger, Alaska Biological Science Center, USGS). Prince William Sound ecosystem boundaries are delineated by the edge of the colored areas and were defined and agreed on by the PWS Ecopath working group.

Aspects of the Ecopath approach and software relevant to the PWS model

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The Ecopath model was originally described J. Polovina (1984, 1995) of the U.S. National Marine Fisheries Service (Honolulu Laboratory). V. Christensen and D. Pauly, previously both at the International Center for Living Aquatic Resources Management (ICLARM), carried further the work (see Christensen and Pauly 1992a), and made it widely available in the form of a well-documented software for computers running MS-DOS (Christensen and Pauly 1992b), and later Windows (Christensen and Pauly 1995, 1996). Both versions allow rapid construction and verification of mass-balance models of ecosystems, as is clear from its present (1999) distribution to 1600 registered users in more than 90 countries.

The data requirements of an Ecopath model are expressed by its two 'Master Equations'. These equations are based on an assumption of mass-balance, and formulate that for any given group its production can be described as:

$$\text{Production} = \text{Catches} + \text{Predation} + \text{Biomass accumulation} + \text{Net migration} + \text{Other mortality}, \qquad \ldots 1$$

and further that

$$\text{Consumption} = \text{Production} + \text{Unassimilated food} + \text{Respiration}. \qquad \ldots 2$$

The first Master Equation is crucial in linking predator and prey in a system. Re-expressed and -arranged the equation reads,

$$\cdot (P/B)_i \cdot EE_i = Y_i + \Sigma B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i \qquad \ldots 3$$

where B_i and B_j are biomasses (the latter pertaining to all consumers of *i*);

P/B_i is the production/biomass ratio, equivalent to total mortality (Z) under most circumstances (Allen 1971);

EE_i is the ecotrophic efficiency, or the fraction of production ($P= B*(P/B)$) that is utilized within the system (including net migration and biomass accumulation);

Y_i is equal the fisheries catch per unit area and time (i.e., $Y = F*B$);

Q/B_j the food consumption per unit biomass of j; and

DC_{ji} the contribution of i to the diet of j (see also Box 1);

BA_i is the biomass accumulation of I (positive or negative, flow rate with units of energy per unit area and time);

NM_i is the net migration of I (emigration less immigration) with unit of energy per unit area and time.

An important aspect facilitating construction of an Ecopath model is that P/B under most circumstances corresponds to total instantaneous mortality rate (Z) in most circumstances (Allen 1971). There are several ways to estimate production (and P/B) directly, however, the combination of cohort-specific abundance and growth data required for many of these methods is usually difficult to assemble. Thus, Allen's formal demonstration of the relationship between P/B with Z is extremely useful, as numerous methods exist, in fisheries science for the estimation of Z from catch-at-age (Ricker 1975), length-frequency (Pauly and Gayanilo 1997), or other data (Pauly 1984).

An attribute of the Ecopath approach is that all of the parameters of its first master equation are amenable to direct estimation, except the ecotrophic efficiency, which is thus often left as the unknown to be estimated when the master equation is solved.

The steps involved in construction of an Ecopath model consist essentially of:

(*i*) Identification of the area and period for which a model is to be constructed;

(ii) Definition of the functional groups (i.e., 'boxes') to be included;

(iii) Entry of a diet matrix, expressing the fraction that each 'box' in the model represents in the diet of its consumers;

(iv) Entry of food consumption rate, of production/biomass ratio or of biomass, and of fisheries catches, if any, for each box;

(v) Balance the model, or modify entries (iii and iv) until input = output for each box;

(vi) Analyze model outputs (e.g., system characteristics, estimated trophic levels) including simulations of functional responses to disturbances and other changes;

Box 1. Basic equations, assumptions and parameters of the Ecopath approach

The mass-balance modelling approach documented in this report combines an approach by Polovina and Ow (1983) and Polovina (1984, 1985) for estimation of biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem (the original 'Ecopath') with an approach proposed by Ulanowicz (1986) for analysis of flows between the elements of ecosystems. The result of this synthesis was initially implemented as a DOS software called 'Ecopath II', documented in Christensen and Pauly (1992a, 1992b), and more recently in form of a Windows software, 'Ecopath 3.1' (Christensen and Pauly 1995, 1996) and Ecopath with Ecosim (Pauly 1998, Walters et al., in press). Unless noted otherwise the word 'Ecopath' refers to the latter, Windows version. The ecosystem is modeled using a set of simultaneous linear equations (one for each group i in the system), i.e.

Production by (i) - all predation on (i) - nonpredation losses of (i) - export of (i) = 0, for all (i).
This can also be put as

$P_i - M2_i - P_i(1-EE_i) - EX_i = 0$ ...1)

where P_i is the production of (i), $M2_i$ is the total predation mortality of (i), EE_i is the ecotrophic efficiency of (i) or the proportion of the production that is either exported or predated upon, $(1-EE_i)$ is the "other mortality", and EX_i is the export of (i).
Equation (1) can be re-expressed as

$B_i*P/B_i - \Sigma_j B_j*Q/B_j*DC_{ij} - P/B_i*B_i(1-EE_i) - EX_i = 0$ ...1)
or
$B_i*P/B_i*EE_i - \Sigma_j B_j*Q/B_j*DC_{ij} - EX_i = 0$ ...2)

where B_i is the biomass of (i), P/B_i is the production/biomass ratio, Q/B_i is the consumption/biomass ratio and DC_{ij} is the fraction of prey (i) in the average diet of predator (j).
Based on (2), for a system with n groups, n linear equations can be given in explicit terms:

$B_1P/B_1EE_1 - B_1Q/B_1DC_{11} - B_2Q/B_2DC_{21} - \ldots - B_nQ/B_nDC_{n1} - EX_1 = 0$

$B_2P/B_2EE_2 - B_1Q/B_1DC_{12} - B_2Q/B_2DC_{22} - \ldots - B_nQ/B_nDC_{n2} - EX_2 = 0$

$B_nP/B_nEE_n - B_1Q/B_1DC_{1n} - B_2Q/B_2DC_{2n} - \ldots - B_nQ/B_nDC_{nn} - EX_n = 0$

This system of simultaneous linear equations can be solved through matrix inversion. In Ecopath, this is done using the generalized inverse method described by MacKay (1981), which has features making it generally more versatile than standard inverse methods.

Thus, if the set of equations is over-determined (more equations than unknowns) and the equations are not consistent with each other, the generalized inverse method provides least squares estimates which minimize the discrepancies. If, on the other hand, the system is undetermined (more unknowns than equations), an answer that is consistent with the data (although not unique) will still be output.

Generally only one of the parameters B_i, P/B_i, Q/B_i, or EE_i may be unknown for any group i. In special cases, however, Q/B_i may be unknown in addition to one of the other parameters (Christensen and Pauly 1992b). Exports (e.g., fisheries catches) and diet compositions are always required for all groups.

A box (or "state variable") in an Ecopath model may be a group of (ecologically) related species, i.e., a functional group, a single species, or a single size/age group of a given species. A term for biomass accumulation (Bacc) may be added to equation (1) in cases where biomass is known to have changed over the period considered in the model.

These steps can be easily implemented if basic parameters can be estimated (see also Box 1), especially as numerous well-documented examples exist of Ecopath applications to aquatic ecosystems (see Pauly and Christensen 1993, and contributions in Christensen and Pauly 1993, and Pauly and Christensen 1996). We sometimes refer here to three ecosystems that have much in common with PWS (the Strait of Georgia, the coast of British Columbia, and the Alaska gyre), documented through the contributions in Pauly and Christensen (1996). In the present report, details are provided, by functional group, on how items (ii) to (vi) were implemented, for the period (1994-1996) in a defined PWS (Figure 2).

Construction of an Ecopath model is followed by model balancing. The first law of thermodynamics states that energy is neither created nor destroyed, but changed from one form to another. The total energy in a closed system remains constant, though the form of that energy changes. The PWS Ecopath model is not based on the assumption of a closed system; rather, the working assumption is that the energy flowing into PWS's biotic system (primary production, and imported secondary production) is equal to the energy used within the defined system and flowing out of it.

For the purposes of the model, the assumption of mass-balance (conservation of energy) is also made for every identified component of the ecosystem. However, the Ecopath formulation includes a biomass accumulation factor so that trends in populations, or ecosystem components, can be represented, and hence the model is not necessarily a steady-state model. The assumption of mass-balance is extremely useful for parameterization of ecosystem models, we always have imperfect knowledge, and mass-balance offers a powerful constraint to the parameterization process. An iterative model balancing approach can serve to increase knowledge about ecosystem components as well as the whole ecosystem, especially if conducted within a collaborative synthesis of information (see the following section on collaboration). This is so because energy flows in and out of each component must be reconciled among connected components. The balancing methodology employed for the PWS model is described in the section on 'Constructing and Balancing the Model' following the 'Model Inputs' section below.

Contributed diet compositions and the overall food web produced by the model were compared to the food web elements previously published for PWS by McRoy and Wyllie Echeverria (1990). This procedure for verification was conducted for every component of the model, and comments regarding similarity are included at the end of this report.

The current project also features examples of the uses of Ecosim and Ecospace to simulate spatial and temporal responses of biotic components to various perturbations and scenarios. This is followed by a discussion of the application of the PWS model for future resource planning, and how it may shed light on the effects of EVOS.

Surface areas of PWS depth zones and habitats

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Estimating biomasses on a Sound wide basis requires estimating the areal extent over which organisms are distributed. For example, sampling in the nearshore is often stratified by depth, habitat type, or both. As a result, raising local estimates to the sound as a whole requires estimation of the relative proportions of each depth or habitat type within the ecosystem. Estimates of area covered by different depth strata are given in Table 1. Estimates of areas covered by different subtidal habitats are given in Table 2, and areas covered by different intertidal shoreline types are given in Table 3.

Table 1. Surface areas of depth strata in Prince William Sound, Alaska.

Depth stratum (m)	**Area (km²)**	**% of area**
Intertidal +3 to 0	300[a]	3.31
0 to 10	709[b]	7.83
10 to 20	709[b]	7.83
20 to 100	2,018[b]	22.28
> 100	5,323[b]	58.76
Totals	9,059[b]	100.00

a. Estimated based on an average 20 m per 1 m of vertical in the intertidal zone, based on data of the Alaska Department of Natural Resources (1991) and unpublished measurements (T. A. Dean and S. Jewett).

b. Based on GIS analysis of NOAA bathymetric data by G. Esslinger, and unpublished by T. A. Dean and S. Jewett

Table 2. Estimates of the percentage of subtidal habitats within each depth in Prince William Sound, Alaska. Estimates for < 20 m are based in part on unpublished side-scan sonar records of substrate type.

Habitat type	**Depth range (m)**			
	2-10	**11–20**	**20 -100**	**>100**
Hard Substrate	85	66	30	10
Bays	42	33	-	-
Points	42	33	-	-
Nereocystis	1	0	-	-
Soft Substrate	15	33	70	90
Eelgrass	15	0	-	-
No vegetation	0	33	-	-

Table 3. Relative importance of habitat type estimated from % of total shoreline (from Sundberg et al. 1996). These estimates do not account for possible differences in beach widths between habitats.

Shoreline type	**% in PWS**	**Habitat type**	**Habitat %**
Exposed rocky	13	exposed rocky	-
Exposed wave-cut platforms	11	exposed rocky	23
Find sand beaches	1	fine textured beaches	-
Coarse sand beaches	0	fine textured beaches	1
Mixed sand/gravel beaches	21	coarse textured beaches	-
Gravel/cobble/boulder	20	coarse textured beaches	-
Exposed tidal flats	0	coarse textured beaches	41
Sheltered rocky	30	sheltered rocky	30
Sheltered tidal flats	3	estuarine	-
Marshes	2	estuarine	5
Total	100	All	100

MODEL INPUTS

The ecosystem components in the 1994-1996 PWS model are organized into groupings defined by both trophic and taxonomic considerations. Within these groupings, components are presented in order of descending trophic level, as estimated by the Ecopath model.

PRIMARY PRODUCERS

Benthic algae and eelgrass

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In Prince William Sound, the nearshore zone, from the upper intertidal (approximately +3 m above mean lower low water) to depths of approximately 20 m, is vegetated by seaweeds and eelgrass. *Fucus gardneri* dominates in the intertidal zone while a variety of kelps (*Agarum cribrosum*, *Laminaria* spp., and *Nereocystis luetkeana*) and eelgrass (*Zostera marina*) are dominant in the subtidal zone.

Intertidal algal biomass in western Prince William Sound was estimated by Highsmith et al. (1994) in 1990 and 1991 following the EVOS using a stratified random sampling design. Sampling was conducted at 3 depth strata within 5 habitat types at both oiled and unoiled sites. Estimates of density and biomass of subtidal algae and eelgrass were made by Dean et al. (1996a, 1998) using a similar stratified random sampling design. We use values from control lo-

Table 4. Estimates of biomass (t·ww·km^{-2}) of intertidal algae in different depth strata and habitat types of PWS (from Highsmith et al. 1994). Depth strata are as follows: MVD1 = high, intertidal, + 2.0 to + 3.0 m, MVD2 = mid intertidal, + 1.0 to + 2.0 m, and MVD3 = low intertidal, 0 to + 1 m (from Highsmith et al. 1994). Habitats are as defined in Table 4. Weighted mean intertidal algal biomass (t ww km-2) (from Highsmith et al. (1994).

Habitat type	Depth stratum	Biomass (t·ww·km^{-2}) May-90	Biomass (t·ww·km^{2}) May-91	Mean
Sheltered rocky	high	918	1,184	
	mid	1,899	1,705	
	low	2,340	1,266	
	Average	1,719	1,385	1,552
Coarse textured	high	80	136	
	mid	665	490	
	low	640	820	
	Average	462	482	472
Estuarine	high	364	438	
	mid	471	1,634	
	low	157	657	
	Average	331	910	620
Exposed rocky	high	822	1,026	
	mid	1,672	1,692	
	low	1,351	3,024	

cations to estimate pre-spill conditions and assume that they are representative of the entire Prince William Sound for the decade from 1980 to 1989, prior to the oil spill.

The dominant alga in the intertidal was *Fucus gardneri,* comprising over 90% of the biomass. The Spring (May) biomass of algae was highest on rocky shores (sheltered rocky and exposed rocky habitats) and was generally higher in the mid and lower tide zones (Table 4). The weighted mean (based on proportional coverage by each habitat type) biomass density was estimated at about 1,058 t ww km^{-2} (**Table 5**). Expressed on a Sound wide basis, this is equivalent to 35 t km^{-2}.

Table 5. Weighted mean intertidal algal biomass (t ww km^{-2}) (from Highsmith et al. (1994).

Habitat type	*Biomass* density (t·km^{2})	% of area	Overall biomass in PWS
Sheltered rocky	1,552	30	465.6
Coarse textured	472	41	193.5
Estuarine	620	5	31.0
Exposed Rocky	1,598	23	367.5
Fine Textured	0	1	0
All	4.242	100	1.057.7

Agarum cribrosum and *Laminaria saccharina* were the dominant subtidal macroalgae in sheltered bays (Dean et al. 1996a). Generally, these two species constituted more than 90% of total macroalgal biomass. *Agarum cribrosum* also dominated on exposed points (more than 60% in terms of number of individuals). Less abundant algae were *Laminaria saccharina* and *L. bongardiana* (= *groenlandica*). *Nereocystis* habitats are located on exposed sites, and the algal diversity was higher than in the other two habitats. The kelp forest structure at these locations consists of a canopy of *Nereocystis luetkeana* with an understory of *L. bongardiana* (61% of the biomass), *L. yezoensis*, *Pleurophycus gardneri*, and *A. cribrosum*. Eelgrass dominated in shallow waters (less than 5 m) in bays, generally at stream mouths.

Biomass estimates from different habitats are given in **Table 6**. The biomass estimate, weighted by proportion of each habitat in

Table 6. Subtidal macroalgal and eelgrass biomass (t·ww·km^{-2}) estimates for different Prince William Sound, Alaska habitats (from Dean et al. 1996a and 1998).

Habitat	Biomass density (t·km^{-2}) (2-10 m)	Biomass density (t·km^{-2}) (11-20 m)
Bays	1,766	529
Points	2,690	678
Nereocystis	6,240	0
Eelgrass	1,232	0
No Vegetation	0	0

Table 7. Estimates of average biomass (t ww km^{-2}) for subtidal algae and eelgrass in Prince William Sound, Alaska (from Dean et al. 1996a and 1998).

Habitat	*Biomass* density (t·km^{-2})	% by area	Biomass (t)
Bays Shallow	1800	21.0	378
Bays Deep	530	16.5	87
Points Shallow	690	21.0	145
Points Deep	680	16.5	112
Nereocystis Shallow	6200	0.5	31
Nereocystis Deep	-	-	-
Eelgrass Shallow	1200	7.5	90
Eelgrass Deep	-	-	-
No Veg Shallow	-	-	-
No Veg Deep	-	33.0	-
Total	-	-	843

Prince William Sound, is 844 tonnes t·ww·km^{-2} (**Table 7**). Expressed on a Sound wide basis, this is equivalent to 132 t·km^{-2}. The total biomass estimate for benthic algae and eelgrass, for both intertidal and subtidal habitats, is 167 t·km^{-2}.

The biomass estimates are based on observations made in summer (May through September). However, we know that in winter months, biomasses of both algae and eelgrass are reduced. Based on some very preliminary estimates given by Rosenthal et al. (1977), we estimate that the winter biomass is about 50% of the summer standing stock. The average of the winter and summer biomass estimates would be 125.25 t·km^{-2}, which can be used as an annual average biomass of macroalgae and eelgrass.

The P/B ratio for algae and eelgrass is about 4 year^{-1}, based on estimates of algal and eelgrass P/B ratios given in Luning (1990).

It is assumed that about 1% of algal and eelgrass production is consumed by herbivores, about 15% is exported as dissolved organics, and about 84% goes to detritus. These are similar to values given by Luning (1990) except that the percentage grazed is about 10% of that suggested by Luning. There are few grazers in Prince William Sound (especially urchins) compared with other kelp communities. Most of the grazing is by small epifaunal invertebrates (especially amphipos, gastropods, and crabs), and large epifaunal invertebrates (mostly crabs and sea urchins).

Some kelp is harvested as part of the herring roe on kelp fishery. This is localized in herring spawn areas and thought to be a very small portion of the yearly production of kelp. No kelp landnings or discards were specified, since the roe-on-kelp fishery was closed during the modeled period (1994-1996).

A note on nearshore groups

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Summaries are provided for several nearshore (depths less than 20 m) groups of organisms in PWS, Alaska. These groups include benthic algae and eelgrass, shallow small epibenthos, shallow large infauna, shallow large epibenthos, and nearshore demersal fish.

The rigor used in deriving these estimates varied by group, and there are still considerable data that could be mined to refine estimates. I have indicated potential sources of data that I am aware of, but have not had time to explore. No confidence intervals are given, but could be obtained with more work. Estimation of confidence intervals is complex and would likely require simulation.

It is important to note that most of the data that serve as the basis for these estimates are from the western portion of Prince William Sound, and this likely produces several biases. The eastern portion of the Sound is shallower and has a higher proportion of soft substrates. Therefore, it is likely that we have overestimated algal and epifaunal biomasses and underestimated infaunal biomass. It also likely that fish assemblages are quite different in the Eastern and Western Sound, leading to potential biases in estimated nearshore demersal fish biomass.

Phytoplankton

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Phytoplankton is the main source of annual primary production in PWS, and its main components are diatoms and phytoflagellates. These organisms form the base of this marine food web, as they turn solar energy into chemical energy. Diatoms are photosynthetic, single-celled protists (division Chrysophyta) whose identifying characteristic is silicified cell walls making up the lid-like valves of a protective frustule (Wetzel 1983). Phytoflagellates are the autotrophic (photosynthetic) group of the protozoan subphylum Mastigophora. They usually possess flagella for locomotion, but unlike their heterotrophic counterparts, they contain chlorophyll and are treated as algae by phycologists (Barnes 1987). Abundances (densities) of these two

Table 8. Monthly changes in production in PWS (based on Goering et al. 1973).

Primary production	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Totals ($t \cdot km^{-2} \cdot year^{-1}$)
$t\ C \cdot km^{-2}$	0.2	0.7	1.3	59.6	19.6	10.6	1.6	3.9	5.4	7.0	3.6	0.2	113.8
$t\ ww \cdot km^{-2}$	2.2	7.4	12.5	596.4	195.6	105.7	15.8	38.5	54.5	70.5	36.4	2.2	1,137.8

groups vary considerably over the course of a year with diatoms blooming in the spring and flagellates numerically dominating in the winter and late summer; both groups are more-or-less equally abundant in the fall. Phytoplankton in PWS is exchanged with the adjacent Gulf of Alaska, but imports and exports are assumed to balance each other for the purpose of this model.

Monthly phytoplankton production estimates were provided by Dr. C. Peter McRoy (UAF Institute of Marine Sciences, pers. comm.) based on data published by Goering et al. (1973). The months of January, February, June, September, and November were missing, so these values were interpolated to calculate the annual primary production in PWS (114 $t\ C \cdot km^{-2}$; Table 8). This estimate is low, by approximately a factor of two, because observations and measurements were made in Port Valdez/Valdez Arm where glacial silt shades the system (Goering et al. 1973). Thus, 114 $t\ C \cdot km^{-2}$ converts to an annual produced biomass wet weight of 1,105 $t \cdot km^{-2}$, assuming 0.1 g C = 1 g wet weight (Dalsgaard and Pauly 1997), and doubling this value leads to a biomass production estimate of 2,210 $t \cdot km^{-2}$. This value must be added to the annual primary production of macroalgae and eelgrass (501 $t \cdot km^{-2}$; from Dean, this vol.) for a total annual primary production estimate of 2,711 $t \cdot km^{-2}$.

P/B values of 190 and ecotrophic efficiency (EE) values of 0.95 were used to allow the model to calculate phytoplankton biomasses, with Q/B values set at zero, as required for autotrophs. Flagellates and diatom groups were aggregated since they were not ecologically distinguishable with the input parameters available to us and since predation on phytoplankton was always equally split between these groups.

Nearshore Phytoplankton

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To ensure dynamic stability of the PWS food web, the phytoplankton group was split into 'nearshore' and 'offshore' groups, with the 20 m isobath serving as boundary (suggested by S. Pimm, U. of Tenn., pers. comm.; *also see* Pauly 1998). Diet compositions were allocated based on the strata (nearshore vs. offshore) of each predator of phytoplankton (nearshore or offshore) except for jellies whose phytoplankton consumption proportion (10% of their diet) was allocated by the proportion of livable phytoplankton space between the two strata (based on a mean euphotic zone limit in PWS of 25 m (D. Eslinger, UAF Institute of Marine Sciences, pers. comm.), 7.2% of livable phytoplankton space is located nearshore of the 20 m isobath and 92.8% is located in the offshore zone). This proportional allocation would reflect feeding opportunities of jellies on phytoplankton. Other input parameters remained the same as offshore phytoplankton.

ZOOPLANKTON

Offshore Zooplankton

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For the purpose of the PWS model, it seemed reasonable to divide the zooplankton into herbivorous zooplankton, omnivorous zooplankton, and carnivorous jelly plankton. Herbivorous zooplankton include copepods, larvaceans, pteropods, and cladocerans. Omnivorous zooplankton include euphausiids, amphipods, larval fishes, chaetognaths, and decapods. Carnivorous jellies are covered in the following section.

This categorization is not strictly correct, but the approximations should work well for the model. Mesozooplankton (our 'herbivores') are all plankters <= 1 mg·individual^{-1}. Macrozooplanktors (our 'omnivores') are animals > 1mg·individual^{-1}. Since some of these animals 'grow through' the mesozooplankton category to macrozooplankton at an older age, categories such as juvenile euphausiids and amphipods are thrown in with herbivores when they are young, and with macroplankters when they mature.

Zooplankton collections, obtained since the spring of 1994 for project H of the EVOS Trustee Council sponsored Sound Ecosystem Assessment (SEA) program, are available for estimates of standing stock from 740 samples collected from 1994-1997. Most of these collections were vertical tows integrating the upper 50 m. A ½-m diameter ring net with 0.33 mm Nitex mesh was used in the field. Some other samples were obtained from hatcheries in PWS. These were collected using a ½-m ring net fished vertically (by hand) in the upper 20-m (0.25-mm Nitex). All collections were processed in the University of Alaska, Fairbanks Institute of Marine Science (UAF/IMS) plankton laboratory using standard subsampling and weighing practices. Numbers and biomass for discrete life stages, species, species composites, genera and more general taxonomic categories were recorded.

For the analysis supporting the development of a mass-balance model, monthly averages were determined over all years (1994-1997) for total zooplankton (summing across all taxonomic categories), and for specific taxa judged to be important for higher-level consumers in Prince William Sound.

Zooplankton densities are highly variable over the course of a year in PWS (Figure 3, and Appendix 3). Wet weight biomass (total, or for specific taxa or size groups) as g·m^{-3}, was determined by converting numbers per m^3 to g·m^{-3} from average wet weights of individuals. Monthly means were then reported for: (1) total zooplankton (all stages and taxa); (2) for zooplankters <= 1 mg wet weight/individual; (3) for zooplankters > 1 mg/individual; (4) for copepods; (5) for pteropods; (6) for amphipods; (7) for larvaceans; (8) for euphausiids; (9) and for a composite (by difference) of everything else (*see* Appendix 3). There were three months for which there were no samples, August, November and January. These means were determined by interpolation.

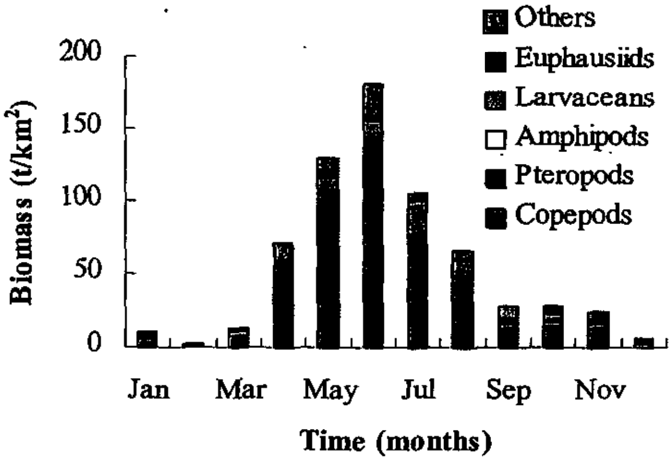

Figure 3. Seasonal changes in PWS zooplankton, upper 50 m, all years, all locations

Monthly estimates (g·m^{-3}) were converted to standing stock in kg·m^{-2} over a depth of 300 m (and 100 m; not used here). Prince William Sound has depths to 720 m. The 300 m depth was chosen to generate stock estimates approximating values for the entire water column over the entire Sound for the mass balance modelling. The means of the monthly estimates were then multiplied by the proportion of PWS area deeper than 20 m to derive offshore PWS zooplankton biomass densities (beyond the 20m isobath) on a PWS-wide basis (Table 9).

The diverse net zooplankton community in PWS is dominated by copepods, some of which produce several generations per year,

Table 9. Annualized Ecopath parameters for zooplankton in PWS.

Zooplankton category	**Biomass ($t{\cdot}km^{-2}$)**	**P/B (year^{-1})**	**Q/B (year^{-1})**	**EE**
Herbivorous zooplankton	30.0	15	50	≥ 0.90
Omnivorous zooplankton	15.4	5	17	≥ 0.90

while others reach up to a year of age. *Pseudocalanus* spp. are the most common small copepods in our samples and produce several broods per year. The larger copepods are dominated by *Neocalanus* spp. and *Calanus marshallae.* These calanoids produce one (*Neocalanus*), at most two (*Calanus*) generations per year. Pteropods, *Clione Limacina* and *Limacina helidina* are numerous, as are euphausiids (*Thysanoessa* spp. and *Euphausia pacifica*). The Pteropods reproduce continuously after the spring bloom, which starts in April; euphausiids in the region are believed to live for 2-3 years. Amphipods were judged to exhibit life histories similar to the euphausiids, and the larvacean production cycle more like that of the pteropods. The 'other zooplankton' consists of a variety of jelly forms (hydromedusae and ctenophores), larval fishes and meroplankton.

There is a huge range in production/biomass (P/B) ratios in the literature (*see* Tranter 1976; Valiela 1995). The values of P/B selected here (5 year^{-1} for herbivorous zooplankton and 15 year^{-1} for omnivorous zooplankton) fall within the ranges of those reported for mixed zooplankton, and for individual groups or species (overall zooplankton, 10 year^{-1}; small zooplankton, 15 year^{-1}; large zooplankton, 5 year^{-1}; copepods , 8 year^{-1}; pteropods, 3 year^{-1}; amphipods, 2 year^{-1}; larvaceans, 3 year^{-1}; euphausiids, 2 year^{-1}; other zooplankters, 2 year^{-1}).

These annual estimates were then distributed across the months generally in proportion to the growth cycle of the zooplankters as observed in their seasonal signal; lower during the winter months, and higher in the late spring and early summer (Appendix 3 and Figure 3).

The amounts of food ingested for each of the groups was determined by applying a gross growth efficiency of 30% to the estimated monthly production values. These consumption estimates (Q) were then divided by the biomass on the different months to provide the Q/B ratios (50 year^{-1} for herbivorous zooplankton and 17 year^{-1} for omnivorous zooplankton). Parsons et al. (1988) list gross growth efficiencies for zooplankton. While the range is quite high, most fall within 20-40%. Harrison et al. (1993) list a Q/B value for herbivorous zooplankton in the Strait of Georgia of 10.5 year^{-1}. The calculated values obtained using a 30% gross growth efficiency range from 7-50 year^{-1} (*see* Appendix 3).

In the absence of a way to measure or calculate ecotrophic efficiency (EE), i.e., the fraction of the production consumed or exported, the default value used by Dalsgaard and Pauly (1997) for a preliminary mass balance model of Prince William Sound is suggested. While this value may be a reasonable annual average, it probably does not apply well to monthly production values. Obvious increases in zooplankton during the late spring and summer months suggest an uncoupling of the system for some of the taxa examined in this study. Appendix 3 lists monthly estimates of EE, generally phased inversely with levels of per capita production. However, the fraction consumed (EE) is not allowed to decline below 0.9 in any month.

Levels of Uncertainty

The information provided here is probably most accurate at the level of monthly biomass in the upper 50 m. Extending this value to greater depths implies an unknown bias. Certainly, zooplankton live at all depths in the region, but at least during the spring and summer, the biomass of most populations is greatest near the surface. I presume that by distributing the upper 50 m derived values of $g{\cdot}m^{-3}$ to a deeper water column there will be a depth below which the overall estimate will become significantly positively biased. On the other hand, the small size of the net used by SEA probably under-represented some of the taxa (euphausiids and amphipods). This negative bias will be partially corrected when surface values are extended over a deeper column. Damkaerr (1977), based on 1-m ring net, reported more than 1 kg·m^{-2} in tows from the deepest part of the Sound to the surface, or roughly an order of magnitude greater than reported here for 'total zooplankton' summed over 300 m in June. This suggests extreme interannual or spatial variability, or very strong negative bias associated with the smaller net used in this study, or something else. Because the amount ingested to account for the calculated zooplankton production is considerably higher than the estimate of annual primary production, I suspect the values of zooplankton standing stock are too high. When the upper 50 m values are distributed over 100 m, the zooplankton ingestion is more in line with primary productivity, particularly since the latter (presented by McRoy, this volume) seems too low by about a factor of 2 (Goering et al. 1973).

The production to biomass (P/B) ratios used here to predict monthly production from monthly standing stock estimates are arbitrarily chosen from a small range of controversial literature values. I suspect that they are accurate only in the most general sense, and may generally be considered conservative.

Ingestion per unit biomass (Q/B) values are calculated from a single value of gross growth efficiency (30%), an average for several zooplankters reported in the literature (range 7-70% year^{-1}). For the larger zooplankton like euphausiids, this growth efficiency may over-estimate food consumption. This approach may introduce a slight positive bias to estimates of food consumed monthly by zooplankton.

Nearshore Zooplankton

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The 'nearshore zooplankton' group in the PWS model consists of omnivorous zooplankton and herbivorous zooplankton collected within the 20 m depth contour. Zooplankton samples were collected from May, 1996 to March, 1997 with 300 μm mesh net vertical tows from the head of four bays in PWS as part of the EVOS Trustee Council sponsored Sound Ecosystem Assessment (SEA) program. Biomass estimates determined from subsample counts and individual weights were pooled for monthly means. Biomass data in April and September were interpolated because no samples were collected. The means of monthly nearshore zooplankton biomass values were expressed on a Sound wide basis by multiplying by the proportion of PWS area in the nearshore zone (0.1586). Summary data are presented in Table 10 and monthly data are presented in Appendix (3).

Production of zooplankton is highly variable and difficult to estimate (Lalli and Parsons 1993; Valiela 1984). P/B estimates for omnivorous and herbivorous zooplankton were derived from estimated annual P/B values for euphausiids (annual P/B=7.9 year^{-1}) and copepods (annual P/B=27.0 year^{-1}), respectively, off southwestern Vancouver Island, British Columbia (Robinson and Ware 1994). Monthly estimates were adjusted in proportion to the biomass data.

Food consumption (Q) for each nearshore plankton group was calculated by assuming that the monthly production value was based on a 30 % growth efficiency, which falls within the range of other aquatic invertebrates (10-40 %) (Parsons et al. 1984). Gross growth efficiency can be seasonally variable dependent on food concentration and temperature (Raymont 1983). Annual Q/B values ranged from 26 to 90 year^{-1}.

Diet composition was set at the same levels as the offshore zooplankton groups, discussed in the previous section. Predation by other groups on nearshore zooplankton was allocated from the offshore zooplankton group in proportion to the water volume in the two areas; for each zooplankton group, 0.6% of its zooplankton proportion was allocated to nearshore zooplankton while the remaining (99.4%) remained in the offshore portion, beyond the 20 m isobath, unless predator distribution information indicated spatial heterogeneity of feeding by particular predators. These percentages correspond to 14.2 km^3 nearshore of the 20 m isobath (assuming a mean depth of 10 m) and 2200 km^3 offshore (integrated to 300 m).

Carnivorous Jellies

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The biomass density estimate of PWS carnivorous jellies (6.39 t·km^{-2}) was estimated using two different data sets, one for jellies in PWS open water areas (J. Purcell, unpublished data) and one for jellies in PWS nearshore areas (R. Foy, unpublished data). This estimate is a weighted mean of the two independently derived estimates, based on the proportion of total area that each zone represents.

The biomass of carnivorous jellies in the offshore surface waters of PWS was estimated to be 7.065 t·km^{-2}. This value was derived by multiplying the volumetric biomass estimate, 94.2 t·km^{-3} (J. Purcell, unpublished data), by 0.3 km, the average depth of PWS, and dividing by four to account for assumed declines in jelly densities with increasing depth.

The biomass density of nearshore jellies was estimated to be 2.79 t·km^{-2}. This estimate was derived by multiplying the nearshore volumetric biomass estimate (278.9 t·km^{-3}; R. Foy, unpublished data) by 0.01 km, the assumed average depth inshore of the 20 m isobath.

Production to biomass ratios (P/B) for carnivorous jellies were derived from maximum daily P/B reported for gelatinous predators in Saanich Inlet, British Columbia (Larson 1986). A maximum daily P/B of 0.1 year^{-1} was assumed for June (when maximum production occurs) while the other months were calculated proportionally to biomass. The annual P/B would then be 8.82 year^{-1}, which is consistent with that of British Columbia gelatinous predators (P/B = 5-10 year^{-1}). The annual Q/B was set at 29.4 year^{-1}, and the diet composition used for carnivorous jellies was 67% herbivorous zooplankton, 23% omnivorous zooplankton, and 10% phytoplankton.

BENTHIC INVERTEBRATES

Shallow Large Infauna

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These are larger (generally greater than 20 mm) infauna found at depths less than 20 m. Clams make up the majority of larger infaunal biomass in the nearshore. These include *Protothaca staminea*, *Saxidomus giganteus*, *Clinocardium* spp., *Macoma* spp. and others. Surveys of subtidal and intertidal clam densities were conducted in Herring Bay, Bay of Isles, and Montague Island portions of the Sound in 1996 and 1997 by G. Van Blaricom, A. Fukayama, S. Jewett, and T. Dean (Holland-Bartels et al. 1997 and unpublished data). Sampling was conducted from the intertidal to

Table 10. Annual summary data for nearshore zooplankton

Group	Biomass[a] (t·km^{-2})	P/B[b] (year^{-1})	Q/B[b] (year^{-1})
Herbivorous zooplankton	0.097	27.0	90.0
Omnivorous zooplankton	0.079	7.9	26.3

a. Means of monthly nearshore biomass values expressed on a PWS-wide basis (times 0.1586; *see* Appendix 3).

b. Sums of monthly P B or monthly Q/B values (*see* Appendix 3)

Table 11. Biomass (t ww km^{-2}) of small intertidal epifauna in different strata and habitat types (from Highsmith et al. 1994). Depth strata and habitats are as defined in Tables 2 and 4. (from Highsmith et al. 1994).

Habitat type	Depth stratum	May 1990	August 1990	May 1991	Mean
Sheltered rocky	High	271	263	362	
	Mid	493	553	1,173	
	Low	397	395	411	
	Mean	387	404	649	**480**
Coarse textured	High	209	117	181	
	Mid	543	573	424	
	Low	328	617	406	
	Mean	360	436	337	**378**
Estuarine	High	3,454	13,456	197	
	Mid	6,440	8,354	95	
	Low	2,815	6,887	91	
	Mean	4,236	9,566	128	**4,643**
Exposed rocky	High	149	66	540	
	Mid	1,324	745	854	
	Low	1,128	181	1,671	
	Mean	867	331	1,022	**740**

depths of 15 m using either shovels (in the intertidal) or a suction dredge (in the subtidal). We assume here that these data are representative of the entire Sound, and are comparable to pre-spill (1980-1989) density estimates.

The estimated clam biomass, for both intertidal and subtidal habitats, was approximately 80 t ww km^{-2}. On a sound wide basis, this is estimated at 12.5 t km^{-2}. There are no data on seasonality, but we suspect that there is no appreciable change in standing stock biomass with season.

The dominant clams are primarily suspension and deposit feeders, and we assume that about 50% of the diet is phytoplankton, and 50% detritus.

Feder and Jewett (1986, Table 12-9) estimated that the infaunal biomass at Hinchenbrook entrance was 343 g m^{-2}, and this produced 4.6 g C·m^{-2} ·year^{-1}, corresponding to 222 g·ww·m^{-2} ·year^{-1}. These estimates were for depths greater than 20 m, from an extremely productive portion of the Sound, and are thus probably not representative of Sound wide conditions. However, we use these data to provide an estimate of a P/B ratio for shallow large infauna, of about of 0.6 year^{-1}. The Q/B ratio for large infauna is estimated at 23 year^{-1}, based on estimates given by Guénette (1996) for the North Pacific.

Some clams (especially *Protothaca*) are harvested. A catch of 0.003 t·km^{-2}·year^{-1} for PWS clams is given in Trowbridge (1996).

Shallow Small Epifauna

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Shallow small epibenthos are defined as non-motile or slightly motile invertebrates of less than 5 cm in size living on or near the bottom at depths less than 20 m. These are generally found on hard substrates or attached to algae/eelgrass. Small epifaunal organisms in the nearshore zone include a variety of invertebrate taxa. Dominant forms include barnacles, littorine and lacunid snails, mussels, limpets, chitons, and amphipods, small crabs, and other snails and crustaceans.

Table 12. Weighted mean biomass (t ww·km^{-2}) of small epibenthic invertebrates in the intertidal zone, Prince William Sound (from Highsmith et al. 1994).

Habitat Type	Biomass density (t·km^{2})	% of area	Biomass in PWS
Sheltered rocky	480	30	144
Coarse textured	378	41	154.98
Estuarine	4,643	5	232.15
Exposed Rocky	740	23	170.2
Fine Textured	0	1	0
All	6,241	**Total**	**701.33**

Highsmith et al. (1994) estimated the biomass of intertidal epifauna within several depth strata and habitat types in PWS in 1990 and 1991 (Table 11). The average biomass at unoiled sites was 701 t km^{-2} (Table 12). On a Sound wide basis, accounting for the whole area, this is equivalent to 23 t·km^{-2}.

Estimates for epifaunal invertebrate abundance in the nearshore subtidal zone were made within three areas (Herring Bay, Bay of

Isles, and Northern Montague Island) by T.A. Dean and S. C. Jewett in 1997 (unpublished data). Airlift samples of invertebrates were collected at systematically selected sites at depths of 1 to 3 m in order to estimate the abundance of food available to harlequin ducks. Several of the dominant taxa, including littorine and lacunid snails, limpets, chitons, amphipods, and other snails and crustacea were counted and weighed. The average biomass was 7.5 t·ww·km^{-2}. This is likely an underestimate of biomass for the Sound as a whole, because densities of invertebrates tend to be higher at more exposed sites that were not sampled, and several common invertebrate taxa (e.g., serpulid polychaetes) were not sampled. However, if we assume that the biomass is representative of the entire subtidal zone in PWS, then the average biomass, on a Sound wide basis, is estimated at 1.2 t·km^{-2}. Thus, the total biomass of small epifauna in both intertidal and subtidal habitats is approximately 8.7 t·km^{-2}.

There are no good quantitative data on seasonality of biomass for small epifaunal invertebrates in the nearshore. However, data in Highsmith et al. (1995) suggest that intertidal biomass peaks in early summer (June) following spring recruitment. We suspect that minimum biomasses occur in late March. This is just after the breakup of ice formations that cause significant mortality to intertidal organisms, and just prior to the Spring recruitment and phytoplankton blooms. We also suspect that there is less seasonality in the subtidal than the intertidal assemblages. We assume here that the minimum biomass occurs in March and is about 75% of the peak in June.

The trophic levels and diets of small epifauna in the nearshore are extremely varied. We estimate that roughly 75% of the biomass consists of barnacles, mussels, and other filter feeders that feed primarily on phytoplankton and detritus. Most of the remaining biomass consists of grazers (e.g. littorines, chitons, and limpets) that feed primarily on smaller algae. We estimate that the composite diet consists of about 40% detritus, 35% phytoplankton, 20% algae, and 5% small nearshore epifaunal invertebrates.

The P/B ratio for small epifauna is assumed to be about 2 year^{-1}, equivalent to that for larger epifauna as described by Feder and Jewett (1986). The Q/B ratio is assumed to be approximately 10 year^{-1}, based on values given in Guénette (1996) for epifauna.

Shallow Large Epifauna

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Shallow large epifauna are defined as generally motile invertebrates that are greater than 5 cm and live on or near the bottom from the intertidal to depths of 20 m. These are mostly sea stars (*Pycnopodia helianthoides, Dermasterias imbricata, Evasterias troschelii,* etc.) and crabs (mostly *Telmessus cheriagonus*).

Dean et al. (1996b) surveyed large epibenthic invertebrates in 4 habitats in Western Prince William Sound in 1990. Based on data from unoiled control sites, we estimate the average density of large epibenthic invertebrates was 0.27 individuals·m^{-2} (Table 13). These include mostly starfish (mainly *Dermasterias* and *Pycnopodia*) and crabs (mainly *Telmessus*). An average *Dermasterias* has a wet weight of about 75g (T. Dean, unpublished data). Based on the assumption that all large epifauna are

Table 13. Density and biomass of large epibenthic invertebrates in 0 to 20 m depths in Prince William Sound, Alaska (from *Dean et al.* 1995b and Jewett et al. 1995; extrapolated from (individuals·100 m^{-2}) and (g·ww·m^{-2}) respectively).

Taxa	**Density (ind.·km^{-2})**	**Biomass (t·km^{-2})**
Pycnopodia helianthoides (adults)	1,000	7.5
Dermasterias imbricata (adults)	1,000	7.5
Evasterias troschelii	200	1.5
Telmessus cheriagonus	300	2.3
Others	200	1.5
Total	2,700	20.0

of about the same weight, this leads to a biomass density of roughly 20 g ww·m^{-2}. On a Sound wide basis, the standing stock biomass is estimated at 3.1 t·km^{-2}.

The diets of *Pycnopodia* (Holland-Bartels et al. 1997) and *Evasterias* (O'Clair and Rice 1985) consist mostly of clams and snails. *Dermasterias* eat a wider variety of benthic invertebrates (Rosenthal et al. 1974). *Telmessus* consume eelgrass and associated small epifauna (McConnaughey and McRoy, 1979). It is estimated that the average diet of large epibenthic invertebrates consists of 80% shallow small epifauna, 19% nearshore small infaunal invertebrates, and 1% eelgrass.

There is no appreciable harvest of nearshore epibenthic invertebrates in PWS. Large epibenthic invertebrates that have been of historical commercial value (crabs and shrimp) are generally restricted to depths greater than 20 m.

The P/B ratio for large epifauna is assumed to be about 2 year^{-1} based on estimates of Feder and Jewett (1986). The Q/B ratio is assumed to be approximately 10 year^{-1}, based on values given in Guénette (1996) for epifauna.

Small Infauna

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Information on the macrobenthos in Prince William Sound are mainly available from the pre-EVOS investigations of Hoskin (1977), Hoberg (1986) and Feder and Jewett (1988) and post-EVOS studies of Feder (1995), Jewett et al. (1995) and Jewett and Dean (1997). The last two investigations, which were conducted in 1990, 1991, 1993 and 1995, targeted depths < 20 m; the others targeted depths > 20 m. Information included in this synopsis is from pre- and post-spill sources. All sampling generally occurred between April and August. Macrobenthos in these investigations refer to all benthic invertebrates larger than 1 mm that were sampled with a 0.1 m^2 van Veen grab or suction dredge. These mainly include infaunal organisms that live within the top 10 cm of substrate and small, slow-moving or sessile epifauna.

Estimates of proportions of subtidal habitats at < 20 m, 20-100 m, and > 100 m in PWS are presented in Table 14. The extent of coverage of < 20 m depth habitats of bays predominated by kelps (*Laminaria* and *Agarum*) and eelgrass (*Zostera*) was estimated using side-scan sonar and systematic surveys by divers along segments of the western portion of the Sound (Jewett and Dean, unpubl.). The extent of hard (unsampleable) and soft (sampleable) substrates at depth > 20 m was estimated by S.C. Jewett (pers. obs.) and T.A. Dean (Coastal Resources Associates, pers. comm.).

Table 14. Proportion of substrate types in different PWS depth zones (%).

Area	**Depth (m)**		
	<20	**20-100**	**>100**
Hard substrate	76.0	30	10
Laminaria/Agarum bays	37.5	----	----
Unsampleable	38.5	----	----
Soft substrate	24.0	70	90
Zostera bays	7.5	----	----
No vegetation	16.5	----	----

Macrobenthic biomass estimates from different habitats in the Sound are presented in Table 15. Estimates from < 20 m depths are mainly from relatively unexposed bays in the Knight Island vicinity where kelps and eelgrass predominate (Jewett et al. 1995; Jewett and Dean 1997). Estimates from 20-100 m

Table 15. Estimates of macrobenthic biomass in PWS.

Area	**Biomass (t·km^{-2})**	**Weighting factor**	**Biomass (t·km^{-2})**
< 20 m	83.8±12.1	0.615	51.5
Laminaria/Agarum	76.0±19.9	0.375	28.5
Zostera bays	87.9±17.7	0.075	6.6
Other	81.9	0.165	13.5
20-100 m	88.1±16.6	0.700	61.7
> 100 m	19.1±3.5	0.900	17.2
Combined > 20 m		--	24.7[a]

a. calculated by adding the products of the biomasses and areal proportions of the two preceding groups. Proportions in Table 14 and Table 8 were used for this calculation.

depths are from western PWS, mainly in the Knight Island/northern Montague Island vicinity (Feder, 1995; Table 4; Hoberg, 1986; Append. 7). Estimates from > 100 m depths are from three fjords in western PWS (Derickson and McClure Bays and Blue Fjord; Hoskin, 1977) and northern PWS (Port Valdez; Feder and Jewett, 1988; Table 2) and non-fjords mainly in the Knight Island/northern Montague Island vicinity (Feder, 1995; Table 4). Not included in the > 100 m stratum estimate is the high biomass of 417 t km^{-2} in the region of Hinchinbrook Entrance (Feder and Jewett, 1986; Table 12-6). This region, which is very dynamic, appears to be exceptionally productive in comparison to other areas > 100 m. I assumed that there is little seasonal biomass variability.

The dominant faunal groups (% biomass) by depth strata are presented in Table 17. Values for < 20 m are estimated from Jewett et al. (1995; Append. P and T). Values for depths 20-100 m and > 100 m are from Hoberg (1986) and Hoskin (1977), respectively. Other sources of information on dominant groups at depths > 20 m report dominance in terms of numerical abundance rather than biomass (Feder and Jewett 1988; Feder 1995).

Estimates of P/B, Q/B and diet matrix of macrobenthos are presented in Table 16. P/B values for depths < 100 m (0.6) are estimated using previously estimated P/B values for specific taxa from Feder et al. (1989; Appendix 3). P/B values for depths > 100 m (1.4) are from Feder and Jewett (1988; Table 3). The Q/B value used here, 32 $year^{-1}$, is the same used for infaunal macrofauna by Guénette (1996). I assumed that the phytoplankton consumed by suspension feeders is composed of one-half diatoms and one-half flagellates.

Deep benthic groups and meiofauna

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Deep large infauna

These are larger infauna (generally greater than 20 mm), mostly clams, found at depths greater than 20 m in PWS. Clams have been sampled at depths deeper than 20 m in PWS (Feder and Blanchard 1998), but I could find no data that can be used to reliably estimate the biomass density of deep large infauna in PWS. Assuming that clam biomass density below 20 m is generally one fourth that of the shallow zone, the density value of 80 t ww·km^{-2} provided by Dean (this vol.) for shallow large infauna was divided by four

Table 17 Dominant macrobenthic groups in PWS (% biomass).

Depth zones (m)	Anthozoa	Polychaete	Bryozoan	Bivalve	Gastropod	Echiuran	Holothurian	Ophiuroid
< 20	<1	11	4	74	5	<1	<1	1
> 20[a]	4	26	<1	26	<1	3	12	8
20-100	6	<1	<1	28	<1	5	20	13
> 100	<1	60	<1	23	<1	<1	<1	<1

a) Figures were calculated by multiplying the values in the following two categories with the corresponding biomass proportions in those two depth zones, then adding the respective products; biomass proportions were calculated from Table 11.

Table 16. Estimates of P/B. Q·B and diet matrix (% abundance) of macrobenthos in PWS.

Depth zones (m)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	Detritivores (Detritus)	Suspension feeders (Phytoplankton)	Predators/ scavengers (Cannibalism)
< 20	0.6	23	0.25	0.60	0.15
20-100	0.6	23	0.77	0.20	0.03
> 100	1.4	23	0.80	0.15	0.05
> 20[a]	0.94	23	0.78	0.18	0.04

a) >20 m values were calculated by multiplying the values in the preceding two categories with the corresponding biomass proportions in those two depth zones then summing the respective products; biomass proportions were calculated from Table 11.

then expressed on a sound wide basis by multiplying by the proportion (0.81) of deep zone area in PWS from Table 1. The deep large infauna biomass estimate is 16.2 t·km^{-2}.

The numerically dominant clams are primarily deposit feeders in the deep zone, and we assume that about 10% of the diet is phytoplankton, and 90% detritus.

P/B ratio for shallow large infauna, of 0.6 year^{-1}, is also used for deep large infauna. The Q/B ratio for large infauna is estimated at 23, based on estimates given by Guénette (1996) for the North Pacific.

Deep Epifauna

This group is made up of both motile and non-mobile invertebrates living on, but not in, the sea floor at depths greater than 20 m. There is inadequate information to reliably estimate biomass of PWS epifauna in the zone deeper than 20 m for any period after the EVOS. Epifaunal biomass has been estimated for one location in PWS prior to EVOS, but information compiled in Feder and Jewett (1986) reveals that the composition of epifaunal assemblages is highly variable among PWS sites (Table 18). The degree of temporal variability of deep epifauna is even less known, though it might be considerable, as indicated by recent fluctuations (declines) in crabs and shrimps throughout Alaska (NMFS 1996). A rough biomass estimate of 1.5 t·km^{-2} was derived by giving equal consideration to the pre-spill biomass value for Port Etches and a pre-spill value derived for the lower Cook Inlet, a nearby setting similar to the central area of PWS (Table 18). The mean of these two values, 1.85 t·km^{-2}, was multiplied by 0.81, the proportion of PWS area deeper than 20 m. A biomass estimate derived from 1975 trawls on the shelf adjacent to PWS was not used in the derivation of the rough estimate, but it is included in (Table 18). Calculated values for Tanner Crab and shrimps are also included in the table for comparison.

The P/B ratio for epifauna is assumed to be about 2 year^{-1}, based on estimates given by Feder and Jewett (1986). The Q/B ratio is assumed to be approximately 10 year^{-1}, based on values given in Guénette (1996) for epifauna.

A catch rate of 0.143 t·km^{-2}·year^{-1} for PWS epifauna is provided in Trowbridge (1996). Included in this rate is pink and other shrimps, king crab (red, blue, brown), and tanner crab.

Meiofauna

The P/B for meiofauna was set at 4.5 and the Q/B was set at 22.5 (Tom Shirley, UAF Institute of Marine Sciences, pers. comm.). The biomass was estimated by Ecopath with the ecotrophic efficiency set at 0.95.

PLANKTIVOROUS 'FORAGE FISHES'

Salmon Fry

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Salmon fry consist of five species of *Oncorhynchus*. The relative contribution of these five species in decreasing abundances is pink (*O. gorbuscha*) > chum (*O. keta*) > red (*O. nerka*) >silver (*O. kisutch*) > king (*O. tshawytscha*). One hundred per cent of the last two species are artificially propagated (by hatcheries) in PWS.

In this section, salmon fry are divided up between those < 6 cm and those ≥ 6 cm in length. Those < 6 cm enter the system either from natural habitats (spawning redds on beaches or natal streams) or hatcheries. Those > 6 cm leave PWS at about 11 cm. The rationale for division of salmon fry into two functional groups is based upon the SEA project findings that suggests a predation size refuge near 6 cm (Willette et al. 1996). Mortality rate of salmon is highest upon entry into the marine system (Parker 1968). Furthermore, mortality nearly compensates biomass increase for fry < 6 cm while average biomass of fry > 6-cm doubles. Splitting into the two functional groups thus also leads to more reasonable means, then to compute a grand mean for juveniles, as required for the single juvenile group, which Ecopath can accommodate for each species.

Approximately 500 million salmon fry enter PWS from hatcheries each year while 300 million enter from natural stocks. The average entry date into PWS from these sources is May 1 (PWSFERPG 1993), and the average weight is 0.25 g (PWSFERPG 1993). This number multiplied by the starting population leads to a biomass estimate of 160 t. There is 32% survival after the 40 day period when the fry are less than 6 cm. Thus, the ending population size is 256 million. This population

Table 18. Estimated biomass of benthic epifauna > 20 m depth, PWS (from Feder and Jewett 1986).

Area (and depth) (m)	Biomass ($t \cdot km^{-2}$)	Species (group) (% weight)
Port Etches[a] (85-150)	0.8	Sunflower star (62), Pink shrimp (28), Tanner crab (4), Mollusks (0.2), Other (5.8)
Rocky Bay[b] (30-100)	---	Echinoderms (87), Crustaceans (5.9), Molluscs (3.2)
Zaikof Bay (20-100)	---	Echinoderms (50), Crustaceans (45)
Outer Simpson Bay (30-50)	---	Sea pens, cockles, brachiopods, basket stars
Outer Port Gravina (50-130)	---	mud stars, pink shrimp
Outer Port Fidalgo (90-170)	---	crinoids, basket stars
Inner Galena Bay (30-130)	---	feather star, shrimps
Columbia Bay (150-275)	---	sea pens, mud stars
Unaquik Inlet (175-212)	---	mud stars, pandalid shrimps
Port Wells (275-400)	---	mud stars, heart urchins, cucumbers
NEGoA shelf[c]	2.1	---
Lower Cook Inlet (>25)[d]	2.9	---
PWS Tanner Crab, 1989[e]	0.24	---
PWS Shrimp, 1989[e]	0.01	---
Mean of selected estimates[f]	1.5	---

a) Feder and Hoberg (1981) in Feder and Jewett (1986);
b) Feder and Hoberg (1981) and Hoberg (1986) in Feder and Jewett (1986);
c) Feder and Matheke (1980) in Feder and Jewett (1986);
d) Feder and Paul (1981) in Feder and Jewett (1986);
e) NMFS (1993);
f) mean of lower Cook Inlet and Port Etches.

Table 20. Ecopath parameters for salmon fry > 6cm (P/B values not used in model parameterization).

Period	B ($t \cdot km^{-2}$)	B min	B max	P/B ($year^{-1}$)	Export ($t \cdot km^{-2} \cdot year^{-1}$)
Jun	0.035	0.029	0.042	--	-0.029
Jul	0.052	0.042	0.062	--	0
Aug	0.069	0.062	0.076	--	0.076
Mean	0.050	0.027	0.073	8.666	0.034
Aggregate (fry 0-12)	**0.072**	–	–	**9.844**	**0.045**

size when multiplied by an average weight of 1.23 g (PWSFERPG 1993) results in a biomass of 315 t. Thus, the average biomass of salmon fry < 6 cm is 238 t. The mortality estimated for the second period, 70 days, reduces the population to 84,480,000 using a mortality rate of 0.0158 day^{-1}. The population biomass, using an average weight of 10.04 g (PWSFERPG 1993), at this time is thus 848 t. This biomass is exported from PWS. The average biomass for fry in PWS > 6 cm is 582 t. Since the import was 160 t, the net export is 422 t. The area of PWS used for the areal density calculations is 9,059 km^2.

The P/B ratio for both salmon fry groups can be approximated on the assumption of linear growth and mortalities, which holds for short intervals. Thus, for a short period $\Delta t = t_2 - t_1$,

$$P/B \approx \frac{\Delta B + (\Delta N \cdot \overline{W})}{\overline{B}}$$

where:

ΔN = change in number of individuals ($N_1 - N_2$);

$\overline{W}$ = mean weight of individual ($(W_1+W_2)/2$);

B = biomass ($N \cdot \overline{W}$);

ΔB = change in biomass ($B_2 - B_1$);

$\overline{B}$ = mean biomass ($(B_1 + B_2)/2$.

The resulting P/B value was then expressed on an annual basis for the model. Using this approach and the preceeding estimates, P/B for salmon fry <6 cm is calculated to be 18.542 $year^{-1}$ (2.032 · (365 days/40 days)). The P/B for salmon fry >6 cm, during their 70 day residence time in PWS, is calculated to be 8.666 $year^{-1}$ (1.662 · (365 days/70 days)). The biomass-weighted average of the two values (9.844 $year^{-1}$) is the P/B of the aggregated group (Table 20 and Table 21).

Salmon fry consumption rate was estimated based on smaller sized fry for which data are available. Consumption rate ranged from 4.5 to 31.5 percent body weight per day (Table 1 in Willette et al. 1996) for an average of 17.2 g. This corresponds to an estimate of Q/B = 62.8 $year^{-1}$. The range on this value is 16.4 to 115 $year^{-1}$.

There is a net export of fry < 6 cm (see, above). The import, i.e., negative export: -160 t, or -0.018 t km^{-2} . The export is 256 t, or 0.029 t km^{-2}. *Net* export is thus (256-160) t or 96 t, i.e., 0.011 t km^{-2}.

There is also a net export of fry > 6 cm. The import, i.e., negative export is -256 t, or -0.029 t km^{-2} . The export is 665 t, or 0.076 t km^{-2}. Net export is thus (665- 256) t, or 409 t. In areal units: 0.046 t km^{-2}.

Fry smaller than 6 cm are present in PWS for 30 days in May and ten days in June. Fry greater than 6 cm are present for 20 days in June, 30 days in July, and 20 days in August. Salmon fry are absent for all other months.

Table 19. *Diet composition (in %) of pink and chum salmon fry in PWS (1994-1996)*[a]

Prey Categories	Pinks	Chums	Means[b]
Small pelagic fishes	36.5	46.4	37.7
Herbivorous zoopl.	30.3	20.6	29.1
Omnivorous zoopl.	15.6	22.2	16.4
Shal. sm. epibenthos	16.4	10.6	15.7

a) Adapted from APEX-SEA data provided by M. Sturdevant (NMFS Alaska Fisheries Science Center);

b) Proportionally weighted means of Pink (0.878) and Chum (0.122) salmon.

Five-eighths of the salmon fry in PWS originate from hatcheries which biases their distribution into a corridor running from Port Valdez to the central north region as far as Esther Island then running south through Knight Island Pass. and around the east side of Knight Island. From here they are distributed southward and out of PWS into the Gulf of Alaska via the southwest passages (Figure 1). Within this area salmon orient themselves to land staying within the 20 m isobath. It is estimated that about 80% of the fry in PWS are found within this area while the balance are distributed more or less evenly in the remaining area, but within the 20 m isobath.

Table 21. Ecopath parameters for salmon fry < 6cm (P/B values not used in model parameterization).

Period	B (t·km^{-2})	B min	B max	P/B^{a} (year^{-1})	Export (t·km^{-2}·year^{-1})
May	0.020	0.018	0.021	--	-0.018
Jun	0.025	0.021	0.029	--	0.029
Mean	0.022	0.018	0.027	18.542	0.011

Diet compositions for pink and chum salmon fry in PWS from 1994-1996 are adapted from APEX-SEA data provided by M. Sturdevant (Table 19, Appendix 4). Since these two species make up 96% of the salmon in PWS, proportionally weighted averages of their diets represent a generalized salmon diet in PWS.

Adult Pacific Herring

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Pacific herring, *Clupea pallasi*, are schooling zooplanktivores that are usually found near the surface, but can occur at various depths and may disperse at night. Adults are defined as equal or greater than 18 cm in length; three year olds are considered adults by length and age distribution, but some do not mature until their fourth year. Herring can live up to 19 years in Alaska (Love 1996).

Most spawning occurs along the north shore of Montague Island at 0-15 m, but the confined spawn at Montague is only a shadow of its former self.

Over half the spawn was formerly in the northeast and north shore of PWS, and the population may now be rebuilding there, and on the east side (mainly Orca Inlet and Sheep Bay) of PWS (E. Brown, UAF Institute of Marine Sciences, pers. comm.). Large summer concentrations of adult herring have been found in SW passages, Esther Passage, Wells Bay and the outer (eastern) coast of Montague.

Adults are widely distributed in the upper 50-100 m, but not as widely as juveniles. Spring and mid-winter distributions are known, but not summer and early fall distributions. They may range offshore to shelf edge of the gulf of Alaska and beyond in summer for food and return in the fall. Substrate for spawning is kelp (over rocky bottom) and eelgrass (over sandy bottom) (E. Brown, R. Foy, and J. Wilcock, UAF Institute of Marine Sciences and Alaska Dept. of Fish and Game, pers. comm.).

Estimates of pre-fishery run herring biomass sharply declined in PWS four years after the EVOS (Figure 4; data include ages 3 and above).

The adult herring biomass estimate of 23,143 t in PWS, or 2.555 t·km^{-2}, is the mean of the estimates from the years 1994-1996 (Table 22). The three-year period of the model occurred after the sharp herring decline of 1993. biomass estimates were based on Age-Structured Assessment modelling (data provided by J. Wilcock, Alaska Dept. of Fish and

Table 22. Estimated Pre-Fishery Herring Run biomass in PWS (1994-1996)$^{a.}$

Year	Pre-fishery run biomass (t)	Biomass density (t·km^{-2})
1994	19.121	2.111
1995	23.933	2.642
1996	26.376	2.912
Mean	23.143	2.555

a) Data provided by J. Wilcock. Alaska Dept of Fish and Game, pers. comm.)

Game, pers. comm.).

The three fisheries sub-sectors that normally catch herring in PWS are spawn on kelp, sac roe by seine and gillnet, and food-and-bait by purse seine or trawl. These fisheries were closed in PWS during the three-year modelling period (1994-1996) except for a food-and-bait catch of 847 t in 1996 for a three-year mean of 282 t, or 0.031 t·km^{-2} (Morstad et al. 1997).

Given that, under equilibrium, F = catch/biomass, a fishing mortality (F) of 0.01 year^{-1} can be estimated from the above figures. Natural mortality (M) was estimated as 0.53 year^{-1}, as the means of age-specific estimates (age 3 to 8) for herring in the Gulf of Alaska (Wespestad and Fried 1983). Since P/B, under equilibrium, equals total mortality (Z; Allen 1971), and Z = F + M, the P/B ratio for herring can be estimated as 0.53 + 0.01 = 0.54 year^{-1}.

The value of Q/B used here, of 18 year^{-1}, is the same as that used for small pelagics (mainly herring) in the Strait of Georgia (Venier 1996a). The diet composition of adult herring was derived from 1994-1996 APEX-SEA data, provided by M. Sturdevant Table 24, Appendix 4).

The estimate for the annual fishery removal rate from 1994-1996 is 2.55 t·km^{-2}·year^{-1}. It was necessary to increase the Pacific herring P/B ratio from 0.54 year^{-1} to 1.54 year^{-1} to accommodate this larger fishery, and balance the model. This P/B value of 1.54 year^{-1} is realistic and justified based on recent information about north Atlantic herring populations (V. Christensen, Fisheries Centre, personal communication, July 1999).

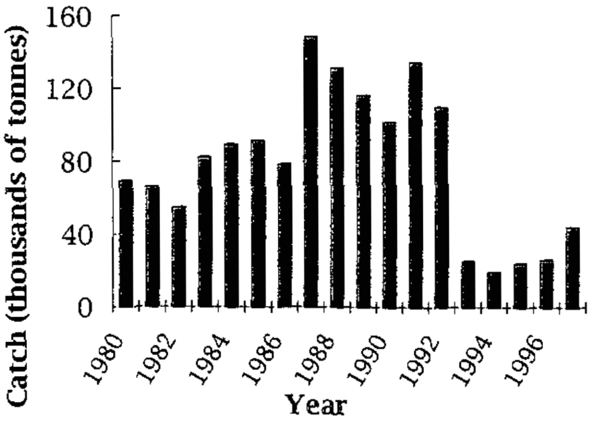

Figure 4. Catch history of herring in the PWS area (data provided by J. Wilcock, Alaska Dept. of Fish and Game).

Table 23. Forage fish biomass estimates for PWS, 1995-1997 (data from E. Brown, UAF Institute of Marine Sciences)[a].

Year	Biomass (t·km^{-2})[a,b]				
	Herring 0	Herring 1	Sandlance	Capelin	Eulachon
1995	1.693	1.664	0	0.163	0
1996	1.454	9.603	0.196	0.529	0
1997	18.968	0.537	1.590	0.000	3.343
Mean	7.372	3.935	0.595	0.231	1.114

a) Estimates are based on extrapolations from school surface area measurements from airplane surveys and based on empirically-derived assumptions about school packing densities and sub-surface biomass distributions relative to water clarity. Large uncertainties in these factors along with seasonal changes in relative abundance of species compound the uncertainty of these ballpark estimates (E. Brown, UAF Institute of Marine Sceinces, pers. comm.).

b) Estimates of total biomass (t) in PWS can be obtained by multiplying values by 9,059 km^2.

Juvenile Pacific Herring

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Juvenile Pacific Herring are defined as less than 18 cm in length; age zero to two year olds are considered juveniles. Like adults, juveniles are widely distributed in PWS.

Table 24. Diet composition (% weight) of herring from 1994-1996 samples[a].

Prey categories	% diet
Herbivorous zooplankton	59.2
Omnivorous zooplankton	32.6
Shallow small epifauna	8.2

a) Functional group composites of the mean proportions among years for each taxonomic group; from APEX-SEA data provided by M. Sturdevant (NMFS Alaska Fisheries Science Center).

Biomass estimates for herring age 0 (7.372 t·km^{-2}) and herring age 1 (3.935 t·kg^{-2}) in PWS were developed by E. Brown (unpublished data) using areal survey information, with the explicit caveat that these estimates contain considerable uncertainty. The biomass estimate for Juvenile pacific herring (13.387 t·km^{-2}; including age 2 herring) was then calculated by applying the age 0-1 ratio of biomass (0.54) to age one herring to acquire an extrapolated age 2 biomass estimate of 2.125 t·kg^{-2}. The biomass estimates for each of the three juvenile age classes were then summed. See Table 23 for the PWS biomass estimates of several forage fish categories. The P/B of 0.54 year^{-1} and the Q/B of 18 year^{-1} are taken directly from the adult Pacific herring group.

Arrhenius and Hansson (1993) revealed bimodal distributions for Baltic Sea herring populations (*Clupea harengus*) at ages zero and four with age zero at almost twice the biomass of age four. The overall ratio of juveniles to adults among eight herring stocks was 0.805, which leads to a juvenile herring estimate of 2.056 t·km^{-2} in PWS when applied to the estimate of adult herring biomass (2.555 t·km^{-2}). Interestingly, this estimate is 85% lower than the empirically-based estimate used for PWS (above). The higher (empirically based) estimate is supported by the apparent need for forage fish by the predator biomass in the PWS model.

To calculate diet composition, juvenile herring were sampled from the heads of four bays in PWS from October 1995 to September 1997 as part of the EVOS Trustee Council sponsored SEA program. Data missing from unsampled months were interpolated. Fish stomachs were processed at the Institute of Marine Science at the University of Alaska Fairbanks. Prey was identified to the lowest possible taxonomic grouping. Relative proportions of prey groups (nearshore zooplankton) were determined for each fish and pooled for monthly means (Table 25, Appendix 3).

Sandlance

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Sandlance, *Ammodytes hexapterus*, are schooling zooplanktivores, which burrow into the sand at night. They are found from the intertidal to about 90 m depth and possibly as deep as 275 m. Sandlance are most commonly seen during spring and summer, and may stay buried in the sediment during fall and winter (Love 1996).

Estimates of PWS sandlance biomass from 1995 through 1997 have been provided by E. Brown (unpublished data). These estimates are presented in Table 23.

A P/B value of 2 year^{-1} and a Q/B value of 18 year^{-1} for sandlance are taken from Venier (1996a) for small pelagics in the Strait of

Table 25. Diet composition (% weight) of juvenile herring from 1995-1997[a]

Taxonomic Group	% of diet
Herbivorous zooplankton	56.2
Omnivorous zooplankton	41.9
Fish egg	1.9

a) Means of monthly proportions for each taxonomic group; provided by R. Foy and SEA program.

Table 26. Diet composition of capelin from 1994-1996 samples[a]

Prey categories	% in diet
Herbivorous zooplankton	0.550
Omnivorous zooplankton	0.416
Shallow small epifauna	0.034

a) functional group composites of the mean proportions among sampling dates for each taxonomic group; summarized from APEX-SEA data provided by M. Sturdevant

Table 27. Diet composition (% weight) of sandlance from 1994-1996 samples[a]

Prey categories	% in diet
Herbivorous zooplankton	72.7
Omnivorous zooplankton	21.0
Shallow small epifauna	6.2

a) functional group composites of the mean proportions among sampling dates for each taxonomic group; summarized from APEX-SEA data provided by M. Sturdevant (NMFS.

Georgia. Sandlance diet composition was summarized from APEX-SEA data provided by M. Sturdevant (Table 27, Appendix 4).

Capelin

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Capelin, *Mallotus villosus,* is a schooling zooplanktivore that spawns in the intertidal during summer, and which was an historically important food for numerous fishes, birds, and mammals because of its high energy content. However, capelin have become much less abundant since the oceanographic warming shift of the mid-1970s.

Estimates of capelin biomass in PWS for 1995 through 1997 (Table 23) are ballpark estimates, and should be treated as such.

Estimates of 2 year^{-1} for P/B and 18 year^{-1} for Q/B are taken from Venier's (1996a) section on small pelagics in the Strait of Georgia; Table 26 summarizes the diet composition of capelin.

Eulachon

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Eulachon, *Thaleichthys pacificus,* are pelagic schooling smelts that live on the outer continental margin and spawn in fresh water (Love 1996). This species is a reproductive transient in PWS, spending only a brief time as they converge on spawning streams.

A mean peak biomass estimate of 1.114 t·km^{-2} was provided by E. Brown for the years 1995-1997 (Table 23). Eulachon did not appear in areal samples in 1995 and 1996, but they appeared in large numbers in 1997 (3.343 t·km^{-2}). The value entered for biomass, however, is 0.371 t·km^{-2} (1/3 of 1.114 t·km^{-2}), to adjust P/B and Q/B to a short PWS residency time.

Values of 2 year^{-1} for P/B and 18 year^{-1} for Q/B, used by Venier (1996a) for small pelagics in the Strait of Georgia are also used for eulachon. The diet composition of eulachon is adapted from the mean of each taxonomic group from two APEX-SEA sampling dates provided by M. Sturdevant (NMFS, Alaska Fisheries Science Center, pers. comm.; Table 29, Appendix 4). Fifty percent of the eulachon diet is specified as imported food, assuming that half their food comes from outside PWS, even considering the above residency time adjustment.

A whole suite of predators feed on eulachon but the extent of this consumption is difficult to estimate due to the ephemeral nature of this species in PWS and the temporal nature of the feeding frenzies that occur when these smelts run. Predators include Pacific cod, sablefish, salmon sharks, spiny dogfish, Pacific halibut, arrowtooth flounder, salmon, baleen whales, orcas, dolphins, pinnipeds, and birds. Indeed, much of the food web partakes directly or indirectly when these summer events occur (E. Brown, UAF Institute of Marine Sciences, pers. comm.; Love 1996). There is some likelihood that overall consumption of eulachon is underestimated in the model.

Squid

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An acoustic/trawl survey was conducted from 23-27 January 1997 in the six areas listed below. Echo-square integration of 120kHz sonar signals was used to determine pollock abundance (Table 28). Trawls were used to determine the squid to pollock ratio (estimation of squid to pollock ratios is problematic because the mesh on the net is 4 inches, through which squid may possibly escape, and because the trawls were fished deep (125-215 meters), below the typical nighttime shallow depth distribution of squid. The product of the number of pollock and the squid/pollock ratio is the predicted numerical abundance of squid, which is believed to be an underestimate due to sampling bias. Adult PWS squid typically weigh 0.5 kg, although squid were not weighed during this survey. The estimate of 170 t of squid in PWS was converted to 0.019 $t \cdot km^{-2}$ by dividing by 9,059 km^2.

The P/B and Q/B values used for squid were taken from the Alaska Gyre model (Christensen 1996); these were 3.0 $year^{-1}$ and 15.0 $year^{-1}$ respectively. Diet composition information is adapted from indices of relative importance in prey composition of *Loligo opalescens* in Karpov and Cailliet (1978). These are shown in Table 30.

Table 29. Diet composition (% weight) of eulachon in PWS, from 1994-1995 samples[a]

Prey Categories	% in diet
Omnivorous Zooplankton	99.4
Herbivorous Zooplankton	0.3
Shallow Sm. Epifauna	0.2

a) Functional group composites of the mean proportions among sampling dates for each taxonomic group: summarized from APEX-SEA data provided by M. Sturdevant (NMFS, Alaska Fisheries Science Center, pers. comm.).

LARGER FISHES

Walleye Pollock

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Walleye pollock (*Theragra chalcogramma*) spawn in southwest PWS and in Port Bainbridge during late March. In early June, age-0 pollock (< 15 cm length) typically appear in surface layer net samples in both offshore and nearshore habitats (Willette et al. 1995a, 1996, 1997), where they continue to be found into early September (Willette 1995b). Age 0 pollock appear to be ubiquitous in the upper 50 m of PWS waters, and they are also associated with aggregations of moon jellies (*Aurelia aurita*). Age 1-2 pollock (15 to 30 cm in length) are typically segregated from the adult population during summer when they are

Table 28. Squid caught from PWS Pollock surveys. Squid value is thought to be an underestimate for Prince William Sound.

Area	No. of Pollock (10^6)[a]	squid/pollock ratio in trawls	Estimated number of squid[b]
South Montague Strait	1.423	0.012	17076
Lower Knight Is Pass	13.369	0.012	160428
Port Bainbridge	7.881	0.091	721
North Montague Strait	3.862	0.012	46344
Green Island	0.304	0.103	31178
Orca Bay	1.492	0.056	83925
Total numbers	28.331	--	339492
			@ ~0.5kg each
Biomass			~170 t

a) Pollock estimates from acoustic data
b) assumed to be an underestimate, due to escapement from trawl.

Table 30. Assigned diet composition (% weight) of PWS squids, modified from diet of *Loligo opalescens* in Monterey Bay (Karpov and Cailliet 1978).

Prey Categories	% in diet
Off. omni. zoo	96.6
Off. herbi. zoo	1.5
Deep epifau.	0.4
Squid	0.3
Near omni. zoo	0.3
Eulachon	0.2
Shal. sm. epifau.	0.2
Shal. sm. infau.	0.2
Capelin	0.1
Pollock age 0	0.1
Near herbi. zoo	0.1

Table 31. Population parameters for walleye pollock in Prince William Sound.

Pollock ages	Biomass ($t \cdot km^{-2}$)	min/ max	Catch (t)	P/B ($year^{-1}$)	min/ max	Q/B ($year^{-1}$)	min/ max
Age 0	0.02	0.01-0.05	0	1.28[a]	0.45-2.34	16.18	12.76-21.97
Age 1-2	0.79	0.39-1.55	0	1.84[a]	0.90-3.23	3.81	2.01-5.71
Age 3+	2.20	1.08-4.32	2100[b]	0.30[c]	--	2.11	0.41-3.81
Age 1+[d]	2.99	--	--	0.707	--	2.559	--

a) From Bailey et al. (1996);
b) From B. Bechtol (Alaska Dept. of Fish and Game, pers. comm.);
c) From Hollowed et al. (1993);
d) Aggregated from the two previous groups; P/B and Q/B values are means weighted by the biomass proportions of those two groups.

commonly encountered in nearshore net samples (Willette et al. 1995a, 1996, 1997). Schools of these age 1-2 pollock migrate through relatively shallow depths (20 – 50m) on the slope outside kelp; they are rarely caught in offshore trawls

Adult pollock (age 3+) are greater than 30 cm in length and are commonly captured in surface layer (0-50 m) trawl samples in the offshore areas of the western passages in PWS during May-June (Figure 1) where they feed heavily of the copepod *Neocalanus* spp. (Willette et al. 1995a, 1996, 1997). After the decline of the seasonal bloom of *Neocalanus* spp., they descend to deeper habitats where they reside for the remainder of the year. During this period, they are distributed throughout PWS, but the biomass is concentrated in the southwest Sound (NMFS 1993). The majority of the adult biomass during summer is found at depths between 100 and 400m (NMFS 1993).

The total biomass of age 3+ pollock residing in PWS (Table 31) was estimated from the product of the area of the Sound and the mean density of pollock measured during acoustic surveys conducted in western PWS during May-July, 1994 (J. Kirsch, Prince William Sound Science Center, pers. comm.). The minimum biomass of age 3+ pollock was assumed to be that obtained from a bottom trawl survey conducted during summer in 1989 (NMFS 1993). Bottom trawls likely provide a minimum biomass estimate, because some portion of the pollock stock occurs above the bottom where they are not vulnerable to this gear type. The maximum biomass of age 3+ pollock residing in PWS was estimated to be that obtained from acoustic surveys of prespawning aggregations in southwest PWS (Thomas and Stables 1995, Kirsch 1997). It is unknown what portion of the spawning biomass in southwest PWS resides in the Sound throughout the remainder of the year. The biomass of age 0 and age 1-2 pollock was es-

Table 32. Summer diet composition matrix (in % of volume) for walleye pollock in PWS.

Prey\ Predators	Age 0	Age 1-2			Age 3+	Age 1+[a]
		pelagic	demersal	composite		
Herbivorous zooplankton	72.2	37.9	53.3	45.7	0.8	7.6
Omnivorous zooplankton	17.4	10.3	16.8	13.6	38.8	35.0
Carnivorous zooplankton	10.0	--	--	--	--	--
Deep large epibenthic invertebrates	--	1.8	1.4	1.6	33.0	28.2
Shallow large epibenthic inverts.	--	34.2	22.5	28.4	7.0	10.3
Capelin	--	0.2	--	0.1	12.9	11.0
Juvenile herring	--	0.2	0.4	0.3	0.2	0.2
Pollock age-0	--	1.7	0.2	0.95	--	0.1
Pollock age 1-2	--	--	--	--	2.0	1.7
Juvenile salmon	--	3.6	0.3	2.0	--	0.3
Squid	--	0.3	1.8	1.1	2.6	2.4
Nearshore pelagic fish	--	9.8	--	4.9	--	0.7
Offshore small pelagic fish	--	--	3.3	1.7	2.7	2.5

a) Age 1+ diet composition values are means of the age 1-2 composite and the Age 3+ values, based on the biomass proportion of each group (0.152 and 0.848)

Table 35. Density (No.·km^{-2}) of nearshore fishes by habitat, western Prince William Sound. Fish groups and habitats are as defined in Laur and Haldorson (1996).

Taxon\Habitat	Bays	Eelgrass	*Nereocystis*	Points[a]
Adult cod	0	210	0	0
Juvenile cod	940	5,540	1,390	2,550
Sculpins	1,050	110	270	3,040
Gunnels	370	560	10	270
Arctic Shanny	2,030	250	40	5,260
Greenlings	50	610	840	450
Ronquils	90	0	20	770
Other	70	30	330	090

a. Points are projections of land that define bays

timated from a simple population model assuming the mean age-specific natural mortality rates used to develop the P/B values in Table 31. Annual food consumption (Q/B) was estimated from the annual growth rate of age 0, age 1-2, and age 3+ pollock assuming a gross conversion efficiency of 25% (Paul et al. 1988). Annual growth was estimated from mean weight at age of pollock sampled in PWS during May-July, 1994 (Willette et al. 1995a). Mean diet composition of pollock during summer (Table 32) was estimated from samples collected during May-July, 1994 (Willette et al. 1995a, 1995b, 1996, 1997).

Age 1-2 and age 3+ pollock groups had to be aggregated in the Ecopath model because the Ecosim routine can link only two ontogenetic stages of a species. These two groups exhibit similar diet composition and probably similar growth rates (relative to the age 0 group). Nevertheless, the age 1-2 fish appear to consume more juvenile fish during summer, whereas the age 3+ fish probably cannibalize age 1-2 fish in winter. Despite these differences, age 0 and age 1-2 groups should not be aggregated, because the age 0 fish are so much smaller and are not predators on other juvenile fish. Perhaps the greatest problem in aggregating the age 1-2 with the age 3+ fish is the cannibalism of the older fish on the younger fish. This may be an important factor in pollock recruitment.

Nearshore Demersal Fishes

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Nearshore demersal fishes are defined as fishes occurring along the shoreline to depths of 20 m and generally found within close association with the bottom. Within Prince William Sound nearshore demersals include greenling, sculpins, arctic shanny, gunnels, ronquils, Pacific cod, tomcod, and others (Rosenthal 1983, Laur and Haldorson 1996). Some rockfish are also considered nearshore demersals, but are treated here as a separate group. Laur and Haldorson (1996) estimated densities of demersal fishes in the Sound in 1990 following the EVOS (Table 35). Diver surveys were conducted in 4 habitats characterized by different vegetation types and exposures: Eelgrass beds in bays, *Laminaria* and *Agarum* beds in bays and more exposed points, and *Nereocystis* beds on very exposed sites in the Sound, especially near the entrances to the Gulf of Alaska. Divers classified fishes in broad size classes (e.g., small and large sculpins) and there were no estimates of length or

Table 33. Mean biomass per fish (kg wet weight) for nearshore fish in western Prince Sound[a].

Taxon	Mean weight (kg)
Adult cod	0.250
Juv. cod	0.005
Sculpins	0.075
Pholids	0.010
Stichaeids	0.010
Greenling	0.200
Ronquils	0.100
Others	0.020

a Estimates were derived from average lengths of fish within each group, and length-weight relationships given in Rosenthal (1983) and Van Pelt et al. (1997). Counts were based on visual estimates from diver observations (T.A. Dean, pers. obs.).

Table 34. Biomass (t·ww·km^{-2}) of nearshore demersal fishes by habitat in western Prince William Sound

Nearshore demersals	Bay	Eelgrass	*Nereocystis*	Points[a]
Adult cod	0.00	5.25	0.00	0.00
Juv. cod	0.47	2.77	0.70	1.28
Sculpins	7.88	0.83	2.03	22.80
Pholids	0.37	0.56	0.01	0.27
Stichaeids	2.03	0.25	0.04	5.26
Greenling	1.00	12.20	16.80	9.00
Ronquils	0.90	0.00	2.00	7.70
Others	0.14	0.06	0.66	0.18
Total	12.79	21.92	22.24	46.49

a. Points are projections of land that define bays

Table 36. Annual landings of salmon in PWS from 1994 to 1996 (commercial and subsistence).

Species	Catch[a] ($N \cdot 10^3$)	Mean weight (kg)[b]	Catch (t)
Pink	26319	1.6	42110
Chum	1273	3.9	4965
Sockeye	390	2.8	1093
Coho	145	4.0	579
Chinook	1	11.2	13
Total	28128	(1.8)	48670

a) Mean landings in PWS from 1994 to 1996, (based on Morstad et al. 1997, Appendices E.2);

b) Weighted means for 1996 (based on Morstad et al. 1997, Appendix A.5).

biomass. We provide rough estimates of biomass based on our estimation of mean length of fish (T.A. Dean, pers. obs., Table 33) and size-weight relationships given in Rosenthal (1983) and Van Pelt et al. (1997).

Species composition varied with habitat and depth, but in all habitats the dominant nearshore demersal fishes (by weight) were greenlings and sculpins (Table 33 and Table 34). The mean biomass density within the different habitats ranged from 12 to 46 t ww km^{-2} (Table 34). On a PWS wide basis, the total biomass of nearshore demersal fishes was 4.2 t ww km^{-2}.

There are no data for P/B or Q/B ratios for nearshore demersal fish in PWS. Based on values for demersal fishes of the Strait of Georgia, Canada, we estimate that the P/B ratio is 1 $year^{-1}$, and the Q/B ratio is 4.24 $year^{-1}$. Of the nearshore demersal fishes, only cod are caught in significant numbers by fishers. Since all of these are taken from segments of the cod population that are deeper than 20 m, we consider there to be no nearshore catches. Many smaller fishes are prey to birds (e.g., pigeon guillemots) and larger individuals are prey to river otters (Bowyer et al. 1994). There is also predation by marine mammals and other fish.

The diets of the fish vary among species (McConnaughey 1978; Rosenthal 1983, Laur and Haldorson 1995). Most of the diet consists of small invertebrates. There are no quantitative data on diet compositions, but based on general descriptions of diets and relative proportions, we estimate that nearshore demersal fishes consume approximately 70% small epifauna (mostly amphipods), 22% large epifauna (mostly crabs), 4% nearshore demersal fish, 2% herbivorous zooplankton, 1% shallow small infauna (mostly polychaetes), and 1% sandlance.

Adult Salmon

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Adult salmon occur in PWS from June through September as they return from the open sea to their spawning grounds, but a given individual salmon transits the sound in only a few weeks. A residence time of one (1) month was chosen as a reasonable estimate for adult salmon in PWS, considering all species occurring there (L. Huato, UBC Fisheries Centre, pers. comm.). Table 36 shows the average landings of salmon in the sound from 1994 to 1996.

The average catch of salmon in PWS for the period 1994-1996 is calculated as 5.373 $t \cdot km^{-2}$ by dividing the estimated annual catch (Table 36) by the total area of PWS (9,059 km^2).

Table 37 presents minimum estimates of the mean biomass of hatchery and wild pink and chum salmon in PWS from 1994 to 1996, based on wild stock escapement (minimum estimates), hatchery returns, and catches.

Run biomass estimates for the three other salmon species in PWS could not be found. However, pink salmon is the dominant species, contributing about 87% of the catch (in weight), while chum contributes about 10% (from Table 36). Run biomass estimates for the remaining 3% of PWS adult salmon—1359 t of sockeye, 720 t of coho, and 16 t of chinook—were made using a biomass/catch ratio of 1.24 derived from pink and chum ratios shown in Table 36 and Table 37. Summing the estimates for each species gives a mean estimate for PWS salmon runs (wild and hatchery) including catches from 1994 to 1996 of 56,174 t, or 6.201 $t\cdot km^{-2}\cdot year^{-1}$. The annual biomass estimate of 0.517 $t\cdot km^{-2}$ was then calculated by dividing this peak estimate by 12, assuming that a given individual salmon has a PWS residence time of one month.

However, this method underestimates salmon in PWS because of observer inefficiency when developing escapement indices. Moreover, run biomass estimates are only a portion of total population biomass in PWS because they do not account for predation on salmon while transiting PWS toward spawning streams. For these reasons, the 1994-1996 run estimate was doubled to arrive at an adult peak salmon biomass estimate of 12.402 $t\cdot km^{-2}$ and a corresponding annual biomass estimate of 1.034 $t\cdot km^{-2}$, used as the entered value. This corrected, one twelfth (1/12) adult salmon biomass estimate was entered in the biomass category while the remaining 11/12 was entered in the immigration column, and 75% of that value was entered as export (the alternative is that the difference is entered as net import).

The adult salmon group poses a difficult problem for the Ecopath model since they are summer transients and feed little while in PWS, if at all. Moreover, their transient nature inhibits useful and accurate calculation of P/B and Q/B values for their within-PWS adult stage. However, instantaneous mortality rates across all life stages have been calculated by Bradford (1995), and his PWS-weighted mean of 6.476 $year^{-1}$ can be used for an adult salmon P/B (see Table 38), even though it is unlikely that P/B is evenly distributed throughout the life cycle.

A Q/B value of 12 $year^{-1}$ applies to pink salmon in the Alaska gyre (L. Huato, UBC Fisheries Centre, pers. comm.; Table 10 in Christensen 1996), and is used for the adult salmon group. The annual Q/B and P/B values may not relate to the role of adult salmon during their spawning stage, but this does not affect the other components of the model (excepting a few that eat adult salmon) because 100% of the food of PWS adult salmon is assigned as import representing the imported secondary production from the Alaska gyre in the form of salmon growth during that ontogenetic stage.

Table 38. Total mortality (Z) for five species of salmon in PWS[a].

Species	Proportions of biomass caught	Total mortality (Z; $year^{-1}$)
Pink	0.865	6.33
Chum	0.102	7.59
Sockeye	0.022	6.55
Coho	0.012	6.40
Chinook	0.000	6.76
Weighted mean[b]	--	6.48

a) From Bradford (1995);
b) Weighted by the catch proportions.

Adult salmon are mostly eaten by resident

Table 37. Mean hatchery and wild pink and chum adult salmon runs in PWS, 1994-1996.

Stock	Estimated pop. ($N\cdot10^3$)[a]	Adjusted pop. ($N\cdot10^3$)[b]	Mean weight (kg)[c]	Biomass of run (t)	Biomass/ catch
Pink	28987	29571	1.6	47314	1.124
Chum	1658	1735	3.9	6765	1.363

a) Based on Morstad et al. (1997, Appendices E.5 and E.9);
b) Adjusted to account for 30% of *wild stock escapement into non-index streams* (B. Bue, Alaska Dept. of Fish and Game, pers. comm.);
c) Weighted means in 1996 (based on Morstad et al. 1997, Appendix A.5).

orcas and eagles (bears are not in the model since most bear feeding occurs in rivers, outside the PWS system as defined here). Salmon that successfully spawn and die before being consumed are considered to become 'nekton falls' (one of the three detritus categories) upon dying, but only a portion of the carcasses of the successful spawners make it back to the PWS system to become 'nekton falls' (the PWS system extends to the upper intertidal, but not up rivers). Most of the unused portions of the 'nekton falls' detritus become inshore detritus, the unused portion of which becomes offshore detritus, which can ultimately be exported from the system.

Adult salmon probably eat very little in PWS as they return to spawning grounds. This is reflected in the Ecopath model by giving them 99% 'imported' food (in the diet composition). The remaining 1% of their food is assigned to herring, sandlance, eulachon, and capelin to achieve a realistic trophic ranking for salmon.

Rockfishes

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Rockfishes, family Scorpaenidae, include over 100 species worldwide including 64 from the northeast Pacific Ocean (Orr et al. 1992). The vast majority of Rockfishes are in the genus *Sebastes*, and are demersal groundfish (often in rocky bottom habitats), but some are classified as pelagic, as they are found in mid-water or near kelp canopies. Rockfishes occupy a variety of niches, but they are presented as an aggregated group in this model.

The total annual rockfish biomass estimate of 0.254 t·km^{-2} in PWS was derived by multiplying the mean PWS landings from 1994 to 1996 by the mean biomass/commercial landings ratio from the greater Gulf of Alaska management region for that time period (Table 39). The accuracy of this biomass estimate is questionable because recreational landings of pelagic and demersal rockfishes in PWS often exceeded commercial landings during the period in question (See below).

Estimates of rockfish P/B (0.17 year^{-1}) and Q/B (3.44 year^{-1}) were taken from Dalsgaard et al. (1998). A generalized diet composition for rockfish was derived by adapting information in Yang (1993) for six species of commercially important rockfish that occur in PWS and from Rosenthal et al. (1980) for two other PWS rockfish species. The diet of a 'composite' rockfish was derived by taking the average of each prey category and using these values as diet proportions (Table 40). Weighted means among species were not used because ratios of estimated exploitable biomasses among species in the Gulf of Alaska were not expected to relate directly to the relative densities of these species in PWS. Furthermore, the resulting diet composition for rockfish is skewed towards those of the commercially important slope and shelf rockfishes and away from other rockfishes such as those that occur in more shallow habitats, or recreationally important species.

Table 39. Biomass estimates for PWS rockfish for 1994-1996.

Year	Biomass /landings[a] (t/(t·year^{-1})	PWS landings (t·year^{-1})[b]	Estimated PWS Biomass (t)	Estimated PWS Biomass (t·km^{-2})
Slope means	31.4	30.571	960.9	0.106
1994	36.6	25.897	947.8	
1995	27.2	42.881	1166.4	
1996	30.5	22.207	677.3	
Pelagic means	23.2	9.027	209.3	0.023
1994	25.6	7.995	204.7	
1995	19.4	12.707	246.5	
1996	24.5	6.165	151.0	
Demersal means	78.9	14.375	1134.6	0.125
1994	77.9	10.032	781.5	
1995	61.3	13.512	828.3	
1996	97.6	19.240	1877.8	
Grand Totals	44.5	53.973	2304.8	0.254

a) Biomass/landings ratios pertain to exploitable biomass and commercial landings in the Gulf of Alaska management region (from NPFMC 1995 and 1997);

b) Commercial landings information from B. Bechtol (unpublished data).

A total landings estimate of total rockfishes in PWS from 1994-1996 (89.255 t, or 0.010 t·km^{-2}) is the sum of commercial landings (Table 39, Table 43) and recreational landings (Table 75).

Parameterization of PWS Rockfish (*Sebastes*) indicates that this composite group is declining in PWS, though this indication is based on limited information. A immigration term of (-0.14 t·km^{-2}·year^{-1}) was used to artificially balance this group by adding immigrating adults to the population every year. This term was added to the migration of rockfish in contrast to our default assumption that the 'composit' rockfish in PWS has no net migration. This 'trick' was used to balance the rockfish group because there was no justification for increasing the given biomass and P/B values, though they contained uncertainty, and be-

Table 40. Diet compositions (*in % weight*) *of rockfish species in* PWS[a]

Prey Group	POP	Rougheye	Northern	Dusky	s-spine TH	Shortraker	China	Black	Mean
Omnivorous Zooplankton	89.7	6.0	96.6	72.3	0.7	--	--	56.7	40.3
Deep epifauna	6.0	65.7	0.2	7.8	80.3	--	70.0	0.2	28.8
Squid	8	20.0	0.3	6.2	0.7	82.0	--	--	13.8
Shallow small epifauna	--	--	--	--	--	--	15.0	7.2	2.8
Deep demersals	1.9	6.9	0.4	--	15.5	--	--	--	3.1
Myctophids	--	--	--	--	--	18.0	--	--	2.3
Herbivorous Zooplankton	1.7	--	2.5	13.7	--	--	--	1.0	2.4
Sandlance	--	--	--	--	--	--	--	32.8	4.1
Shallow large epifauna	--	--	--	--	--	--	15.0	0.2	1.9
Deep Infauna	--	1.4	--	--	1.2	--	--	--	0.3
Nearshore demersals	--	--	--	--	--	--	--	1.4	0.2
Age 0 pollock	--	--	--	--	0.9	--	--	--	0.1
Capelin	--	--	--	--	0.7	--	--	--	0.1
Herring	--	--	--	--	--	--	--	0.5	0.1

a) Diet compositions for China and Black rockfishes were adapted from prey indices in Rosenthal et al. (1988). Diet compositions for all other species are from Yang (1993).

cause a 'balanced' model, without explicit declines, is convenient for exploring trophic relationships. The other alternative is to add a negative biomass accumulation term to explicitly display the indicated declines in biomass for this composite group. The upshot of this balancing 'trick' is that the negative biomass accumulation value ($-0.14\ t\cdot km^{-2}\cdot year^{-1}$) represents rockfish decline at that rate.

Nearshore Rockfish

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Diver surveys in the nearshore (less than 20 m) in 1990, 1996, and 1997 found few rockfish in this zone (T. Dean and S. Jewett, unpublished data). Only juvenile copper rockfish were at all abundant. Densities (No. per 100 sq. m) in various habitats are shown in Table 42.

Our estimates are probably low for *Nereocystis* since we sampled only at relatively shallow depths there (less than 10 m) and most rockfish are deeper. Our data suggest that rockfish make up a very small proportion of the biomass of nearshore benthic fishes.

Rosenthal (1980) indicated that rockfish can be very abundant. However, most of his data were from *Nereocystis* beds on the outer margins of the Sound (Danger Island, Schooner Rocks, Zaikof Point). These are sites on the margin, or in some cases excluded from our current PWS boundary definition. These are very special habitats and not very well represented within the Sound proper. (We estimate

Table 42. Densities of juvenile copper rockfish in different PWS habitats.

Habitat	No.·km^{-2}
Eelgrass beds	0.002
Bays	0.004
Points	0.079
Nereocystis	0.027

Table 41. Estimated biomass of demersal fish species in PWS, 1989[a].

Species	Biomass (t)
Fishes	
Walleye Pollock	7140
Pacific Cod	2040
Sablefish	1470
Arrowtooth Flounder	19300
Flathead sole	3000
Rex sole	1510
Skates	3402
Halibut	1880
Rougheye Rockfish	844
Invertebrates	
Shrimp	101
Tanner Crab	2200

a) NMFS (1993)

that *Nereocystis* habitat makes up less than 1 % of total nearshore habitat). While Rosenthal found rockfish at depths less than 20 m in these habitats, they were more abundant in deeper waters.

According to Love (1996), copper rockfish eat plankton, and adults eat octopods, shrimps, crabs, and small fishes. This is similar to the diets of some of the commercially-important species used to generate the diet composition of a generalized rockfish (see previous section).

Miscellaneous Demersal Fishes

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Biomass information was limited for some species of explicitly defined fishes. Two methods were used to derive preliminary estimates of biomass: (1) the mean PWS landings for a particular species from 1994 to 1996 was multiplied by the mean biomass/landings ratio from the greater Gulf of Alaska management region for that period, (2) biomass estimates from a 1989 multispecies trawl survey (post spill) were extracted from appropriate areas and used as a proxy for 1994-1996 estimates or for comparison to the results of method (1). These estimates are shown in Table 41 and Table 43, and in the following sub-sections. P/B and Q/B values taken from other models are shown in Table 44.

Table 43. Reported PWS commercial landings (unpublished data provided by B. Bechtol, Alaska Dept. of Fish and Game).

Group	Landings (t)			
	1994	1995	1996	Mean
Lingcod	4.662	1.298	2.962	2.998
Pacific Cod	752.184	708.362	307.863	594.185
Sablefish	126.249	254.295	116.045	166.854
Pollock	2.570	2947.865	1659.676	1548.997
Flounders	0	1.584	11.156	4.281
Skates	0	1.072	7.120	2.753
Sharks (all)	0	0.158	9.014	3.081
Rockfish	43.924	69.100	47.612	53.974
Pelagic	7.995	12.707	6.165	9.027
Demersal	10.032	13.512	19.240	14.375
Slope	25.897	42.881	22.207	30.571

Table 44. P/B and Q/B values from other Ecopath models

Group	P/B (year^{-1})	Q/B (year^{-1})
Pacific Cod	1.200[a]	4.000[a]
Sablefish	0.566[a]	6.420[a]
Lingcod	0.580[b]	3.300[b]
Other Flounders	0.775[b]	3.210[b]
All Rockfish	0.170[b]	3.440[b]

a) from Livingston (1996), for the Bering Sea ecosystem;
b) Dalsgaard et al. (1998), for the Strait of Georgia ecosystem.

Deep Demersals (skates and flatfishes)

For the purposes of this deep-demersal group, flatfishes include flathead sole and rex sole, and skates include big skate, Aleutian skate, and Alaska skate. The biomass estimate of 0.873 $\mathrm{t \cdot km^{-2}}$ is based on the sum of post-spill 1989 biomass estimates of these flatfishes and skates listed in Table 41 above (from NMFS 1993). Biomass/landings ratios from the Gulf of Alaska region were not used to convert landings to biomass in this case because catches of this group were increasing during this period. For example, the commercial fishery landings in PWS for flounders and skates increased from zero in 1994 to 18.3 t, or 0.002 $\mathrm{t \cdot km^{-2}}$, in 1996.

Estimates of P/B (0.775 year^{-1}) and Q/B (3.21 year^{-1}) were calculated by taking the mean of the flatfish estimates in Dalsgaard et al. (1998). Diet composition values were estimated from considerations in Love (1996).

Pacific Cod

Pacific cod (*Gadus macrocephalus*) is a schooling species found near soft or gravel bottoms mostly between 45 m and 275 m. They spawn in deeper water, but move shallow to feed during late spring and summer, particularly the juveniles (Love 1996).

The Pacific cod biomass estimate of 0.555 $\mathrm{t \cdot km^{-2}}$ in PWS was derived by multiplying the mean PWS landings from 1994 to 1996 by the mean exploitable biomass/landings ratio of Pacific cod from the greater Gulf of Alaska management region for that time period (Table 45). This estimate is 247%

Table 45. Biomass estimates for PWS Pacific cod for 1994-1996.

Year	Biomass/ landings[a]	PWS landings[b]	Estimated PWS biomass (t)	Estimated PWS biomass ($t \cdot km^{-2}$)
1994	6.231	752.184	4686.859	0.517
1995	8.417	708.362	5962.283	0.658
1996	10.726	307.863	3302.139	0.365
Mean	8.458	594.185	5025.617	0.555

a) Biomass/landings ratios apply to the Gulf of Alaska management region and are derived from NPFMC (1995 and 1997);
b) Landings information from B. Bechtol (unpublished data).

greater than the 0.225 $t \cdot km^{-2}$ estimate adapted from the 1989 post-spill PWS multispecies trawl survey data (NMFS 1993). Nevertheless, 0.555 $t \cdot km^{-2}$ could well be an underestimate since the estimation method does not account for pre-recruits.

A P/B value of (1.2 $year^{-1}$) and a Q/B value of (4.0 $year^{-1}$) were taken from Livingston (1996) estimates for the southern BC shelf model. Diet composition information in Table 46 was adapted from Yang (1993). Shallow and deep prey allocations were made by an assumed 25% feeding in areas shallower than 20 m. Note that 12.5% of the prey of Pacific cod is fishery discards. This prey item was added to the Pacific cod diet as an import (see Sablefish discussion).

Lingcod

Lingcod, *Ophiodon elongatus,* are large predatory greenlings (Hexagrammidae) that live mostly on or near the bottom in relatively shallow water feeding on fishes, squids, and octopods, or guarding large egg masses if male. Lingcod, like rockfish discussed above, have both commercial and recreational importance in PWS. Explicit identification of these groups in the model may help provide insights into the impacts of changing exploitation levels as user demographics change in the future.

The mean recreational landings of lingcod in PWS between 1994 and 1996 was 20.6 $t \cdot year^{-1}$ Adding this to the mean commercial landings of 3 t during the same period gives an annual fishery extracted biomass of 23.6 t (0.003 $t \cdot km^{-2}$). Application of a conservative biomass/catch ratio, like that for Pacific cod (8.5), results in preliminary lingcod biomass estimate of 200.6 t in PWS, or 0.022 $t \cdot km^{-2}$. The resulting lingcod estimate may not be realistic as the actual lingcod biomass/landings ratio is likely different than that of Pacific cod. A PWS biomass of 0.022 $t \cdot km^{-2}$ is probably an underestimate for lingcod.

Estimates of lingcod P/B (0.58 $year^{-1}$) and Q/B (3.3 $year^{-1}$) were taken from Dalsgaard et al. (1998). Diet composition values for lingcod are adapted from a discussion in Cass et al. (1990).

Sablefish

Sablefish (*Anoplopoma fimbria*) are schooling fish that live on or near muddy or sandy bottoms from 180 m to over 900 m when adult (Love 1996). Juveniles are found shallower than 180 m.

The sablefish biomass estimate of 0.195 $t \cdot km^{-2}$ in PWS was derived by multiplying the mean PWS landings from 1994 to 1996 by the mean biomass/landings ratio from the greater Gulf

Table 46. Diet composition (i% weight) of Pacific Cod[a]

Prey group	% in diet
Discards	12.5
Shallow epifauna	11.9
Deep epifauna	35.6
Infauna	5.3
Squid	2.5
Shallow demersal	7.9
Deep demersal	7.9
Capelin	1.9
Arrowtooth	5.8
Pollock	7.4
Eulachon	0.3
Herring	0.4

a) From Yang (1993).

Table 47. Biomass estimates for PWS sablefish 1994-1996.

Year	Biomass/ landings[a]	PWS landings[b]	PWS Biomass (t)	Biomass (t·km^{-2})
1994	10.216	126.249	1289.760	0.142
1995	10.885	254.295	2768.001	0.306
1996	10.610	116.045	1231.238	0.136
Mean	10.570	166.854	1763.647	0.195

a. Biomass/landings ratios apply to the Gulf of Alaska management region and are derived from NPFMC (1995 and 1997);
b. Landings information from B. Bechtol (unpublished data).

of Alaska management region for that period (Table 47). This estimate is 20% greater than the 0.162 t·km^{-2} adapted from the 1989 post-spill PWS multi-species trawl survey data (Table 41), but it is likely still an underestimate since exploitable biomass is only a fraction of total biomass.

The P/B value used for Sablefish in PWS (0.566) was derived by taking the mean of juvenile and adult mortality estimates weighted by the proportions of juvenile and adult biomasses used for the southern BC shelf model by Livingston (1996). McFarlane and Beamish (1983) presented a natural mortality rate for juveniles between age 0 and age 4 of 0.6 year^{-1}, and Stoker (1994) presented a natural mortality rate for adults of 0.08 year^{-1}. The proportion of juvenile to adult biomass on the Southern BC shelf is 15:1. Likewise, a Q/B value of 6.42 year^{-1} was calculated by taking the weighted mean of the Q/B values given for juvenile and adult sablefish by Livingston (1996). Therefore, derivation of sablefish P/B and Q/B values for PWS is based on the assumption that proportion of juvenile to adult biomass is the same there as on the southern BC shelf. The mean commercial landings for the three years was 0.018 t·km^{-2}.

Table 48. Diet composition (% weight) of sablefish[a]

Prey group	% in diet
Discards	29.1
Age 0 Pollock	10.5
Age 1-2 Pollock	10.5
Age 3 Pollock	10.5
Squid	8.0
Omni. Zoopl.	6.7
Eulachon	5.5
Jellies	5.4
Deep epifauna	5.1
Deep demersal	4.8
Herring	2.2
Pacific Cod	0.8
Infauna	0.4
Capelin	0.3

a. Compiled from Yang (1993).

Diet composition for sablefish in Table 48 was based on Yang's (1993) study in the Gulf of Alaska. This study also revealed that sablefish consumed all size classes of pollock (0, 1-2, and 3+). Equal allocation among pollock age classes is based on the assumption of equal proportions consumed by sablefish. Note that 29% of sablefish prey is fishery discards based on information from the Gulf of Alaska. The 'nekton falls' group, which include discarded fish carcasses, are fed to Sablefish, but some food is imported into their diet, reflecting consumption outside the system.

Arrowtooth Flounder

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Arrowtooth flounder (*Atheresthes stomias*) is a large predatory flatfish which may be the single most abundant fish species in the Gulf of Alaska (Wilderbuer and Brown 1993). The biology of arrowtooth flounder is not well known. Sexual maturity occurs at a length of about 30 cm and spawning off the coast of Washington takes place during winter (Rickey 1995). Larvae occur in the surface layer 0-200 m during summer (Taylor 1967) where they feed on copepods and eggs (Barraclough and Fulton 1968). The biomass of arrowtooth in PWS appears to have increased substantially from 4,000 to 40,000 tons between 1978 and

Table 49. Population parameters for arrowtooth flounder in PWS.

Arrowtooth stages	Biomass (t·km^{-2})[a]	Biomass min-max[a]	P/B (Z; year^{-1})[b]	Q/B (year^{-1})[c]
Juveniles	0.57	0.08-1.05	0.22	3.03
Adults	4.00	0.60-7.36	0.22	3.03

a. NMFS (1993);
b. Wilderbuer and Brown (1993);
c. Smith et al. (1991).

1989 (Parks and Zenger 1979, NMFS 1993). In 1989, arrowtooth comprised about 55% of the bottomfish biomass in the Sound (NMFS 1993). Ecopath input parameters for arrowtooth flounder are presented in Table 49. Despite its high abundance, there is no directed fishery on arrowtooth flounder in the PWS region.

Approximately 56% of the juvenile biomass and 80% of the adult biomass of arrowtooth flounder occurs in southwestern PWS (see Appendix 6). The remainder of the juvenile biomass is found in Orca Bay and Port Fidalgo (NMFS 1993). Juveniles tend to be distributed between 20 and 200m; whereas, adults typically occur between 100 and 400m. In the present study, minimum and maximum biomass densities were calculated from the lower and upper 95% confidence intervals on the mean biomass estimated during a 1989 trawl survey (NMFS 1993). The annual food consumption of arrowtooth was estimated from a laboratory analysis of the energetics of yellowfin sole (Smith et al. 1991). Size at age data indicate that arrowtooth and yellowfin sole exhibit very similar growth rates in the Gulf of Alaska (Wilderbuer and Brown 1993). The diet of juvenile arrowtooth during summer is dominated by shrimp and capelin, whereas adult diets are dominated by walleye pollock (Table 50).

Table 50. Summer diet composition matrix (% weight) for arrowtooth flounder in PWS (from Yang 1993).

Prey\Predator	Juveniles	Adults
Omnivorous zooplankton	15.0	3.0
Deep large epifauna	25.0	4.0
Capelin	44.0	14.0
Juvenile herring	5.0	7.0
Adult herring	5.1	4.0
Pollock age-0	3.7	21.8
Pollock age 1-2	1.2	45.2
Squid	1.0	1.0

Pacific Halibut

International Pacific Halibut Commission staff

Seattle, Washington, USA

We estimated biomass (total biomass of age 8 and older, round weight) by calculating relative abundance from catch/effort and bottom area for Prince William Sound and IPHC Area 3A, and scaling to the 3A biomass (see Table 51). Density (catch/effort) times area is usually proportional to abundance, and the ratio of relative abundance for the two areas times absolute abundance in one area (3A) equals absolute abundance in the other area (PWS). This calculation must be treated with caution, because the catch/effort data in PWS are very limited. The total catch in PWS is only 1.5-2.5% of the 3A catch, and the number of ship logs collected for catch/effort in PWS is a low proportion of the total landings there. The ratio of PWS biomass to 3A biomass is similar to the ratio of PWS catch to 3A catch, so we think the estimates are in the right ballpark. However, we would be inclined to use the estimated values as a range, rather than a trend. The mean biomass of Pacific halibut in PWS for the period 1994-1996 is 6133 t, or 0.677 $t{\cdot}km^{-2}$ (Table 51).

Our estimate of total mortality (Z) comes from adding the calculated fishing mortality (F) to a constant estimate of M (=0.2 $year^{-1}$); i.e., 1993: 0.33; 1994: 0.34; 1995: 0.30; 1996: 0.32; 1997: 0.34. The mean Z for the 1994-1996 period, 0.32 $year^{-1}$, is used as the P/B estimate. A Q/B of 1.73 $year^{-1}$ was taken from

Table 51. Biomass of Pacific halibut in PWS

Year	PWS catch (t)	3A catch (t)	No. skates	PWS catch/effort (t/skate)	3A catch/effort (t/skate)	3A biomass (t)	PWS catch fraction	PWS biomass (t)	PWS biomass fraction	Density ($t{\cdot}km^{-2}$)
1993	214	13753	259	0.1071	0.2364	320508	0.0156	7476	0.0233	0.825
1994	220	15023	213	0.1084	0.1997	291199	0.0147	8140	0.0280	0.899
1995	214	11092	435	0.0780	0.2357	275251	0.0193	4691	0.0170	0.518
1996	295	11909	910	0.1110	0.2675	260614	0.0248	5569	0.0214	0.615
1997	366	14926	1532	0.0824	0.2639	238751	0.0245	3839	0.0161	0.424

a. Area 3A extends along the continental shelf from Cape Spencer to the west end of Kodiak Island, including PWS.

Table 52. Diet Composition (% weight) of Halibut[a]

Prey group	% in diet
Pollock	57.4
Deep epifauna	14.1
Discards	7.1
Salmon	5.3
Shallow epifauna	4.7
Juv. Arrowtooth	4.2
Deep demersal	3.8
Shallow demersal	1.3
Pacific Cod	1.0
Capelin	0.9
Squid	0.2

a) Adapted from Yang (1993).

Venier (1996b) who derived it from an empirical equation in Christensen and Pauly (1992, p. 14). This value is close to the mean of the following two Q/B values suggested by P. Livingston for the gulf of Alaska (unpublished data): Halibut consume 0.4% body weight daily for individuals 50-79 cm in length ($0.004 \cdot 365 = 1.46$ annual ration Q/B for Ecopath) and 0.3% body weight daily for individuals greater than 80 cm in length ($0.003 \cdot 365 = 1.095$ annual ration Q/B for Ecopath).

The diet composition of Halibut in Table 52 is adapted from Yang (1993). Halibut occur from depths of 6 m to over 1,000 m, and generally migrate to shallow waters during summer to feed (Love 1996). The deep/shallow zone allocations were based on the assumption that 25% of demersal fish and epifaunal biomass was taken in waters shallower than 20 m. Yang (1993) showed that 57.4% of GoA halibut diet in the summer of 1990 was walleye pollock, and that all three size classes were consumed. Biomass of consumed pollock was thus allocated equally among pollock age classes in the model. However, only juvenile arrowtooth flounder (<30 cm) were consumed by halibut.

The commercial catches of halibut in PWS are given in Table 51, and the recreational catches are given in **Table 75.** The total catch estimate is the grand mean of the sum of recreational and commercial catches from 1994-1996: 626 t, or $0.069\ t \cdot km^{-2}$.

Sharks

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This group is composed of salmon sharks (*Lamna ditropis*), spiny dogfish (*Squalus acanthias*), and sleeper sharks (*Somniosus pacificus*). Personal observations and anecdotal evidence suggest that shark abundance has increased dramatically throughout the 1990s. Anecdotal accounts of increasing numbers of dogfish in PWS are supported by a time series of relative abundance (CPUE) for dogfish calculated from International Pacific Halibut Commission longline survey data (Figure 5; data provided by IPHC biologist Dan Randolf).

Currently there are no quantitative estimates of biomass for these species in PWS. Given the potential trophic and ecological importance of these predators in PWS, research is needed to obtain more realistic estimates of biomass, abundance, and diet composition. The estimates in this section were made to provide input parameters for the Ecopath modelling exercise, but caution is advised when considering the usefulness of these preliminary estimates for other purposes, as some

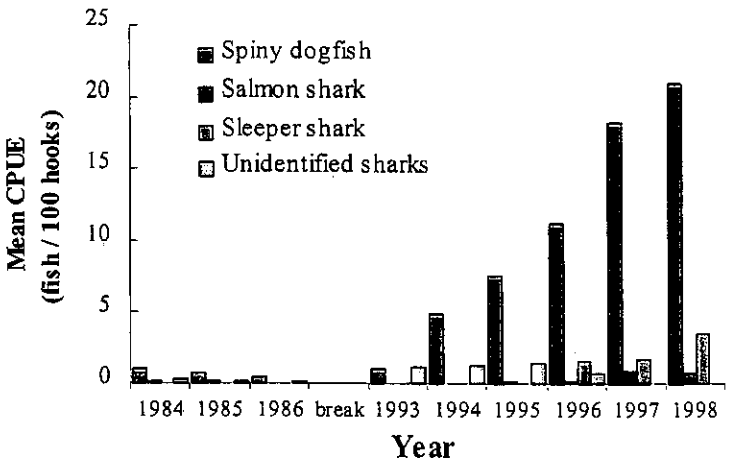

Figure 5. Average annual shark bycatch per 100 hooks. Compiled from IPHC longline survey data collected in the GoA between Nuka Point and Cape St. Elias.

Table 54. Biomass and Q/B estimates for PWS Sharks.

Population parameters	Salmon sharks	Sleeper sharks	Spiny dogfish	PWS sharks
Biomass (t)	4000	1000	1000	--
Daily ration (%)	5	1	1	0.58
Residency time (year)	0.5	1	0.5	--
Overall Q/B (year^{-1})	18.25	3.65	3.65	7.00
PWS-adjusted Q/B (year^{-1})	9.13	3.65	1.825	

are little more than rough approximations.

Biomass estimates of four thousand tonnes of salmon sharks in Prince William Sound (0.442 $t\cdot km^{-2}$), and one thousand tonnes each of spiny dogfish and sleeper sharks (0.11 $t\cdot km^{-2}$) resulted in an overall shark biomass estimate of 0.662 $t\cdot km^{-2}$. Derivations for Q/B were based on daily ration estimates of 1% body weight per day for spiny dogfish and sleeper sharks, and 5% body weight per day for salmon sharks. These Q/B estimates were corrected using peculative estimates of annual residency durations of 180 days for salmon sharks and spiny dogfish, and 365 days for sleeper sharks. A weighted average of these adjusted Q/B estimates were then calculated based on the relative biomass estimates for each species. The derivation of Shark Q/B estimates are shown in Table 54. The P/B estimate of 0.1 year^{-1} for these species are based on a natural mortality estimate for spiny dogfish (Polovina 1996). Immigration is assumed to approximately equal emigration.

Commercial shark bycatch in Alaska waters is poorly documented. Shark bycatch is frequently recorded as 'unidentified shark', 'shark', or 'other fish.' To account for fishery removals of PWS sharks, a discard flow of 0.0038 $t\cdot km^{-2}\cdot year^{-1}$ was equally apportioned between commercial and recreational fisheries. This flow represents 10% of the production of PWS sharks (the product of the specified biomass and P/B estimates), corrected with the overall shark residency multiplier (0.58; Table 54). Dividing the resulting flow equally among commercial and recreational fisheries results in an estimate (0.0019 $t\cdot km^{-2}\cdot year^{-1}$ each) that is very close to the specified estimate for shark discards associated with commercial fisheries in PWS (0.0022 $t\cdot km^{-2}\cdot year^{-1}$; Table 76). Thus, the former value was used for recreational discards, and the latter for commercial, resulting in an adjusted total specified shark discard of 0.004 $t\cdot km^{-2}\cdot year^{-1}$. Incorporation of these catch estimates are needed to avoid inconsistency in model parameterization (i.e., not including parameters of the model we know are not zero).

In 1997 the Alaska Board of Fisheries closed all commercial shark fishing and heavily regulated the sport fishery in Alaska state waters. No Federal Management plan exists specifically for sharks in the Gulf of Alaska and the Aleutians. Sixgill and blue sharks also occur in the PWS area but are not explicitly included in this exercise, i.e., their biomass is assumed to be part of the overall 'shark' biomass estimates specified herein.

The salmon shark, a large pelagic predator, is the sister species to the better known porbeagle (*Lamna nasus*), and is also closely related to the white shark (*Carcharodon carcharias*), and mako sharks (*Isurus oxyrinchus* and *I.*

Table 53. Prey items and % diet composition of sleeper shark (*Somniosus pacificus*), collected in Gulf of Alaska in 1996 (Mei-Sun Yang, NMFS, Alaska Fisheries Science Center, pers. comm.).

Sleeper shark prey	Frequency (%)	% in diet
Gastropoda (snail)	9.09	0.49
Fusitriton sp. (snail)	9.09	0.19
Cephalopoda (squid and octopus)	27.27	0.17
Teuthoidea (squid)	36.36	0.62
Octopus dofleini (octopus)	72.73	4.63
Crangonidae (shrimp)	9.09	0.01
Pagurid (hermit crab)	9.09	0.01
Teleostei (unidentified fish)	45.45	0.33
Oncorhynchus sp. (salmon)	9.09	4.49
Gadidae (gadid fish)	9.09	0.49
Theragra chalcogramma (walleye pollock)	9.09	5.22
Atheresthes stomias (arrowtooth flounder)	63.64	67.2
Sebastes sp. (rockfish)	9.09	2.06
Pleuronectid (unknown flatfish)	18.18	0.86
Hippoglossoides elassodon (flathead sole)	9.09	0.98
Fishery offal	9.09	12.3

paucus). Salmon sharks live at least 25 years and average size range in PWS appears to be between 180-230cm total length (Lee Hulbert, unpublished data). Length and age at maturity estimated to occur at 140cm PCL and 5 years for males, and 170-180cm PCL and 8-10 years for females. *L. ditropis* is ovoviviparous with an annual fecundity of up to 5 pups (Tanaka 1980); the gestation period is not documented. Based on mating occurring in the late summer and parturition occurring in the spring, gestation may be around 9 months (K. Goldman, Virginia Institute of Marine Science, pers. comm.). Salmon sharks are opportunistic predators. Their diet includes salmonids (*Oncorhynchus*), rockfish (*Sebastes*), lancetfish (*Alepisaurus*), daggertooth (*Anotopterus*), sablefish (*Anoplopoma*), spiny dogfish (*Squalus acanthias*), lumpfishes (Cyclopteridae), lanternfishs (Myctophidae), sculpins (Cottidae), pollock (*Theragra chalcogramma*), Pacific tomcod (*Microgadus proximus*), herring (Clupeidae), halibut (Pleuronectidae), squid (Teuthoidea), and benthic crustaceans (Nagasawa 1998, Tanaka 1980, 1986, Castro 1983, Sano 1960, 1962). Temporal abundance of salmon sharks in PWS is not documented. Distribution and abundance of salmon sharks are associated with aggregations of prey (Blagoderov 1994) and have been observed in spring (April-May) during the sac roe herring fishery and fall (September-October) during the herring bait fishery. Peak abundance appears to occur during July and August, corresponding with the return of adult salmon to PWS. Neave and Hanavan (1960) observed no obvious pattern of change in distribution of salmon sharks in the Gulf of Alaska between May and September. An occasional salmon shark is taken in trawl gear during the PWS winter pollock fishery (Robert Bercelli, Alaska Dept. of Fish and Game, pers. comm.).

Table 55 lists the frequency of occurrence of salmon shark prey taxa in 11 stomachs collected from mid to late July, 1998 (K. Goldman, Virginia Institute of Marine Science, unpublished data). Eight sharks were collected in Montague strait, two in Aialik Bay, and one was collected in Resurrection Bay. Weight data for individual prey was unavailable; breakdown of diet composition by percent biomass is based on estimated weights of prey taxa.

Spiny dogfish are adaptable predators that often congregate in packs. They can grow to 130 cm and over 9 kg. Dogfish age and length at maturity vary greatly with region, and have been estimated to range from 16-35 years and up to 94 cm for females (Love 1996, Smith 1998). They are ovoviviparous and average 7 pups per parturition. Gestation period is the longest of any vertebrate at 22-24 months (Saunders and McFarlane 1993). Diet composition of dogfish in PWS has not been documented, but diet composition information is available from British Columbia during the 1970s (Table 56). They are known to prey heavily on schools of spawning capelin, and aggregations of dogfish are often associated with herring returning to coastal waters of British Columbia. Principal food appears to be herring (Clupeidae), sandlance (*Ammody-*

Table 55. Derivation of estimated diet composition of salmon sharks in PWS[a]

Salmon shark prey taxa	**Frequency in 11 stomachs**	**Frequency (%)**	**Mean weight (kg)**	**Biomass (%)**
Salmonids (*Oncorhynchus*)	5	26	2.2	40
Sablefish (*Anoplopoma*)	5	26	2	36
Pollock, Cod (Gadidae)	1	5	1	4
Rockfish (*Sebastes*)	1	5	0.3	1
Herring (Clupeidae)	2	11	0.05	0.4
Spiny dogfish (*Squalus acanthias*)	1	5	2	7
Squid (Teuthoidea)	3	16	0.1	1
Halibut (Pleuronectidae)	1	5	3	11

a) It is unlikely that these estimates of diet composition have representative value for PWS as a whole, due to the low sample size and the subsequent extrapolation to percent biomass.

Table 56. Spiny dogfish prey composition (% weight) sampled off the coast of British Columbia (Jones and Geen 1977).

Spiny dogfish prey	% in diet
Unidentified teleosts	17.56
Herring (Clupeidae)	14.42
Euphausiid (Euphausiacea)	12.87
Plankton	9.09
Shrimp (*Pandalus* sp.)	7.57
Crab (T. Brachyura)	6.68
Gadid fish (Gadidae)	5.37
Flatfish (Pleuronectidae)	3.89
Eulachon (Osmeridae)	3.65
Octopus (Octopus sp.)	2.87
Combjellies (Ctenophora)	2.26
Elasmobranchs	1.99
Squid (*Loligo* sp.)	1.61
Jellyfish (Coelenterata)	1.15
Sandlance (Ammodytidae)	1.11
Rockfish (*Sebastes*)	0.98

Table 57. *Generalized shark diet composition estimates for PWS. Percent biomass contribution to shark diet are averages weighted by relative biomasses of three shark species*[a].

Generalized "shark" prey	Biomass ($t \cdot year^{-1}$)[b]	*% in diet*
Adult Salmonids	1,437	13
Adult Sablefish	1,294	12
Adult gadid fish	161	1
Juvenile gadid fish	193	2
Walleye pollock	188	2
Rockfish	145	1
Herring	533	5
Sandlance	40	0
Smelt	131	1
Halibut	395	4
Flathead sole	35	0
Arrowtooth flounder	2,415	22
Other flatfish	171	2
Teleostei	12	0
Spiny dogfish	252	2
Elasmobranch fish	72	1
Squid	120	1
Octopus	272	2
Euphausiids	462	4
Combjellies	81	1
Jellyfish	41	0
Plankton	327	3
Crab	240	2
Shrimp (*Pandalus*)	272	3
Misc. benthic inverts	416	4
Fishery offal	441	4
Unidentified teleost	643	6

a) Generalized shark diet composition (salmon shark, sleeper shark, and spiny dogfish) is based partly upon conjecture. Salmon shark estimates were based on just 11 stomach samples from summer, and are thus unlikely to represent an annual diet. Future changes in relative abundance of the shark species, and diet composition, would act to compound uncertainty.

b) Based on an estimated daily ration of 1%

c) $BW \cdot day^{-1}$

tes), smelts (Osmeridae) and euphausiids. Their diet also includes some 27 other fish species and 13 varieties of invertebrates, many of which are commercially important (Hart 1980). Dogfish are known predators of juvenile Pacific salmon (Orsi et al. 1998). Temporal patterns of residence for spiny dogfish in PWS are unknown.

Pacific sleeper sharks are a large demersal species that average ~200cm in PWS (Hulbert 1999 unpublished data). Very little is known of sleeper shark life history. Age and size at maturity are unknown. They are thought to be ovoviviparous, but gestation time and litter size have not been documented. Sleeper sharks are said to be voracious and versatile feeders of fish. Principal prey include flatfish - halibut, soles and other flatfishes - salmon, and rockfish. Other foods include octopods and squids, crabs, and carrion (Hart 1980). Sleeper shark diet has also been shown to include marine mammals, including harbor seal, Phoca vitulina (Bright 1959), and southern right whale dolphin, Lissodelphis peronii (Crovetto et al. 1992). Table 53 presents a sleeper shark diet composition based on stomach contents from the Gulf of Alaska. Temporal patterns of residence for sleeper sharks in PWS are not documented.

ADF&G longline sablefish surveys (May and October) catch an occasional sleeper shark, but it is unknown whether they remain in the sound during winter (Robert Bercelli, Alaska Dept. of Fish and Game, pers. comm.).

Prey collected from Pacific sleeper shark stomachs in PWS during the ADF&G longline sablefish survey in September 1999 included adult coho and pink salmon (Hulbert unpublished data). The sharks were caught at depths ranging from 350-550 m. Adult pink and coho salmon depth data recorded on data storage tags during July and August 1999 never exceeded 90 m (Walker, et al. 1999). Based on this information, sleeper sharks could be making vertical foraging igrations. At high latitudes sleeper sharks are known to venture into the littoral and intertidal zones and occasionally come to the surface (Hart 1973). Sleeper shark diet has also been shown to include marine mammals, including harbor seal, Phoca vitulina (Bright 1959), and southern right whale dolphin, Lissodelphis peronii (Crovetto et al. 1992). Seals are considered common prey of the Greenland shark, Somniosus microcephalus, the Atlantic congener of the Pacific sleeper shark (Compagno 1984). The behavior of these species can be expected to be very similar, and sleeper sharks may prey on marine mammals in PWS (Bruce Wing 1999 pers. comm.).

The consumption / biomass (Q/B) estimate for the 'PWS sharks' group in early versions of the model was based on a conservative daily ration estimate of 1% per day. The Q/B estimate was then corrected for PWS residency time for each species, and the resulting species-specific Q/B estimates were averaged (weighted by PWS biomass).

New information indicating that salmon sharks may consume 5% of their body weight per day rather than the initial assumption of 1%. This corresponds with a Q/B of 18.3 year-1 and to a residency time-corrected Q/B of 9.1 $year^{-1}$ for that species , which in turn leads to a Q/B value of 7 $year^{-1}$ for overall PWS sharks by using a biomass-weighted average, also corrected for residency time (Table 54). This adjustment was based on an increase in daily ration estimates from 1% to 5% in salmon sharks due to metabolic considerations.

Table 57 presents a generalized shark diet composition by combining the estimated annual diet compositions for all three species of sharks, weighted by proportions of biomass represented by each species.

BIRDS

Invertebrate-Eating Sea Ducks

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This group is comprised of the primary benthic invertebrate-eating sea ducks that occur in Prince William Sound (i.e., 8 species listed in Table 58). Excluded from this analysis are rare sea ducks (e.g., eiders) and fish-eating sea ducks (i.e., mergansers). Data summarized in Table 58 were used to calculate an annual mean biomass of 0.005 $t \cdot km^{-2}$ and a Q/B ratio of 450.5 $year^{-1}$. The ratio of production to biomass (P/B) was considered to be equal to 0.2 $year^{-1}$, the estimated mortality for each of these species.

Population estimates are from the most recent U.S. Fish and Wildlife Service (Migratory Bird Management) surveys (Agler and Kendall 1997).

Table 58. Ecopath parameters for invertebrate-eating sea ducks in PWS

Species	Winter population	Summer population	Body weight (kg)	Winter biomass (t)	Summer biomass (t)	Prey consumed ($kg \cdot bird^{-1} \cdot day^{-1}$)	Food consumption ($t \cdot year^{-1}$)
Harlequin Duck	17,151	10,619	0.60	10.29	6.37	0.66	3,472
Goldeneyes	35891	0	0.90	32.30	0	0.99	7,532
Surf Scoters	6492	3024	1.10	7.14	3.33	1.21	2,225
White-winged Scoters	6203	0	1.35	8.37	0	1.49	1,952
Black Scoters	1837	0	1.15	2.11	0	1.27	492
Oldsquaw	6852	0	0.90	6.17	0	0.99	1,438
Bufflehead	6875	0	0.45	3.09	0	0.50	721
Total	81,301	13,643	--	69.48	9.70	--	17,835

Table 59. Diet composition (% weight) of invertebrate-eating sea ducks in PWS

Species	Mussels	Clams	Snails	Chitons	Crustaceans	Limpets
Harlequin Duck	10	0	35	10	35	10
Goldeneyes	90	--	10	--	--	--
Surf Scoters	75	10	5	--	5	5
White-winged Scoters	30	30	30	--	10	--
Black Scoters	85	--	--	--	15	--
Oldsquaw	20	20	20	--	40	--
Bufflehead	5	5	40	0	45	5
Means	45	9.3	20	1.4	21.4	2.9

Biomass estimates are simply the number of individuals multiplied by average body weight. Note that both numbers and biomass are seasonally variable.

Prey weight consumed per day was estimated based on relationships described for Barrow's goldeneyes (Holland-Bartels 1997). Goldeneye field metabolic rate (FMR) was estimated to be 1674kJ·day^{-1} using an equation for flapping flight sea birds (Birt-Friesen et al. 1989). Prey energy density of mussels was estimated to be 1.65kJ·gram^{-1} wet weight including shell (Palmerini and Bianchi 1994; Mary Ann Bishop, unpubl. data). Thus, the estimate of wet weight consumed per day for goldeneyes was 1015g. Based on goldeneye average body weight of 900g, individuals consume an average of 110% of their body weight daily. This seems high but may be accurate given the high water content and low energy density of mussels, especially when their shell is included. This figure was applied to other species, which assumes (1) no variation in FMR with body weight and (2) energy density of all prey items is similar to mussels.

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Food consumption per year is estimated by calculating bird days (adjusted for seasonal changes in abundance) and multiplying by daily food requirements.

Diet data in Table 59 are gathered from published sources (Vermeer 1981, Koehl et al. 1982, Sanger and Jones 1982, Vermeer and Bourne 1982, Vermeer 1982, Goudie and Ankney 1986, Goudie and Ryan 1991, Patten 1994). Sea duck diets vary considerably by site and few studies have been conducted in Prince William Sound; the data presented represent my assimilation and summary from all available sources.

Seabirds and Seabird Predators

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Although the seabird population of Prince William Sound is a rich and diverse collection of species (Isleib and Kessel 1973) with differing foraging strategies (Klosiewski and Laing 1994, Ostrand et al. 1998), their distribution is consistent across taxa, with most bird observations occurring within 1 km of the shoreline (Ostrand and Maniscalco 1996). Within the nearshore zone, seabirds have been associated with shallow water habitats. However, this relationship was not apparent during 1997 (U.S. Fish and Wildl. Serv., Anchorage, unpubl. data).

Population estimates in Table 60 are from 1996 U.S. Fish and Wildlife Service surveys (Agler and Kendall 1997). Bird population estimates were based on counts of adult birds and did not include estimates of offspring abundance. Mortality among seabird offspring is high (Ashmole 1971). However, we speculate that little of this biomass is returned to the Prince William Sound marine system. Much mortality of eggs and chicks is due to predation by avian predators (Hatch and Hatch 1990) and possibly mammals (Seto and Conant 1996). Avian nest predators are composed of marine [Glaucous-Winged Gulls (*Larus glaucescens*)] and terrestrial [Common Ravens (*Covus corax*) and Northwest Crows (*Corvus caurinus*)] birds (Parrish 1995). We assume that none of the biomass consumed by terrestrial predators and only a portion of that consumed by marine predators is returned to the sea. We further speculate that young seabirds leave Prince William Sound soon after fledging, hence mortality among these individuals does not contribute biomass back into the system. Therefore, we have considered only the adult population in this modelling exercise. The summer population and biomass is dominated (>20,000 individuals of each species) by Glaucous-winged Gulls, Black-legged Kittiwakes (*Rissa tridactyla*), and *Brachyrampus* murrelets (Marbled Murrelet, *B. marmoratus* and Kittlitz's Murrelet, *B. brevirostris*). The winter population and biomass differs and is dominated by Mew Gulls (*Larus canus*), murres (mostly Common Murre, *Uria aalge*), and *Brachyrampus* murrelets. In addition, Bald Eagles (*Haliaeetus leucocephalus*) are a major contributor to avian biomass (>1.5 kg km^{-2}) during both seasons.

Body weight estimates for Alcids were taken from De Santo and Nelson (1995), cormorant estimates from Johnsgard (1993), and all other species from Dunning (1993). Daily food consumption estimates for Black-legged Kittiwakes and Pigeon Guillemot (*Cepphus columba*) were obtained from studies conducted in Prince William Sound (U.S. Fish and Wildl. Serv., Anchorage, unpubl. data). Bald Eagle and Peregrine Falcon (*Falco peregrinus*) consumption estimates were obtained from Stalmaster and Gessaman (1984) and Nelson (1977), respectively. For all other species daily food consumption was calculated using the following formula of Birt-Friesen et al. (1989):

$$\log_{10}(\text{daily energy}) = 3.08 + 0.667 \log_{10}(\text{body weight})$$

where energy is expressed in kJ and body weight in kg. We assumed a 75% efficiency in converting energy consumed and a local energy content of 4.5 kJ gm^{-1} of forage fish (D. Roby, Oregon State Univ, Corvallis, pers. comm.). Hence, we divided daily energy by 0.75 and then divided that product by 4.5 kJ gm^{-1} to obtain daily consumption in wet weight.

Food habits for Pigeon Guillemot (*Cepphus columba*), Marbled Murrelets, Black-legged Kittiwakes, Glaucous-winged Gulls, and Mew Gulls (Table 61) were obtained from local studies (U.S. Fish and Wildl. Serv., Anchorage, unpubl. data). Tufted Puffin (*Fratercula cirrhata*) data were also collected in Prince William Sound (Piatt et al. 1998). Bald Eagle, Peregrine Falcon, and cormorant food habits were taken from Grubb and Hensel (1978), Nelson (1977), and Robertson (1974), respectively. All other food habits data were obtained from Sanger (1987).

Estimated production biomass ratio (P/B) values of 0.078 year^{-1} for piscivorous seabirds and 0.05 year^{-1} for seabird predators was determined by calculating the average adult mortality, weighted by species biomass. Adult mortalities for Black-legged Kittiwakes (U.S. Fish and Wildl. Serv., Anchorage, unpubl. data) and Bald Eagles (Bowman et al. 1993) were obtained from local studies. Mortality values for Tufted Puffins, Horned Puffins (*Fratercula corniculata*), and Parakeet Auklet (*Cyclorrhynchus paittacula*) were not available so we used an Atlantic Puffin (*Fratercula arctica*) value (del Hoyo et al. 1996). Similarly, Herring Gull (*Larus argentatus*) mortality (Ashmole 1971) was used for Mew Gulls. Mortality values for Fulmars and Shearwaters, Marbled Murrelets, Ancient Murrelets (*Synthliboramphus antiquus*), Glaucous-winged Gulls, all cormorants, Arctic Terns (*Sterna paradisaea*), and Peregrine Falcons were obtained from Ashmole (1971), Beissinger (1995), De Santo and Nelson (1995), Reid (1987), Johngard (1993), Coulson and Horobin (1976) and Ambrose and Riddle (1988), respectively.

Table 60. Population estimates and Ecopath input parameter estimates for seabirds in Prince William Sound.

Species	Summer population[a]	95% CI	Winter population[a]	95% CI	Body weight (g)	Summer biomass ($kg \cdot km^{-2}$)	Winter biomass ($kg \cdot km^{-2}$)	P/B ($year^{-1}$)	Prey weight ($g \cdot day^{-1}$)	Q/B ($year^{-1}$)	Food consumption ($kg \cdot km^{-2} \cdot year^{-1}$)
Seabirds											
Fulmars and Shearwaters	1877	958	0	0	810	0.2	0.0	6.0	309.5	139.5	12.8
Fork-tailed Storm-petrel	15800	11451	0	--	43	0.1	0.0	--	43.7	370.7	14.3
Double-crested Cormorant	74	110	367	230	2350	0.0	0.1	15.1	629.8	97.8	5.8
Pelagic Cormorant	263	225	590	552	2000	0.1	0.1	17.0	565.6	109.5	10.0
Unid.: red-faced or pelagic	1067	1508	12056	4005	2000	0.2	2.7	17.0	565.6	109.5	153.9
Bonaparte's Gull	1600	1343	0	0	212	0.0	0.0	15.0	126.6	217.9	4.2
Mew Gull	14200	5526	20300	11702	400	0.6	0.9	15.0	193.3	176.4	138.4
Glaucous-winged Gull	25100	6547	13900	5442	1010	2.9	1.6	15.0	358.6	129.6	289.8
Black-legged Kittiwake	48227	18882	5279	2129	390	2.2	0.3	7.0	190.1	177.9	218.3
All terns	5400	1710	0	0	110	0.1	0.0	13.0	81.7	271.2	9.1
Arctic Tern	4852	1656	0	0	110	0.1	0.0	13.0	81.7	271.2	8.2
All Murres	3300	2177	46100	19571	1004	0.4	5.3	11.0	357.2	129.8	366.8
Pigeon Guillemot	2982	905	2500	1056	487	0.2	0.1	20.0	220.4	165.2	25.1
Brachyramphus *murrelet*	82200	18917	44300	13158	221	2.1	1.1	15.0	130.1	214.9	341.2
Ancient Murrelet	188	185	0	0	206	0.0	0.0	23.0	124.2	220.0	0.5
Parakeet Auklet	800	419	0	0	297	0.0	0.0	5.0	158.5	194.8	2.6
Tufted Puffin	5000	2126	0	0	773	0.4	0.0	5.0	300.0	141.7	31.0
Horned Puffin	500	390	0	0	612	0.0	0.0	5.0	256.7	153.1	2.7
Sum (mean)	213430	--	145392	--	--	9.5	12.3	(7.8)	--	(150.6)	1634.7
Seabird Predators											
Bald Eagle	3046	741	3893	832	4700	1.6	2.1	5.0	489.0	36.5	70.0
Peregrine Falcon	6	7	0	0	1130	0.0	0.0	23.0	150.0	48.5	18.0
Sum (mean)	3052	--	3893	--	--	1.6	2.1	(5.0)	--	(38.9)	88.0

a) Summer: May-October; Winter: October-April.

Table 61. Diet composition (% weight) of Seabirds in Prince William Sound

Predators\Prey	Adult salmon	Salmon fry 6-12cm	Inshore detritus	Sand-lance	Juv. herring	Capelin	Nearshore demersals	Pollock 0	Pollock 1-3	Squid	Herb zoo.	Omni. zoo.	Shal. sm. epiben.	Sea-birds	Other marine	Non-marine
Seabirds																
Fork-tailed Storm Petrel	-	-	-	-	-	-	-	5	-	60.0	10.0	25.0	-	-	-	-
Sooty Shearwater	-	-	-	5.0	-	70	-	-	-	22.0	-	3.0	-	-	-	-
Double-Crested Cormorant	-	-	-	5.0	3.0	-	92.0	-	-	-	-	-	-	-	-	-
Pelagic Cormorant	-	-	-	18.9	-	-	74.3	-	-	-	-	6.8	-	-	-	-
Mew Gull	-	-	40.0	20.0	20.0	20	-	-	-	-	-	-	-	-	-	-
Glaucous-winged Gull	-	-	40.0	12.0	12.0	6	-	-	-	-	-	1.2	30.0	-	-	-
Black-legged Kittiwake	-	4.0	3.0	19.0	61.0	12	-	-	-	-	-	5.0	-	-	-	-
Arctic Tern	-	-	-	1.0	1.0	1	-	-	-	-	-	97.0	-	-	-	-
Common Murre	-	-	-	20.0	-	40	-	-	25.0	-	-	15.0	-	-	-	-
Pigeon Guillemot	-	-	-	17.4	3.9	-	62.4	-	11.8	-	-	-	-	-	4.5	-
Marbled Murrelet	-	-	-	43.0	48.0	-	-	-	-	-	-	-	-	-	9.0	-
Ancient Murrelet	-	-	-	-	-	-	-	-	13.0	2.0	-	-	-	-	5.0	-
Tufted Puffin	-	24.0	-	-	22.0	-	-	-	13.0	-	-	-	-	-	41.0	-
Horned Puffin	-	-	-	18.0	-	65	-	-	1.0	2.0	-	-	-	-	12.0	-
Mean	-	1.0	10.8	22.0	22.4	14	8.7	0	6.0	0.7	0.1	6.2	5.3	-	2.7	-
Seabird predators																
Bald Eagle	10.0	-	10.0	-	-	-	5.0	-	-	-	-	2.5	-	30	10.0	25
Peregrine Falcon	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-
Mean	8.0	-	8.0	-	-	-	4.0	-	-	-	-	2.0	-	50	8.0	20

Consumption of Herring Eggs by Birds

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Consumption of herring eggs is incorporated into bird diet compositions in the previous two sections at an 'annual' resolution (as 'inshore detritus' for the purposes of the model). Additional information on this phenomenon is provided in this section to document the smaller spatial and temporal resolutions at which some energy flows occur.

Herring eggs are deposited on kelp and along the shoreline at Montague Island and northeast PWS during a few weeks in the spring. Herring eggs are thus an ephemeral resource for migratory birds in PWS, but these deposited eggs can be a substantial food source, particularly considering their high energy content. The estimated biomass of herring eggs in PWS was 1,413 t in 1995 and 1,484 t in 1996, with a mean of 1,449 t, or 0.160 $t \cdot km^{-2}$ when expressed on a Sound wide basis. However, the 1990 biomass estimate was almost nine times greater than the 1995-1996 period, at 12,826 t (J. Wilcock, ADF&G, unpublished data).

At northern Montague Island in 1994 and 1995, information on the abundance and distribution of the five most numerous avian herring spawn predators was collected using boat and aerial surveys. These species included Glaucous-winged Gulls, Mew Gulls, Surf Scoters, Surfbirds, and Black Turnstones. In 1995, problems with aerial videography prevented an estimate of Mew Gull and Glaucous-winged Gull abundance. For each species, a daily herring spawn consumption per individual bird was determined using a bioenergetic model based on field metabolic rate, energy content of spawn, and proportion of energy acquired from herring spawn. Energy acquired from herring spawn was determined based on stomach content analyses of birds collected in Montague Island spawn areas during 1994 and 1995. Glaucous-winged Gulls, Surf Scoters, and Mew Gulls were consuming only spawn (Table 62). Intake of herring eggs by birds ranged from 1.06 kg per Surf Scoter per day to 0.16 kg per Black Turnstone per day, with other birds consuming intermediate quantities (Table 63). Total herring spawn consumption in 1994 at the northern Montague Island study area was estimated to be 729 t.

As part of a separate EVOS study, in 1997, Glaucous-winged Gulls were collected in winter and spring at northern Montague Island, from Stockdale Harbor to Port Chalmers. Spring gull collection was conducted during four time periods: prior to spawn, active spawn deposition, spawn incubation, and post spawn hatch. Glaucous-winged Gulls consumed adult herring prior to and during active spawn deposition, switching to spawn once deposition was complete in an area (Table 64). In 1997, spawn covered many other areas at Montague, therefore, estimates of gull numbers for all spawn areas are not available.

Table 62. Percent occurrence (% occ.) and aggregate % weight (% wt.) of prey items contained in gut samples of birds collected from within spawn areas on northern Montague Island, April-May 1994, 1995.

	Glaucous-winged Gull (n=13)[a]		**Mew Gull (n=9)[a]**		**Surf Scoter (n=8)[a]**		**Surfbird (n=20)**		**Black Turnstone (n=14)**	
Species	**% occ.[b]**	**%wt.[c]**	**% occ.**	**%wt.**	**% occ.**	**%wt.**	**% occ.**	**%wt.**	**% occ.**	**%wt.**
Fish										
Herring Egg	100	100	100	96	100	100	75	70.5	69	74.0
Bivalves										
Mytilus		-	-	-	-	-	80	27.7	19	1.6
Crustaceans										
Balanus		-	-	-	-	-	5	0.2	19	23.6
Amphipod sp.	-	-	-	-	-	-	-	-	6	0.9
Amphithoe sp.	-	-	-	-	-	-	5	<0.1	-	-
Hermit crab	-	-	-	-	-	-	10	0.3	-	-
Gastropods										
Alia sp.	-	-	-	-	-	-	10	0.7	-	-
Lirularia sp.	-	-	-	-	-	-	5	<0.1	-	-
Littorina sitkana		-	-	-	-	-	10	0.1	-	-
Margarites sp.	-	-	-	-	-	-	10	0.4	-	-
Unid. gastropod	-	-	-	-	-	-	5	<0.1	-	-
Insects										
Diptera Larvae	-	-	11	4.2	-	-	-	-	-	-
Nematods										
Nematode	8	<0.1	-	-	-	-	-	-	-	-
Unid. organic material	8	<0.1	-	-	-	-	-	-	-	-

[a] Aggregate weight based on 12 glaucous-winged gulls, 8 mew gull, and 7 surf scoters;

[b] Percent occurrence: number of individuals with prey item x100 / total number of individuals;

[c] Percent aggregate weight = total weight of prey item for all individuals x100 / total weight of all prey items for all individuals.

Herring eggs are not explicitly defined as a group in the PWS Ecopath model at the present time for the sake of simplicity. Consumption of herring eggs by modeled avian groups (i.e., Mew Gulls, Surf Scoters, Glaucous-winged Gulls), is represented as consumption of inshore detritus (Ostrand and Irons, this vol.; Table 61). Avian herring spawn predators (Black Turnstones, Surfbirds) are sufficiently transitory that their exclusion from the model is somewhat justified. However, such transitory species are part of the PWS ecosystem, and in the future, herring eggs may be considered as an explicit group and their transitory predators explicitly included.

Table 63. Daily herring spawn consumption by avian species based on bioenergetic model. Northern Montague Island 19 April - 15 May 1994 and 27 April - 19 May 1995.

Species	Mean weight (kg)/bird	Aggregate energy for eggs (%)	Eggs consumed per day (kg)	Total bird days (1994)	1994 spawn consumed (t)	Total bird days (1995)	1995 spawn consumed (t)
Glaucous-winged	1.33	100	0.73	825,156	601.1	–	–
Mew Gull	0.45	95	0.32	213,755	67.8	–	–
Surf Scoter	1.16	100	1.06	42,392	44.9	24,558	26.0
Surfbird	0.21	93	0.19	73,742	14.3	102,248	19.8
Black Turnstone	0.14	99	0.16	6,297	1.0	12,432	1.9

Table 64. Percent occurrence and percent aggregate weight of prey items in gut samples (esophagus/proventriculus) of glaucous-winged gulls. Northern Montague Island, 13 Dec 96-24 Feb 97 (winter), and 14 Apr 97-12 May 97 (spring).

Species	Winter (*n* = 10)		Spring (*n* = 30) Prespawn (*n* = 8)		Spring (*n* = 30) Spawn (*n* = 4)		Spring (*n* = 30) Postspawn/ Prehatch (*n* = 14)	
	% Occ[a]	% Wt[b]	% Occ	% Wt	% Occ	% Wt	% Occ	% Wt
Eggs: Herring Eggs	-	-	-	-	25	5.9	100	92.4
Fish: *Clupeas Pallasi*	-	-	37.5	69.4	-	-	-	-
Offal	10	4.1	-	-	-	-	-	-
Unidentified Fish	-	-	25	28.6	100	94.1	7.1	7.6
Stars: *Evasterias trochelli*	20	69.0	-	-	-	-	-	-
Pycnopodia helianthoides	30	23.0	-	-	-	-	-	-
Pisaster ochraceus	10	3.3	-	-	-	-	-	-
Unidentified Sea Star	10	0.4	12.5	2.0	-	-	-	-
Crustaceans: *Cancer* sp.	10	0.03	-	-	-	-	-	-
Unidentified Organic Matter	20	0.2	-	-	-	-	-	-

[a] Percent Occurrence: number of birds with prey type / total birds

[b] Percent Aggregate Weight: weight of prey type / total weight of all prey items

MAMMALS

Baleen Whales

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Baleen whales are represented by humpback whales, for which however, we have no recent population estimates for Prince William Sound. Waite et al. (in press) use abundances of 140 to 200 to represent a range for the population in Prince William Sound, the south side of the Kenai Peninsula and adjacent waters. The range found during the post-EVOS studies in 1989 and 1990 probably still holds (O. von Ziegesar et al. 1994). Total numbers that use the study area of the model in a given year probably range from 60-90 whales (O. von Ziegesar, unpub. data). Some of these stay all winter, or at least there are humpback whales in the Sound during all months of the winter. There are probably the fewest between mid-January to mid March, but there may be as many as 10-20 even during these months (O. von Ziegesar, unpub. data). We have done no winter surveys, but observations from winter herring surveys indicate humpback whales are associated with the herring all fall and winter. The amount these whales eat is estimated at 30 $g \cdot kg^{-1} \cdot day^{-1}$. and an average humpback is estimated to weigh 32.7 t (from Dolphin 1987). In the summer a majority of prey are euphausiids based on sonar scans (M. Nerini, formerly with NMFS National Marine Mammal Lab., unpub. data) and scats observed opportunistically (O. von Ziegesar, unpub. data), although they certainly feed on sand lance and herring as well. It appears that the diet shifts toward herring in the fall (late September, October) and into winter, but this is from observational data from herring researchers in late fall and winter. Estimated population parameters for baleen whales are listed, along with those for other whales, in Table 65.

Table 65. Cetacean input parameters for PWS

Group	Biomass ($t \cdot km^{-2}$)	+/- (t)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)
Baleen whales	0.1486	0.0743	0.05	10.95
Small cetaceans	0.0088	0.0044	0.10	29.20
Transient orcas	0.0019	0.0013	0.05	6.00
Resident orcas	0.0113	0.0075	0.05	8.67
Aggregated orcas	0.0132	--	0.05	8.29

a) P/B and Q/B estimates for PWS were derived by multiplying annual estimates for the group by the estimated fraction of a year spent in PWS (0.25).

Sea otter

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The purpose of this section is to provide estimates of biomass, mortality, prey consumption and dietary composition for sea otters (*Enhydra lutris*) in Prince William Sound, Alaska. Biomass estimates are derived from an aerial survey conducted in 1994. Sea otters in Prince William Sound are distributed by bathymetric contours as follows; shoreline to 40 m contour = 0.85. 40-100 m contour = 0.10 and >100m = 0.05 (Bodkin and Udevitz 1996). Prey data were obtained from field observations in 1996 and 1997. We assume biomass, mortality, and prey composition remain constant over time. We assume sea otters require 25 % of their weight/day in prey (not including shells) (Costa 1982), and used conversions from Kvitek (1992) to estimate wet weight of clams from shell length. Food habits data were extracted from Holland-Bartels (1997) and unpublished data from the authors. Estimates of sea otter population parameters are found in Table 66.

Methods

Table 66. Estimates of sea otter population parameters for PWS.

Biomass[a] ($t \cdot km^{-2}$)	95% CI (±; $t \cdot km^{-2}$)	P/B[b] ($year^{-1}$)	Range ($year^{-1}$)	Q/B[c] ($year^{-1}$)	Range ($year^{-1}$)
0.0450	0.0150	0.13	0.10-0.15	117	100-140

a) Biomass derived from 1994 survey of PWS including Orca inlet in which the population size was estimated at 14,352 individuals (see above tables);
b) Corresponds to instantaneous rate of total mortality;
c) Ration for an average sized individual.

Table 68. Correction factors for population estimates

Observer	No. of ISUs	Factor	S.E.
J.B.	42	1.92	0.20
G.E.	55	1.39	0.08

We conducted a survey throughout all of Prince William Sound, including Orca Inlet, in July of 1994. The aerial sea otter survey methodology consists of two components: (1) strip and (2) intensive search units (Bodkin and Udevitz 1991, 1996). Sea otter habitat was sampled in two strata, high density (shoreline - 40 m contour) and low density (40 - 100m contour), distinguished by distance from shore and depth contour. Survey effort was allocated in proportion to expected sea otter abundance (0.85 for high abundances, and 0.15 for low abundances) by adjusting the systematic spacing of transects within each stratum. Transects with a 400 meter strip width on one side of a fixed-wing aircraft were surveyed by a single observer at an airspeed of 65 mph (29 $m \cdot s^{-1}$) and altitude of 300 feet (91 m). The observer searched forward as far as conditions allow and out 400 m, indicated by marks on the aircraft struts, and recorded otter group size and location on a transect map. A group was defined as one or more otters spaced less than three otter lengths apart. Intensive search units (ISUs) were used to estimate the proportion of sea otters not detected on strip transect counts. ISUs were flown at intervals dependent on sampling intensity throughout the survey period, and were initiated by the sighting of a group, then followed by five concentric circles flown within the 400-m strip perpendicular to the group that initiated the ISU. Two observers were used in 1994, resulting in separate estimates of detection for each observer.

Food habits and foraging success of nearshore feeding sea otters were measured during shore based observations in 1996 and 1997. High power telescopes (Questar Corp., New Hope, PA) and 10X binoculars were used to identify prey type (lowest possible taxon), prey number, and prey size (small <5 cm, medium 5-9 cm, and large >9 cm), and dive success (prey captured or not) during foraging 'bouts'. A 'bout' consisted of observations of repeated dives for a focal animal while it remained in view and continued to forage (Calkins 1978). Assuming each foraging bout records the feeding activity of a unique individual, bouts were considered independent while dives within bouts were not. Thus the length of any one foraging bout was limited to one hour after which a new focal animal was chosen.

Results

In July 1994, we conducted an aerial survey of sea otters in PWS (Bodkin and Udevitz in press), which included 7,328 km^2, of which 2,987 km^2 were considered high density stratum and 4,341 km^2 low density stratum. The results of the survey are presented in Table 67. It is likely that the estimate of abundance generated from this survey methodology are negatively biased by about 5-10%, due to detection probabilities of 90-96% during survey development experiments (Bodkin and Udevitz 1991). Although there may be small scale (10s of km) movements of sea otters seasonally, we believe that the overall abundance of sea otters in Prince William Sound does not vary seasonally.

We calculated a mean sea otter weight of 23.0 kg based on actual weight of >116 sea otters captured and weighed in western PWS in 1996 and 1997. This includes 79 females and 37 males, roughly in proportion to the sex ratio in the population. We estimated an instantaneous mortality rate of 0.13 $year^{-1}$ based on an average age of 7 years in the live population. We assumed that immigration approximates emigration.

A total of 1425 foraging dives were observed between 19 May and 23 July, 1996, including 631 dives during 70 forage bouts at Knight Is-

Table 67. Otter counts, unadjusted population size estimates and adjusted population size estimate in the 1994 sea otter survey, PWS.

Type of estimate	*Population* estimate (N)	s.e.
Unadjusted[a]	1085	2051
Adjusted[b]	14352	2418

a) 1973 otters were observed on the 681 km^2 transects;
b) See correction factors (Table 68).

land (mean of 9 dives/bout), and 794 dives during 58 bouts at Montague (mean of 13.7 dives/bout). A total of 1,271 foraging dives were observed between 23 May and 15 August, 1997, including 604 dives during 49 forage bouts at Knight Island (mean of 12 dives/bout), and 667 dives during 58 bouts at Montague (mean of 11.5 dives/bout).

Prey composition was similar between areas and was dominated by clams. Butter clams (*Saxidomas giganteus*) were the most commonly identified species followed by soft shell clams. Prey types other than clams included small crabs (primarily *Telmessus*), fat innkeepers (*Echiurus*), and sea stars (*Evasterias* and *Leptasterias*) all of which were uncommon or missing from the diet at Knight. Sea urchins (*Stongylocentrotus droebachiensis*) were rare in the diet in both areas, though urchins were present in scats examined in both areas (4 of 44 examined at Knight (9%), and 6 of 43 examined at Montague (14%), possibly reflecting seasonal differences in sea urchin utilization.

Prey composition for the purpose of this report is summarized by faunal category in Table 69 and is a compilation of food habit data collected during the summer of 1996 and 1997. It is likely that prey composition varies geographically within the Sound, but our results are similar to results of others (Calkins 1978, Doroff and Bodkin 1994). It is also possible that seasonal differences in prey species composition exist but we have no data to address this possibility

Table 69. Diet matrix for sea otters in PWS[a].

Taxa	% in diet	PWS model component	% in diet
Clams	80	Shallow large infauna	40
Mussels	12	Deep large infauna	40
Crabs	4	Shallow large epifauna	16
Other	4	Deep large epifauna	4

a) Fraction refers to weight, or volume, of energy units (NOT frequency of occurrence)

Pinnipeds

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This group consists of harbor seals (*Phoca vitulina richardsi*) and Steller sea lions (*Eumetopias jubatus*). Harbor seals occur in most coastal areas throughout PWS, particularly Northwestern, Southwestern, and Eastern areas. Sea lions are far less abundant than harbor seals in the PWS as defined here.

Harbor seals occur in PWS throughout the year. Data from 50 seals satellite tagged during 1992-1997 indicate that most PWS harbor seals show strong site fidelity, remaining near the haulouts where they were originally tagged. Some seals make feeding trips to the Gulf of Alaska (GoA), the Copper River Delta, or between the northern and southern sound, especially during fall through spring. Usually these seals return to PWS during their feeding trips. Occasionally longer movements are made (to Cook Inlet or Yakutat) and seals may or may not return to PWS. Twelve newly-weaned harbor seal pups tagged in 1997 also made relatively local movements, with occasional trips to the GoA by a few. Since satellite tags remain attached only until the following molt (usually 9-11 months after tagging), the tags do not provide information about any long-term movements that might occur. However, several tagged seals have been recaptured 1-3 years later near the original capture location.

Based on GoA samples collected in the 1970s,

Table 70. Ecopath input parameters for harbor seals in PWS, 1992-1997

Species	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Export (t·km^{-2}·yr^{-1})
Harbor Seal	0.05 (± 0.04-0.06)[a]	0.06	25.55[b]	0.002

a) Based on the range of population estimates since 1990 (does not represent 95% CI);

b) Converted by the editors from Q = 2,044 kg·seal^{-1}·year^{-1} in PWS cumulative mortality of harbor seals from birth to 4 years was estimated at 77% (Pitcher and Calkins 1979). At 4-7 years, mortality was 9-11% per year. Mortality remained fairly constant at 9-10% per year until age 20, increasing to about 14% after age 20. Mortality may be substantially different in other areas. For example, in British Columbia where the harbor seal population has been rapidly growing, subadult mortality was about half what it was in the GoA (Bigg 1969). There are no recent data for the GoA (including PWS). Maximum recorded age for harbor seals in Alaska is 32 years. In the GoA, sex ratio is about 50:50 until seals reach 20 years of age. Then, the ratio is approximately 78% females.

Table 70 shows estimated population parameters for harbor seals in PWS. The estimated population size of harbor seals in PWS is 5,500 (range 4,600 - 6,400). This value is the mean (range) of Trend A + Trend B x 1.61 correction factor. It does not include every seal in PWS, and no confidence intervals are available. The average size of adults in the GoA during the mid 1970s was 84.6 kg for adult males and 76.5 kg for adult females. Assuming a 50:50 population of males and females, and a PWS population size of 5,500, there would be 443 t of harbor seal in PWS. Adding 10% for Steller sea lions gives about 487 t of pinnipeds in PWS, or 0.054 $t \cdot km^{-2}$.

Daily consumption by harbor seals ranges from 6-8% of body weight per day (Ashwell-Erickson 1981; Ashwell-Erickson and Elsner 1981), and depends on the caloric content of the prey and season. Captive feeding experiments showed that harbor seals consume ~4% daily of their body weight in March through August and ~8% in winter. About 40% of the total annual net energy required by the harbor seal population is necessary to sustain 0-3 year olds (50% of the energy goes to growth from birth to weaning stages, compared with 2-7% from weaning to three years, and less than 2% from 2-24 years). Values given in Table 70 for PWS harbor seal P/B, Q/B, and export are used here for PWS pinnipeds.

Harbor seal diet varies by age and season. There are no recent stomach contents data for PWS harbor seals. Based on data from the mid 1970s, in order of descending frequency of occurrence, pups ate capelin, pollock, tomcod, and cephalopods; yearlings ate herring, pollock, squid, capelin, eulachon; other subadults ate pollock, herring, tomcod, cod, capelin, flatfish, squid; and adults ate pollock, herring, cod, eulachon, octopus, squid, tomcod, flatfish, and salmon. By month the most commonly eaten prey were: February - pollock, herring, cod, and cephalopods; March - pollock, capelin, herring, and cod; April - herring, pollock (capelin, eulachon); May/June - eulachon and pollock; July - eulachon, herring, pollock, and tomcod; September/October - pollock, tomcod, herring, cod, and flatfish; November - pollock, squid, octopus, and cod. Flatfishes were also eaten, but the amount is unknown. Recent data from analysis of fatty acid signatures in blubber indicates that these same species were still present in harbor seal diets in the mid 1990s. Additional analytical models must be developed before the relative importance by species can be estimated for the fatty acids data. An estimated pinniped diet composition is shown in Table 71.

The kill of harbor seals is about 250 $year^{-1}$, or 0.002 $t \cdot km^{-2} \cdot year^{-1}$. Steller sea lions are not hunted.

Table 71. Pinniped diet composition (% weight) in PWS, 1992-1997

Prey	Harbor seals	Pinnipeds[a]
Pollock	47	52
Herring	11	12
Squid	6	12
Salmon	10	10
Capelin	4	5
Nearshore pelagics	5	--
Octopus	5	--
Shallow Small Epifauna	--	5
Eulachon	2	2
Pacific Cod	1	2
other	9	--

a) Adapted from harbor seal diet by R. Hobbs (including *Steller sea* lions)

Orcas

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Transient Orcas

There are 11 transient killer whales (in group AT1) that seem to spend most of their time in the PWS 'region' and other transients that come and go from other regions in the Gulf of Alaska. About 8 of those are in the Prince William Sound region at any given time (C. Matkin unpublished data). We do not know how these numbers change in the wintertime. For the purpose of this exercise we assume that average residence time in the study area for the 19 whales is 3 months with a range from 1 to 6 months. The average weight of a killer whale is 3550 kg (Baird 1994). Barrett Lennard et al. (1995) has the best estimates of killer whale food consumption; for transients, this was 58.7 kg of marine mammal·day^{-1} (lower for transients than residents because of higher caloric values for pinniped and small cetacean prey). A 25% correction was added (for wild/captive diet extrapolation) for transients and residents, though this is questionable (C. Matkin; and Barrett Lennard, pers. comm). From observations of transient killer whales the diet consisted of 32% harbor seal, 39% Dall's porpoise, 6% harbor porpoise, and 23% unidentified marine mammals. (Saulitis et al., unpublished data). For the purpose of this study we have prorated the unidentified marine mammals into the three identified species.

Resident Orcas

There are 112 resident type killer whales that center their range in PWS. This center seems to have recently shifted a bit westward, into the Kenai Fjords region. For the purpose of this exercise we assume that average residence time in the study area for the 112 whales is 3 months with a range from 1 to 6 months. Barrett-Lennard et al (1995) has the best estimations of killer whale food consumption. The rate for resident killer whales fish consumption was estimated at 84.3kg of fish·day^{-1} (176K kcal·day^{-1}). A 25% correction factor was applied here to increase this daily consumption figure for both types of killer whales but one of us (C. Matkin) thinks that this adjustment is questionable. The average weight of a killer whale is 3550 kg (Baird 1994). Also from this study we found 95% of the scale samples collected from resident fish kills were coho salmon, the rest being divided between chum and chinook salmon (Saulitis et al., unpublished data). Although there may be some bias in the sampling, the dependence on specific salmon species, particularly coho salmon is probably real. Observations indicate that resident killer whales begin feeding on herring in April. We have no way of knowing how the diet changes for either residents or transients during the November-March period.

Table 72. Estimated diet compositions of orca categories in PWS

Prey	Transient orcas[a]	Resident orcas[a]	Aggregated orcas[b]
Harbor seal	39.7	–	5.7
Dall's porpoise	46.7	–	6.7
Harbor porpoise	13.7	–	2.0
Salmon	--	75.0	64.2
Herring	--	25	21.4

a) Diets from Matkin and Hobbs (above);
b) A generalized orca diet was derived by multiplying the diet proportions for each orca group by their biomass proportions in PWS (transient: 0.144; resident: 0.856).

Orca aggregation and disaggregation

(Thomas A. Okey)

The biomass used for the aggregated orca group (0.003) is ¼ of the sum of the biomasses of each orca group because the average residence time in PWS is 3 months. The Q/B and the P/B values were derived by calculating means weighted by the relative biomass of each orca group presented above (Table 65). Aggregated diet composition was likewise calculated by multiplying the prey proportion for each orca group by their biomass proportion of each orca group (Table 72).

The single killer whale group was finally resplit into two distinct groups: transient orcas and resident orcas

The PWS Ecopath model working group initially decided to distinguish killer whales into two groups, transients and residents—as the diets of these two types of orcas are highly distinct in the wild (Ford 1994, 1999). Thus, two orca groups were included in the earliest versions of the PWS Ecopath model. However, these groups were aggregated to make room for other groups in the model that needed to be dis-aggregated, in order to avoid exceeding a maximum of 50 groups in the model. This made the task of orca dis-aggregation simple since original authored sections existed for these groups (see above) enhanced with additional prey information (McRoy and Wyllie Echeverria 1990).

As the result of dis-aggregating orcas, the 'small cetacean' group (porpoises) and the 'pinnipeds' group needed adjustment in order to balance the model. The small cetacean P/B value was increased from 0.15 to 0.24, and the pinniped biomass was increased from 0.066 to 0.072 t·km^{-2}.

Sea otters were added to the diet of transient orcas at a low level (1.5%) because transient orcas have recently been observed to switch to consuming sea otters (*Enhydra lutris*) throughout the Aleutians and in Prince William Sound (Estes et al. 1998, Hatfield et al. 1998, Garshelis and Johnson 1999). Otters were added to the transient orca diet at a small level because orcas could have a profound effect on otter populations in PWS, as they have in the Aleutians, even if otters are a small proportion of the transient orca diet (Estes et al. 1998). With this inclusion, transient orcas could now switch to eating more otters when otter densities are high and other orca prey are scarce. Several other species of fishes were added to the orca diets at 1% levels to facilitate prey switching (see verification section).

Small Cetaceans

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The small cetacean group is composed primarily of Dall's porpoise and harbor porpoise. Dall's porpoise are most common during the summer and early fall and less common in late fall, winter and spring and may leave the Sound at that time (C. Matkin, unpublished data). Harbor porpoise are more often sighted in the fall, winter and spring than the summer and often the largest groups appear in late March and early April (C. Matkin, unpublished data). For this exercise we assume that the temporal behavior of these two porpoise species is complementary so that their peak populations are in September for Dall's porpoise and March for harbor porpoise. The diet preferences shift toward those of Dall's porpoise in the summer and fall and harbor porpoise in the winter and spring. Dahlheim et al. (unpub. data) estimate the density of harbor porpoise at 0.048 ·km^{-2} (CI = 0.030 - 0.066) in the region that includes Prince William Sound. Hobbs and Lerczak (1993) estimate the density of Dall's porpoise in the Gulf of Alaska at 0.11 ·km^{-2} (CI = 0.07 - 0.16). An average Dall's porpoise weighs 136 kg, and an average harbor porpoise weighs 55 kg (Wynne 1992). Thus, the annual biomass density estimate for small cetaceans is the mean of the biomass density estimates of Dall's and harbor porpoise.

Harbor porpoise in captivity typically eat between 4% and 9.5% of their body weight per day (Kastelein et al. 1997). We use 8% as an intermediate value for active porpoise and apply it to Dall's porpoise also. Typically Dall's porpoise feed on epi- and meso-pelagic squids and fishes (mostly <30 cm in length). In the northwestern North Pacific Ocean Dall's porpoise feed primarily on squids (Gonatidae) and lanternfish (Myctophidae) (Jefferson 1988). Although harbor porpoise feed primarily on gadoid and clupeoid fishes in the range of 10 - 25 cm, they also feed on a variety of cephalopods and other small fishes (Leatherwood et al. 1982, Kastelein et al. 1997). Relative fractions of components of the diets are unknown, so the above groups were roughly apportioned for this exercise based on availability in the model. The general parameters used for this group are presented in Table 65.

DETRITUS

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For the purposes of this model, detritus is defined as organic carbon that is readily accessible and usable by organisms in the system. The overall estimate for PWS detritus (134 $tC{\cdot}km^{-2}$) is the sum of a water column estimate (14 $tC{\cdot}km^{-2}$) and a conservative sediment estimate (120 $tC{\cdot}km^{-2}$)(see below). Detritus pools in the sediment and the water column were each split into nearshore and offshore detritus groups according to respective sizes of these zones, thereby expressing each of the pools on a PWS-wide basis. The resulting split estimates were then combined within zones to estimate the detritus masses of nearshore (19.52 $tC{\cdot}km^{-2}$) and offshore (114.48 $tC{\cdot}km^{-2}$) detritus groups. Approaches to calculating the detritus mass for these two groups are described in the following sub-sections.

A third detritus group, 'nekton falls,' consists of 'dead discards' from PWS fisheries and salmon carcasses that re-enter the system. The 'nekton falls' group is discussed in the 'fisheries' section and the 'adult salmon' section in this volume.

Benthic detritus pool

Feder and Jewett (1988) developed a carbon budget for Port Valdez, in PWS, in which the pool of benthic detritus (organic carbon; OC) was estimated to be 120 $gC{\cdot}m^{-2}$ (120 $tC{\cdot}km^{-2}$), based on an estimate by Naidu and Klein (1988). This is probably a minimum estimate for the larger Prince William Sound since the percent organic carbon measured in Port Valdez sediment was lower than almost all 24 PWS stations investigated in 1990 by Feder and Blanchard (1998) (Table 74), and because the organic carbon-limited benthos of Port Valdez is less abundant than the benthos of the outer Prince William Sound and the adjacent shelf (Feder and Jewett 1988, H. Feder, UAF IMS, pers. comm., November 1999). Although the OC in Port Valdez sediment may be locally supplemented by some terrigenous sources (which are less labile, i.e., useful as food sources), seasonally-dense zooplankton densities may disproportionately limit sediment OC thereby uncoupling planktonic production from the benthos. Benthic systems are more tightly coupled with overlying planktonic systems in certain nearshore nearshore continental shelf systems of Alaska, thereby receiving higher depositions of usable organic carbon (Grebmeier and Barry 1991), and this may be more true for outer PWS than Port Valdez (H. Feder, pers. comm., November 1999).

Estimates of degradable organic carbon in the mixed surface layer of sediment (0-20 cm) throughout the worlds oceans also indicate that the PWS benthic detritus estimate of 120 $tC{\cdot}km^{-2}$ may underestimate the pool of organic carbon in PWS; degradable organic carbon on continental margins is estimated to range from 450-760 $tC{\cdot}km^{-2}$, while on abyssal plains it may range from 53-103 $tC{\cdot}km^{-2}$ (Emerson et al. 1987). However, the long term persistence of 'degradable' organic carbon detected in these sediments indicates that some fractions of the degradable OC in this surface mixed layer might be unusable by benthic fauna. In this light, benthic assemblages could exist in a state of carbon limitation even in situations of apparently excess organic carbon. Such limited accessibility of organic carbon by benthic fauna is supported by evidence that only a low proportion of sea floor OC is used, and a high proportion is refractory (O'Reilly 1985). Therefore, the low proportion of sediment OC that is usable by benthos may offset the underestimate of organic carbon for PWS, due to the tendency for under-representation of PWS OC by Port Valdez data and the expression of OC in dry weight. Esti-

Table 74. Percent organic carbon in sediment from locations in and around Prince William Sound and from earth's continental margins and abyssal plains. Means are presented with standard errors, except for range data from Port Valdez.

Locations of samples	Percent OC
13 PWS sites (40m depth)[a]	1.57 ± 0.44
13 PWS sites (100m depth)[a]	1.24 ± 0.28
26 PWS sites (40m & 100m)[a]	1.41 ± 0.26
Port Valdez[b]	0.1 – 0.6
4 GoA shelf and slope sites[c]	0.55 ± 0.09
Earth's continental margins[d]	1.02
Earth's abyssal plains[d]	0.34

a) 1990 data from Feder and Blanchard (1998);
b) range from Feder and Jewett (1988);
c) from Seminov (1965) *in* Feder and Jewett (1986); these values likely underestimate %OC in the more OC-rich northern gulf region, which includes PWS;
d) estimates from Emerson et al. (1987).

mation of the extent of such compensation was not attempted, due to uncertainty in these variables.

Pelagic detritus pool

The standing mass of pelagic detritus in Prince William Sound was estimated to be 14 tC·km^{-2} based on a contributed value for primary production of 228 tC·km^{-2}·year^{-1} (doubled from P. McRoy's contributed value of 114 tC·km^{-2}·year^{-1}, *see* Phytoplankton section) and a mean PWS euphotic depth of 25 (D. Eslinger, pers. comm., 5/1998) using the following empirically derived equation from Pauly et al. (1993);

$$\log_{10}D = -2.41 + 0.954 \log_{10}PP - 0.863 \log_{10}E$$

where D is the mass of standing pelagic detritus in tC·km^{-2}, PP is the primary production in tC·km^{-2}·year^{-1}, and E is the euphotic depth in m.

This new estimate of the standing mass of pelagic detritus in PWS (14 tC·km^{-2}) was used as wet weight in the PWS model, as an applicable conversion from C to wet weight was not identified for detritus. The model may thus underestimate the wet weight of standing detritus, but these values can be easily modified in the future by users who can identify a useful conversion factor.

The pelagic detritus pool and the benthic pelagic pools were apportioned into nearshore and offshore detritus categories by calculating the relative space for each pool in the area corresponding with each category. For example, 0.64% of the pelagic detritus space (volumetric) occurs inshore of the 20m isobath, while 99.36% occurs offshore (integrated to 300m mean depth). Likewise, 16% of the benthic detritus space (area) occurs inshore of the 20m isobath, while 84% occurs offshore. The splits of the pools apportioned to each zone were then combined for zone-specific estimates of detritus mass (Table 73). The large discrepancy between inshore and offshore values arises because the detritus pool in each area must be expressed on a sound-wide basis like the other groups in the model.

Input of terrestrial organic material

An estimate of the flux of labile terrestrial organic carbon to PWS sediments (9.6 t·km^{-2}·year^{-1}) was explicitly specified in the model. This import was split evenly between the inshore and offshore detritus groups (4.8 t·km^{-2}·year^{-1} each) even though the area corresponding to the nearshore detritus group is 16% of the total PWS area, with the effect of the nearshore zone receiving five times the input of terrestrial detritus as the offshore zone.

Several studies indicate that terrigenous sources of organic carbon make up a considerable proportion of the total organic carbon that reaches

Table 73. Estimated mass of detritus pools in PWS split into nearshore and offshore zones. Zones are delineated by the 20m isobath. Density values for each area are expressed on a sound-wide basis for compatibility with other groups in the model.

Detritus group	Mass of detritus (tC·km^{-2})		
	Pelagic	Benthic	Combined
Nearshore	0.09	19.43	19.52
Offshore	13.91	100.57	114.48

the sea floor of continental margins (e.g., Fahl and Stein 1997, Hedges et al. 1997, Macdonald et al. 1998). On the Canadian Beaufort shelf, terrestrial POC comprised 39% of the total POC reaching the sea floor (primary produced POC made up the remaining 61%) (Macdonald et al. 1998), but in portions of lower Cook Inlet, which is adjacent to PWS, Lees and Driskell (1981) found that the majority of detritus on the bottom is from terrigenous sources (*also see* Feder and Jewett 1986). Thus, the 24 $t{\cdot}km^{-2}{\cdot}year^{-1}$ estimate of net flux of terrigenous organic carbon to the PWS sea floor is the product of Naidu's (1988) estimate of 48 $t{\cdot}km^{-2}{\cdot}year^{-1}$ for net flux of organic carbon to the sediments of Port Valdez and 50%, which represents the proportion of terrigenous origin OC in PWS sediments, based on the information presented above. However, a large proportion of terrigenous organic carbon (e.g., 60%) has been found to go unused (Macdonald et al. 1998 *also see* Hedges et al. 1997). The proportion of used to unused terrestrial OC might vary considerably among nearshore benthic systems, but its application here results in an adjusted estimate of 9.6 $t{\cdot}km^{-2}{\cdot}year^{-1}$ for the flux of liable terrigenous organic carbon to the PWS sea floor.

Adjusting assimilation efficiencies

Unassimilated food / consumption ratios for plankton and benthic groups were changed from the 0.2 default to 0.4, meaning that the assimilation efficiencies (unassimilated food / consumption) were set to 60% rather than 80% for these groups.

Default assimilation efficiencies of 80% (unassimilated food / consumption = 0.2) in the Ecopath software are unrealistic for detritivores and herbivores because much of the organic material ('food') consumed by these groups is of low quality in the sense that it has a low energy to mass ratio, or the energy can be difficult to utilize because some material is difficult to digest. Thus, assimilation efficiency takes food quality into account, and the efficiency of the feeding and digestion of the prey organisms. Lower trophic level organisms (i.e., especially herbivores) consume food that is of lower quality as defined here.

Erroneously high assimilation efficiencies caused early versions of the PWS model to be unrealistically 'tight' in energy terms. This 'tightness' was manifest in the detritus. Detritus in the system did not build up at all when assimilation efficiencies were too high. This was not acceptable because the system's microbial community is implicit in the detritus, rather than explicit like all other biotic groups. In this model scenario, then, a considerable flux of 'extra' detritus must exist in order to feed the microbial community and account for other non-biological losses of OC.

This energetic tightness of the system exacerbated the dynamic instability identified by Powell and Pimm (1999). Buildup of detritus as the result of the downward adjustment of assimilation efficiencies can be inferred from the decreases in the ecotrophic efficiencies of detritus groups (Figure 1) and considerable increases in flows to trophic level two (Figure 2), as consecutive adjustments are made to plankton and benthic groupings. This surplus detritus should help to increase the stability of the model.

However, the 'instabilities' experienced by Powell and Pimm (1990) have other causes in addition to the 'energetic tightness.' Notably, these analyses all assume strictly top-down scenarios, i.e., assuming that all prey are always accessible to their predators, which is probably unrealistic. Such approaches, which feature full access of predators to prey, lead to artificial competitive exclusion, artificial cyclic behaviors, and the loss of functional groups due to diet overlaps and due to the assumption that increases in mortality rates are proportional to increases in predation (C. Walters, UBC Fisheries Centre, personal communication, 18 September 1999). This unrealistic behavior can easily be generated on Ecosim (by setting the vulnerabilities to '1'). However, our Ecosim runs were performed with lower vulnerability, corresponding to a mix of top-down and bottom-up interactions structuring the food web.

Powell and Pimm (1999) also found that higher trophic level organisms had higher instabilities than those at lower levels. This is to be expected in a fully top-down control model, because the complex stabilizing behaviors of higher trophic level organisms, such as compensatory prey switching and searching, are not accounted for. This is discussed by Powell and Pimm (1999; page 39, bullets 2 and 4). In this light, their finding that higher trophic levels in the early versions of the PWS model were less stable than lower trophic levels verifies reality, and indicates the need for inclusion of prey switching, refugia, spatial and temporal heterogeneity, and inefficiency of predation into dynamic simulations, as Ecosim and Ecospace do.

Although the adjustment of assimilation efficiencies led to a considerable increase of the detritus flux available to the microbial community, it did not change the character of the dynamics of particular working simulations in Ecosim. Further refinement of assimilation efficiencies in the future will further increase the usefulness of the Prince William Sound model.

PWS FISHERIES

PWS fishery catches were explicitly assigned to three fishery sectors: subsistence, recreational, and commercial. The commercial sector could be further broken down further into gear types, but this was not done at this stage.

Economic information about the fisheries can be incorporated in order to conduct fisheries-related economic analyses, but no fisheries economic information has been incorporated into the model at this time.

Fishery Landings Estimates for PWS, 1994-1996

Commercial landings in PWS

Estimates of commercial landing and discard rates in PWS are shown in Table 76. These estimates were developed from estimates of commercial groundfish (and shark) landings in Prince William Sound for 1994-1996 (Table 43; data provided by B. Bechtol, Alaska Department of Fish and Game); mean salmon landings in PWS from 1994-1996 (commercial and subsistence; Table 36; based on Morstad et al. 1997); and PWS herring landings (Figure 4; data provided by J. Wilcock, Alaska Department of Fish and Game); other information in this report (e.g. K. Frost, this volume), and the methods described in this section.

Recreational landings in PWS

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Recreational landings estimates were compiled using two data sources: (1) the number of fish harvested was estimated through a postal survey using a large random sample of resident and non-resident license buyers (Howe et al 1995-97); (2) the species composition of the sport harvest and average weights were estimated through a port sampling program located in the Valdez harbor, conducted from late May - early September. Recreational groundfish catch estimates for the years 1994-1996 in PWS are shown in Table 75.

Halibut average weights are based on lengths and a length-weight relationship generated by staff of the International Pacific Halibut Commission. Rockfish average weights were estimated from length measurements using species-specific or assemblage-specific length-weight relationships from 1991-1995 data from all over South-central Alaska. Lingcod average weights are based on measured lengths and a length-weight relationship using fish weighed in 1992-1996.

One potential problem with rockfish estimates is that the species composition at Valdez may not be representative of PWS as a whole. Another is that the species composition is very different by user group (guided/unguided) in Valdez, and that the proportions of harvest by each user group in Valdez are not representative of PWS as a whole. Guided anglers on charter boats in Valdez tend to fish the outer waters of PWS around Montague and Hinchinbrook Islands, and catch mostly black and yelloweye rockfish. Unguided anglers tend to fish inner, more protected waters, and catch more coppers and quillbacks. Estimates were not stratified by user group - when originally done no user group information was available for PWS harvest estimates. We explored the 1996 estimates to see the effect of this error; if 75% of the PWS catch is by unguided anglers (estimate from postal survey) and if we assume that the species composition of the rockfish harvest by private anglers all over PWS is similar to private anglers from Valdez, then we could be overestimating harvest biomass by 20% or more. This is because we are overestimating the harvest of larger black and yelloweye rockfish, and underestimating the harvest of smaller copper and quillback rockfish.

A third problem with the sport harvest data for Prince William Sound is that there is an unknown amount of error due to misreporting of areas fished, which would likely result in a slight underestimation of the halibut, rockfish, and lingcod harvested from PWS waters. The error arises from the fact that some anglers report harvest by the port of landing rather than from the waters they fished.

Fishery Discard Estimates for PWS, 1994-1996

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Fishery discards that were assumed to be dead were explicitly included and treated in the model. Species-specific estimates of discards are shown in Table 76 and were explicitly incorporated into the discard input interface and added to species-specific landings estimates to obtain discard-adjusted estimates of catch (i.e., catch = landings + discards). Discarded marine organisms entered a new and separate detritus category, 'nekton falls.' This general name was used instead of 'dead discards' because post-spawner salmon carcasses were also added to this group. This detritus group is then fed on by detritivores, scavengers, and other fish predators, in which discards were specified in diet compositions.

Commercial discards. – Discard flows from the commercial fishing fleet were estimated using reported discard information from the Alaska Department of Fish and Game (Charlie Trowbridge, unpublished data), but primarily from the fishery observer program of the National Marine Fisheries Service (M. Furuness; unpublished data; 10/1999). Annual discards for the PWS groundfish fisheries during the 1994-1996 period were estimated by calculating the ratios of discards in each species category to total catch (calculated from observed PWS cruises from 1994-1996 including hook and line, pot, and trawl fisheries) and applying these group-specific ratios to the total 1994-1996 PWS commercial catch estimate (provided by B. Bechtol, ADF&G; 8/1998), not including salmon and herring fishery catches. Discards associated with the herring fishery were then calculated based on rough estimates of discards for each PWS herring fishery sector (by J. Wilcox; pers. comm., 25 Oct 1999). Salmon fisheries were assumed to have zero discards.

Recreational discards. – Estimates of the flow of discards from the recreational fisheries in PWS were developed based on the statewide postal survey of recreational fishing in which

Table 75. Estimated recreational groundfish landings in PWS (t round weight):

Year	Halibut	Pelagic rockfish	Demersal rockfish	Slope rockfish	Total rockfish	Lingcod ^{b}
1994	338^{a}	14.810^{b}	20.984^{b}	0.54^{b}	36.333^{b}	17.360
1995	383^{b}	14.054^{b}	25.014^{b}	0^{b}	39.068^{b}	26.885
1996	429^{b}	8.708^{b}	21.628^{b}	0.105^{b}	30.441^{b}	17.631
Mean	383	12.524	22.542	0.215	35.281	20.625

a) From Meyer (1995);
b) Estimates from S.C. Meyer (Alaska Dept. of Fish and Game, pers. comm.).

respondents report the number of individuals of each species category that that they kept and released (Howe et al. 1995-1997). Mean weights of fish from the Valdez area were then applied to these PWS-wide data for to estimate total mass of 'kept' and 'released' fish. Ballpark estimates of mortality rates were then applied to the estimates of released fish mass for a rough estimate of the mass of 'dead discards,' which enters the 'nekton falls' detritus category in the PWS model. The mortality rates that were applied to the released fish was 0.75 for the entire recreational rockfish complex and 0.05 for both lingcod and Pacific halibut.

A caveat on these estimates of landed and released fish is required here because of the following limitations:

1. Recreational fishers are not particularly skilled at marine fish identification;
2. Landings and reporting from Seward may not represent fishing activity in PWS;
3. Average fish weights calculated from the Valdez area may not accurately represent all of PWS.

The fate of these discards was assigned to the detritus group 'nekton falls,' as described previously. The amount of post-run salmon carcasses re-entering the defined PWS system from adjacent rivers and spawning beds was taken as 25% of the estimated amount of escaped adult salmon (56,174 t, or 6.201 $t \cdot km^{-2} \cdot year^{-1}$), resulting in 1.55 $t \cdot km^{-2} \cdot year^{-1}$ being imported into the 'nekton falls' detritus group.

Table 76. Estimates of mean annual PWS fishery landings and discards (1994-1996).

Group	**Landings ($t \cdot km^{-2} \cdot year^{-1}$)**			**Dead discards ($t \cdot km^{-2} \cdot year^{-1}$)**	
	Commercial[a]	**Recreational**[b]	**Subsistence**	**Commercial**	**Recreational**[g]
Adult salmon	5.3726	-	0.0002[c]	-	-
Adult Pacific herring	2.5455	-	-	0.0551[e]	-
Pollock 1+	0.1710	-	-	0.0103[f]	-
Deep epibenthos	0.1430	-	-	-	-
Shallow demersals	0.0700	-	-	0.0001[f]	-
Pacific cod	0.0656	-	-	0.0016[f]	-
Pacific halibut	0.0268	0.0423	-	-	0.0015
Sablefish	0.0184	-	-	0.0008[f]	-
Rockfish	0.0060	0.0039	-	0.0005[f]	0.0020
Shallow large infauna	0.0030	-	-	-	-
Adult arrowtooth flounder	0.0004	-	-	0.0019[f]	-
Deep demersal fishes	0.0003	-	-	0.0023[f]	-
Sharks	0.0003	-	-	0.0022[f]	0.0019[h]
Lingcod	0.0003	0.0023	-	-	0.0002
Juv. arrowtooth flounder	0.0001	-	-	0.0019[f]	-
Juv. Pacific herring	-	-	-	0.1189[e]	-
Pinnipeds	-	-	0.0020[d]	-	-
Totals	8.4234	0.0485	0.0022	0.1958	0.0037

a) adapted from data from Bill Bechtol (ADF&G; see Table 44) ;
b) from estimates from S. Meyer (see Table 58 in this volume);
c) from Morestad et al. (1997);
d) from K. Frost (this volume);
e) based on ballpark estimates by J. Wilcox. ADF&G (pers. comm.. 25 Oct 1999);
f) based on postal surveys by Howe et al. 1995-1997;
g) group-specific discard ratios calculated from data provided by M. Furuness. NMFS; these ratios were applied to PWS landings data provided by B. Bechtol, AKF&G.
h) see Hulbert (this volume)

Constructing and Balancing the PWS Model

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The input parameters estimated in the previous sections by the PWS Ecopath working group were entered into the 'basic input' and 'diet composition' spreadsheets of the Ecopath with Ecosim software application (available free from http://www.ecopath.org/). Fishery and migration information provided in the previous sections, as well as detritus fate information was likewise entered into appropriate spreadsheets in the Ecopath software. In the PWS model, detritus fate information consists of the allocation of unconsumed and un-exported production from each group between nearshore (< 20 m depth) and offshore detritus categories.

The PWS model contains 48 ecosystem components - presently 50 is the maximum number that the Ecopath software can accommodate. Groups were considered for aggregation when this limit had been reached and more groups needed to be added to achieve optimal realism. Groups that were most similar affinities, in terms of their basic inputs, were identified using an automatic aggregation routine, and then aggregated. Resident orcas and transient orcas were the first groups to be aggregated, as their trophic levels were similar.

After the initial model construction, the ecotrophic efficiency (EE) terms were examined to evaluate the balance among components, and within the whole system. If a particular group was 'unbalanced' within the model (i.e., when its ecotrophic efficiency was greater than 1), this indicated that biomass or production/biomass values for the group were underestimated, or that consumption by other groups was overestimated.

Estimates of these parameters for the connected groups can then be adjusted to bring the groups and the model into balance. However, since there are multiple connections among groups, a change in the estimate for a predator, for example, may in turn change the degree of balance with *its* predators in addition to its prey. Thus, a haphazard approach to model balancing may result in arbitrary parameter adjustments and lead to unnecessary erosion of model realism. A semi-systematic method was employed to address this problem by developing a hierarchy of parameter adjustments; groups were ranked by degree of imbalance indicated by the amount that its EE exceeded 1.0; groups were also qualitatively ranked based on the balancer's degree of confidence in the contributed parameters. The balancer's degree of confidence was based on the weight of the available evidence.

One contributor pointed out that the general technique used to balance the first model iteration tended to adjust the biomass and production estimates upward in unbalanced groups rather than adjusting predator consumption rates downward (T. Dean, personal communication). This occurred for two reasons: (1) the assumption that biomass uncertainty is more likely underestimation than overestimation, (2) lowering consumption rates spreads effects of the adjustment across all prey rather than just the unbalanced one, and (3) adjusting diet compositions also influences more than just the target groups and can erode model realism, as well as refine it. The potential interjection of bias relating to these assumptions was considered during the final re-balancing. This resulted in improved agreement of the calculated phytoplankton production estimate with the initial phytoplankton production estimate provided by C. P. McRoy (see Phytoplankton section).

Adjustments to the contributed parameter values, made during balancing, are documented in the following sections.

Phytoplankton and primary production

Phytoplankton biomass was calculated by the model using P/B values of 190 and ecotrophic efficiency (EE) values of 0.95 for each of the two phytoplankton groups - nearshore and offshore phytoplankton. The annual phytoplankton production required for the model to run is calculated by the model as 3,040 t·km^{-2}·year^{-1}. This value is 38% greater than the initial phytoplankton production estimate of 2,210 t·km^{-2}·year^{-1} for PWS (*see* Phytoplankton section in this report). This initial estimate was based on samples from Port Valdez and Valdez Arm, and likely contained an underestimating bias due to turbidity caused by glacial silts. The alternative explanation is that the current model is *inflated* (see above). Both could be true. Total production, including macroalgae and eelgrass, was calculated to be 3,666 t·km^{-2}·year^{-1}, again 35% greater than the initial 2,711 t·km^{-2}·year^{-1} estimate for the total *primary* production of PWS from 1994-1996.

Macroalgae and eelgrass

The P/B for macroalgae and eelgrass was increased from 4 year^{-1} to 5 year^{-1} to balance the offshore detritus group. The biomass of offshore detritus was too low to support the demand on it by detritivores, and increasing the production of macroalgae/eelgrass effectively increases the contribution of drift algae to detritus.

Capelin

This group was balanced by shifting predation pressure from this group to juvenile herring, of which there was plenty in the model. Thus, predators were fed juvenile herring rather than so much capelin. In addition, the biomass value (0.231 t·km^{-2}) was increased 60% to 0.367 t·km^{-2}, and the P/B value was bumped from 3 to 3.5 year^{-1}.

Sandlance

Again, predators of sandlance were fed larger proportions of juvenile herring, and smaller proportions of sandlance.

Herring

The Adult herring group was balanced by increasing the biomass estimate by 10% to 2.810 t·km^{-2}.

Squid

The biomass estimate for squid (0.019 t·km^{-2}) was highly uncertain mainly because the data used for the estimate came from a sampling program that was designed for estimating pollock (*see* squid section in this report). The biomass estimate was increased to 3 t·km^{-2} to balance this group, implying either that this group is undersampled, or that the contribution of squid to its specified predators is overestimated.

Pollock

The pollock age 0 group was balanced by increasing the P/B estimate to the upper end of its confidence range (*see* Table 31) and doubling the biomass from the upper end of its confidence range (0.05 t·km^{-2}) to 0.11 t·km^{-2}. The pollock age 1+ group was balanced by shifting some of the predation by its predators to other groups in the diet matrix. The aggregated biomass estimate (2.99 t·km^{-2}) for pollock age 1+ was then multiplied by 2.5 to balance the group.

Sablefish

The sablefish biomass estimate was multiplied by 1.5 (from 0.195 t·km^{-2} to 0.293 t·km^{-2}) to balance this group. This original was thought to be an underestimate (see Sablefish section in this report). In addition, some of the contribution of sablefish to the diets of predators was shifted to Pacific cod (which was less than fully exploited trophically), in order to balance the Sablefish group.

Pacific cod

The biomass estimate of 0.555 t·km^{-2} derived for Pacific cod in PWS resulted in a calculated ecotrophic efficiency (EE) value of less than 0.5 indicating that over half the PWS biomass of Pacific cod die of old age and become detritus rather than being preyed upon. The estimate adapted from the 1989 post-spill PWS multispecies trawl survey data (0.225 t·km^{-2}) produced an EE that was slightly over 1. Thus, a value intermediate of the two independent estimates (0.3 t·km^{-2}) was used to achieve a reasonable EE of 0.884.

Juvenile Arrowtooth Flounder

The given biomass value (0.57 t·km^{-2}) was multiplied by 1.5 to 0.855 t·km^{-2}, a value well within the given confidence range.

Deep Epibenthos

This group was balanced by increasing the initial biomass estimate of 1.5 t·km^{-2} to 30 t·km^{-2} and increasing the P/B from 2 year^{-1} to 3 year^{-1}

Rockfish

Both the rockfish biomass estimate and predation on this group are highly uncertain. This group remained unbalanced after the biomass estimate was multiplied by four, and predation on this group was shifted to other groups. If these adjusted input parameters do not underestimate biomass and P/B, and the group remains unbalanced (EE is greater than 1), then the model indicates that PWS rockfish are declining. An import value of 0.14 t·km^{-2}·year^{-1} was entered in the migration sheet to represent rockfish decline, and allow model balancing (see Rockfish section for further discussion).

Deep Demersals

This group was balanced by increasing the biomass estimate by 10% to 0.96 t·km^{-2} and the P/B estimate by 30% to 1.008 ·year^{-1}.

Shallow Small Epifauna

The biomass estimate used for this group was developed using data from the intertidal zone (Highsmith *in* Dean, this volume). This group was balanced by tripling the biomass from 8.7 to 26.1, based on evidence that shallow small epifauna can attain tremendously high abundances and biomass in the shallow subtidal (Vetter 1994 and 1995; Okey 1997). The P/B was also increased from 2.0 to 2.8 to obtain balance for the group.

Macrofauna

The deep small infauna group was balanced by doubling the biomass estimate and increasing the P/B from 0.96 ·year^{-1} to 3 ·year^{-1} The shallow small infauna group was balanced by multiplying its P/B by six, from 0.6 year^{-1} to 3.6 ·year^{-1}. This value was then nudged [1] to 3.8 ·year^{-1}

Deep large infauna

This group was balanced by increasing the initial biomass estimate (16.2 t·km^{-2}) by 75% to 28.35 t·km^{-2}.

Shallow large infauna

The ecotrophic efficiency (EE) for shallow large infauna was less than 0.25. To increase the utilization of this component to a more realistic level, the ratio of deep and small large infauna (clams) in the sea otter diet was adjusted from equal allocations of 80% (40% and 40%) to 70% shallow prey (<20 m depth) and 10% deep prey (>20 m depth). This adjustment assumes that otters exploit shallow clam resources before venturing deeper.

Zooplankton

The biomass estimate of offshore omnivorous zooplankton was increased by 60% from 15.4 t·km^{-2} to 24.64 t·km^{-2}, and its P/B was increased to 11.06 ·year^{-1} (40% above the 7.9 t·km^{-2} value given for nearshore omnivorous zooplankton) to achieve balance in that group. Its Q/B was then increased from 17 to 22.13 year^{-1} to limit the P/Q to 0.5 year^{-1}, but this is more in line with the estimates for nearshore omnivorous zooplankton. The P/B of offshore herbivorous zooplankton was increased 60% from 15 t·km^{-2} to 24 t·km^{-2}. Nearshore omnivorous zooplankton biomass was increased 30% from 0.079 ·year^{-1} to 0.103 year^{-1} The biomass of nearshore herbivorous zooplankton was increased 40% from 0.097 year^{-1} to 0.136 year^{-1}

Small Cetaceans

To balance this group relative to the specified predation by orcas, the maximum specified biomass range value (0.0132 t·km^{-2}) was increased by 15%, and the P/B value was increased from 0.10 to 0.15 year^{-1}.

Orcas

Five new categories were added to the Orca diet at a symbolic 1% level because they were identified by McRoy and Wyllie Echeverria (1990; see below) as part of the PWS Orca diet. This refinement was not necessary to balance the model, but it was preferred, as it allows prey switching in the dynamic simulation routines Ecosim and Ecospace, and presumably make for more realistic simulations. Sea otters were added to the transient orca diet (see orca section).

Pinnipeds

This group was balanced by using the upper end of the given density estimate for harbor seals in PWS, are 0.06 t·km^{-2} (Frost, this volume), and adding 10% to account for Steller sea lions, resulting in a biomass estimate of 0.066 t·km^{-2} for pinnipeds in PWS.

Lingcod

The lingcod group was balanced by multiplying the initial biomass estimate by 3.5.

Salmon fry 0-12 cm

A P/B value of 7.154 year^{-1} was used instead of the calculated 9.844 year^{-1}. It is 27% smaller.

Sharks

The increased consumption by sharks in the model led to several groups consumed by sharks going unbalanced. This necessitated adjustment of the shark diet composition rather than adjusting parameters of its prey groups without justification. Adjustment of shark diet composition is justified due to the levels of uncertainty in its construction. In general, this diet balancing involved shifting predation pressure from the unbalanced group to the adult salmon group, which still had a relatively low EE value (0.454). This particular approach to balancing was strongly supported by August 1999 observations of high incidences of adult salmon in the diets of sleeper sharks in addition to salmon sharks (L. Hulbert, pers. comm., 21 September 1999; n = 16 stomachs). Table 77 indicates proportion of shark diet composition shifted to adult salmon according to species.

Table 77. Proportion of shark diet composition shifted from the following species to adult salmon.

Species	Proportion
Sharks	0.015
Pacific halibut	0.020
Sablefish	0.040
Adult arrowtooth	0.020
Juv. arrowtooth	0.008
Pacific cod	0.060
Deep demersals	0.004
Rockfish	0.006
Total	0.173

Final input parameters

The final input parameters and detritus fate information for the PWS Ecopath model, after the above balancing adjustments were made, are listed in Table 78; input diet composition values are listed in Appendix 5, and three immigration terms were entered: Adult salmon: 3.0 t·km^{-2}·year^{-1}; Eulachon: 3.0 t·km^{-2}·year^{-1}; and Rockfish: 1.4 t·km^{-2}·year^{-1} (the value for rockfish represents decline in the group and was needed for balancing).

Table 78. Basic input parameters and detritus fate for the Prince William Sound model, 1994-1996. TL is the trophic level calculated by Ecopath, OI is the omnivory index indicating the degree of omnivory, P/B is production/biomass, Q/B is consumption/biomass, and EE is the ecotrophic efficiency expressing the proportion of the production lost to export or predation. Detritus fate is a percentage allocation of the remaining production between detritus pools. Values in bold were calculated by Ecopath; values not bolded are empirically-based input estimates, contributed by a collaboration of experts on PWS (Okey and Pauly 1999).

Group	Trophic level	OI	Biomass $(t \cdot km^{-2})$	P/B $(year^{-1})$	Q/B $(year^{-1})$	EE	Detritus fate (%)			
							N. falls	Inshore	Offshore	Export
Transient Orca	**5.4**	**0.01**	0.001	0.05	6.04	-	1	-	50	49
Resident Orca	**4.9**	**0.21**	0.015	0.05	8.67	-	1	-	50	49
Sharks	**4.5**	**0.98**	0.662	0.10	7.00	**0.753**	1	-	99	-
Halibut	**4.5**	**0.36**	0.677	0.32	1.73	**0.865**	1	-	99	-
Porpoise	**4.5**	**0.20**	0.015	0.24	29.20	**0.989**	1	30	69	-
Pinnipeds	**4.4**	**0.14**	0.072	0.06	25.55	**0.994**	1	30	69	-
Lingcod	**4.3**	**0.35**	0.077	0.58	3.30	**0.816**	-	40	60	-
Sablefish	**4.0**	**0.87**	0.293	0.57	6.42	**0.774**	-	-	100	-
Adult flounder	**4.2**	**0.12**	4.000	0.22	3.03	**0.792**	-	-	100	-
Adult salmon	**4.2**	**0.06**	1.034	6.48	13.00	**0.660**	-	30	-	70
Pacific cod	**4.1**	**0.47**	0.300	1.20	4.00	**0.936**	-	-	100	-
Juv flounder	**4.0**	**0.12**	0.855	0.22	3.03	**0.956**	-	-	100	-
Avian raptors	**3.9**	**1.58**	0.002	5.00	36.50	-	-	25	-	75
Seabirds	**3.8**	**0.55**	0.011	7.80	150.60	**0.425**	-	40	40	20
Deep demersals	**3.8**	**0.80**	0.960	0.93	3.21	**0.984**	-	-	100	-
Pollock 1+	**3.8**	**0.25**	7.480	0.71	2.56	**0.982**	-	-	100	-
Rockfish	**3.7**	**0.26**	1.016	0.17	3.44	**0.969**	-	20	80	-
Baleen whales	**3.7**	**0.16**	0.149	0.05	10.90	-	1	-	99	-
Juv. salmon	**3.5**	**0.31**	0.072	7.15	62.80	**0.931**	-	30	70	-
Nearshre demersal	**3.3**	**0.24**	4.200	1.00	4.24	**0.710**	-	100	-	-
Squid	**3.3**	**0.01**	3.000	3.00	15.00	**0.938**	-	-	100	-
Eulachon	**3.2**	**0.63**	0.371	5.00	18.00	**0.998**	-	40	20	40
Sea otters	**3.2**	**0.18**	0.045	0.13	117.00	**0.005**	-	50	50	-
Deep epibenthos	**3.2**	**0.62**	30.000	3.00	10.00	**0.958**	-	-	100	-
Capelin	**3.1**	**0.02**	0.367	3.50	18.00	**0.962**	-	50	30	20
Adult herring	**3.1**	**0.01**	2.810	1.54	18.00	**0.955**	-	-	100	-
Pollock 0	**3.1**	**0.01**	0.110	2.34	16.18	**0.945**	-	50	50	-
Shal large epibenth.	**3.1**	**0.03**	3.100	2.10	10.00	**0.750**	-	80	20	-
Sea ducks	**3.1**	**0.00**	0.005	0.20	450.50	-	-	40	40	20
Sandlance	**3.1**	**0.01**	0.595	2.00	18.00	**0.841**	-	50	50	-
Juv. herring	**3.0**	**0.01**	13.406	0.73	18.00	**0.919**	-	30	70	-
Jellies	**3.0**	**0.11**	6.390	8.82	29.41	**0.004**	-	10	90	-
Deep sm infauna	**2.3**	**0.23**	49.400	3.00	23.00	**0.916**	-	-	100	-
Near omni-zoo	**2.3**	**0.19**	0.103	7.90	26.33	**0.980**	-	70	30	-
Omni-zooplank	**2.3**	**0.19**	24.635	11.06	22.13	**0.978**	-	10	90	-
Shal sm infauna	**2.2**	**0.18**	51.500	3.80	23.00	**0.941**	-	100	-	-
Meiofauna	**2.1**	**0.11**	**4.475**	4.50	22.50	**0.950**	-	20	80	-
Deep lg infauna	**2.1**	**0.09**	28.350	0.60	23.00	**0.931**	-	-	100	-
Shal sm epibent	**2.1**	**0.05**	26.100	2.30	10.00	**0.975**	-	70	30	-
Shal lg infauna	**2.0**	**0.00**	12.500	0.60	23.00	**0.516**	-	100	-	-
Near herbi-zoo	**2.0**	**0.00**	0.136	27.00	90.00	**0.978**	-	70	30	-
Herbi-zooplankt	**2.0**	**0.00**	30.000	24.00	50.00	**0.976**	-	10	90	-
Nearshr phytopl	**1.0**	**0.00**	**5.326**	190.00	-	**0.950**	-	70	30	-
Offshore phytopl	**1.0**	**0.00**	**10.672**	190.00	-	**0.950**	-	10	90	-
Macroalgae & grass	**1.0**	**0.00**	125.250	4.00	-	**0.135**	-	50	50	-
Nekton falls	**1.0**	**0.21**	2.000	-	-	**0.953**	-	80	20	-
Nearshore detritus	**1.0**	**0.30**	19.520	-	-	**0.542**	-	-	100	-
Offshore detritus	**1.0**	**0.46**	114.480	-	-	**0.587**	-	-	-	100

Verification of web structure

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The food web structure (diet compositions) of the PWS Ecopath model was compared with food web diagrams constructed for 35 individual species by McRoy and Wyllie Echeverria (1990). This approach was used to verify the existence of trophic links, not the magnitude of flows, though indications of 'principal prey' by these authors shed some light on relative flows. Inconsistencies are highlighted in the following sections; no comment was made when food webs were consistent.

Seabirds

Diet compositions of seabird species in Table 61 correspond well with individual food webs in McRoy and Wyllie Echeverria (1990), except for tufted puffins which the latter authors suggest consume capelin, sandlance, squid, euphausiids, and nearshore small epibenthos.

Avian predators

McRoy and Wyllie Echeverria (1990) included juvenile fishes, forage fishes, young sea otters, young seals, and young sea lions in the diet of bald eagles. These groups are represented by the 'other marine' category in Table 61, though predation on some of these groups is probably rare.

Small cetaceans

McRoy and Wyllie Echeverria (1990) indicate that salmon is a major prey of Dall's porpoise, whereas salmon were not considered part of the small cetacean diet in the current model. Beluga whales were also not included in the small cetacean category for Prince William Sound. It was decided that visitation of individuals from the Cook Inlet stock (~800 individuals) would have produced a PWS biomass too low to exist as a group in the model (and likely too low to be functionally important).

Pinnipeds

Squid was specified as 6% of the harbor seal diet in the PWS Ecopath model, whereas it was not included by McRoy and Wyllie Echeverria (1990). Squid was, however, included in the diet of northern fur seals.

Baleen whales (humpback whales)

McRoy and Wyllie Echeverria (1990) include both capelin and pollock as prey of humpback whales, whereas these two species were left out of the diet specification for humpback whales in the PWS Ecopath model. Conversely, sandlance was specified in the model's humpback whale diet, yet it was not included in McRoy and Wyllie Echeverria (1990).

Orcas

McRoy and Wyllie Echeverria (1990) identified five categories of primary prey of Orcas not specified in the PWS model: halibut, sablefish, Pacific cod, pollock, and greenlings. The model specified one category not included in their compendium—herring.

Trophic levels

Another aspect of food web structure that was verified are the trophic level estimates for PWS generated by Ecopath. These were found to closely correspond to those estimated by the ratios of stable nitrogen isotopes (Kline and Pauly 1998).

Ecosim and Ecospace Methodology

Once the Ecopath model was constructed and balanced, the effects of perturbations, or changes in fishing, were simulated over a selected time horizon (typically 10 years) by adjusting the mortality regime over that same period for one or more component of the ecosystem. This method was used to simulate a number of 'what if' scenarios provided during the model specification workshop in March 1998. These are listed in Box 2.

Adjusting the mortality regime enables a simulation of responses from connected components of the ecosystem based on their relationships and the rates of trophic flow among them. These mortality adjustments were drawn into Ecosim's graphical interface of mortality rate, using a mouse. Simulations can be repeatedly re-run as the user adjusts mortality rates. Scenarios were saved and archived within the software to be accessed and re-run at any time in the future.

The recently-developed Ecospace routine (Walters 1998, Walters et al., in press) was used to simulate changes in spatial distributions of Prince William Sound groups starting with information on habitat preferences as well as spatial distributions of habitats and organisms provided by contributors. Ecospace simulates dynamic, two-dimensional re-distribution of ecosystem components based on trophic interactions (flow) among organisms, their relative preferences for spatially-specified habitats, and their movement rates and vulnerability to predators in the various specified habitats.

A spatial representation of Prince William Sound and its various marine habitats was created in the spatial 'mapping' interface of the Ecospace routine. This was done by overlaying a geographically-referenced grid system over a scanned map of Prince William Sound using a computer drawing application. The grid was then reproduced with an Excel spreadsheet and hard copies were laid over one another. Boxes that covered mostly land were colored in and then transferred to Excel's coloring function. This map was then used for electronic and hard-copy distribution to contributors as a standardized template for specifying the distributions of organisms and habitats, on a resolution useable in the Ecospace application. This same template was used to create

Box 2. Hypothetical 'what if' scenarios for simulations runs

1. What if fishing pressure on herring increases or decreases; what if there is one stock of herring? two? three?
2. What if somebody decides to fish sandlance or capelin? This is probably far-fetched, but model simulations would likely show important trophic impacts of removing important forage fishes.
3. What if an earthquake raises the upper 10m of intertidal above sea level?
4. What if PWSAC goes broke and the hatcheries close?
5. What if there is another oil spill?
6. What if human impacts from the road to Whittier result in damage to intertidal habitats in the western part of PWS?
7. What if recreational fishing pressure removes 90% of the rockfish from PWS?
8. What if there is a major warm-water episode for 2 years, such that the upper 200 m of water over the shelf in the GoA is elevated by 2 °C ?
9. What if the bloom and sustained productivity lasts only for 3 weeks instead of the usual 12 weeks in PWS ?
10. What if the harbor seals continue to decline at 8% per year ?
11. What if dungeness crab return to PWS?
12. What if salmon prices drop or increase?
13. What if pollock disappear from PWS?
14. What if salmon farming were allowed in PWS?
15. What if a road were established to Cordova?
16. What if cruise ship traffic increases into Cordova?

the map of land and habitats in Ecospace.

An area 178 km wide (E-W) and 167 km tall (N-S), encompassing Prince William Sound, was re-constructed by coloring grid cells in the Ecospace mapping interface. Each grid cell was designated as land, or one of the following six habitats:

1. Nearshore rocky;
2. Shallow Soft Bottom;
3. Sandy/Muddy intertidal;
4. Open Water/Deep Soft Bottoms;
5. Productive entrances;
6. Deep fjords.

This specification was quickly accomplished by drawing with a mouse while toggling different category tools.

Preference for each habitat was then specified for each ecosystem component in the model, by going to 'ecology parameters' in the menu, as were other parameters such as 'relative movement in bad habitat', and 'vulnerability to predation in bad habitat'. Default settings proposed by the Ecospace software, and based on the developer's experience, were used as a guide for setting these parameters during this initial analysis. Redistribution of biomass densities of each species in PWS was then evaluated in the context of different hypothetical scenarios of system changes and forcing.

RESULTS

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The goal of the construction of a balanced trophic model of Prince William Sound using Ecopath was to incorporate all the biotic components of the marine ecosystem (implicitly or explicitly) in a cohesive description of the food web and to provide a functional venue for synthesis of existing ecosystem information to achieve that goal. This collaborative effort resulted in the construction of the most explicit Ecopath model constructed to date, including a total of 48 ecosystem components (Figure 6; *also see* Okey and Pauly 1999). Trophic connections have been omitted from the box diagram (Figure 6) because these connections are too numerous to display in a useful manner. The nature of the trophic interactions in this model is summarized by a matrix of mixed trophic impacts (Figure 7).

The Ecopath model of Prince William Sound was designed to view the system at a particular resolution, which is necessarily lower than that possible in concentrated studies of smaller sub-sections of the system, and thus some of the detailed information collected by other research projects in PWS cannot be incorporated into this analysis. However, the approach *is* designed to enable a whole-system view using parameters that are basic to understanding populations and the ecosystem, and which should be information rich and highly refined. Relatively accurate estimates of these parameters were available, or calculable, for enough groups to enable construction of a useful PWS model at the intended resolution.

It is important to highlight the potential for refinement and learning provided by a balanced trophic model. This model of PWS represents a possible scenario of relationships among groups (during the modeled period) as defined by the contributed information and the known constraints to the system. Estimates for relatively unknown components, for which confidence in the estimates is low, were refined based on these constraints and subsequent balancing. However, this is just a focal point in the refinement process, the most useful result of which is the re-visiting of ecosystem data and estimates by researchers and research program managers. In this sense, the balanced trophic model of PWS may become a powerful tool for formulating questions and guiding research in PWS and beyond. Thus, the Ecopath model of PWS, using the Ecosim and Ecospace simulation routines, should be useful in several ways beyond the goal of synthesis of existing information into a comprehensible description of the system's biotic components and their trophic relationships.

The Ecopath model of PWS presented here is a static model that represents the average annual state of the ecosystem based on the three years of data that were included in this synthesis (1994-1996). Ecosystem components fluctuate in the real PWS, as in other systems, and these fluctuations are driven by both biotic interactions and physical forcing. However, the Ecosim routine enables a simulation of environmental forcing, both at seasonal and longer term scales. For example, seasonal changes in primary production can be imposed on the system, while a 20-year shift in the regional climate regime can be simultaneously imposed. These physical forcing functions can be applied to selected groups in the model. Fluctuations in these forced groups would subsequently drive fluctuations in other components of the system.

The next step in the development of the PWS model is to incorporate explicit seasonality into the model using empirical seasonal data for various groups and interpolated data for groups without explicit seasonal data. Such interpolation can be undertaken by, for example, using empirically-derived relationships between temperature and metabolism (i.e., consumption rates). However, this can best be done as an exercise of its own, using the version of ecopath recently developed to accommodate explicitly seasonal inputs (Martell 1999). Characterization of seasonal changes currently consist of estimates and discussions within individual sections of this report, and to analyses using Ecosim forcing functions on the current (annual average) Ecopath model of PWS.

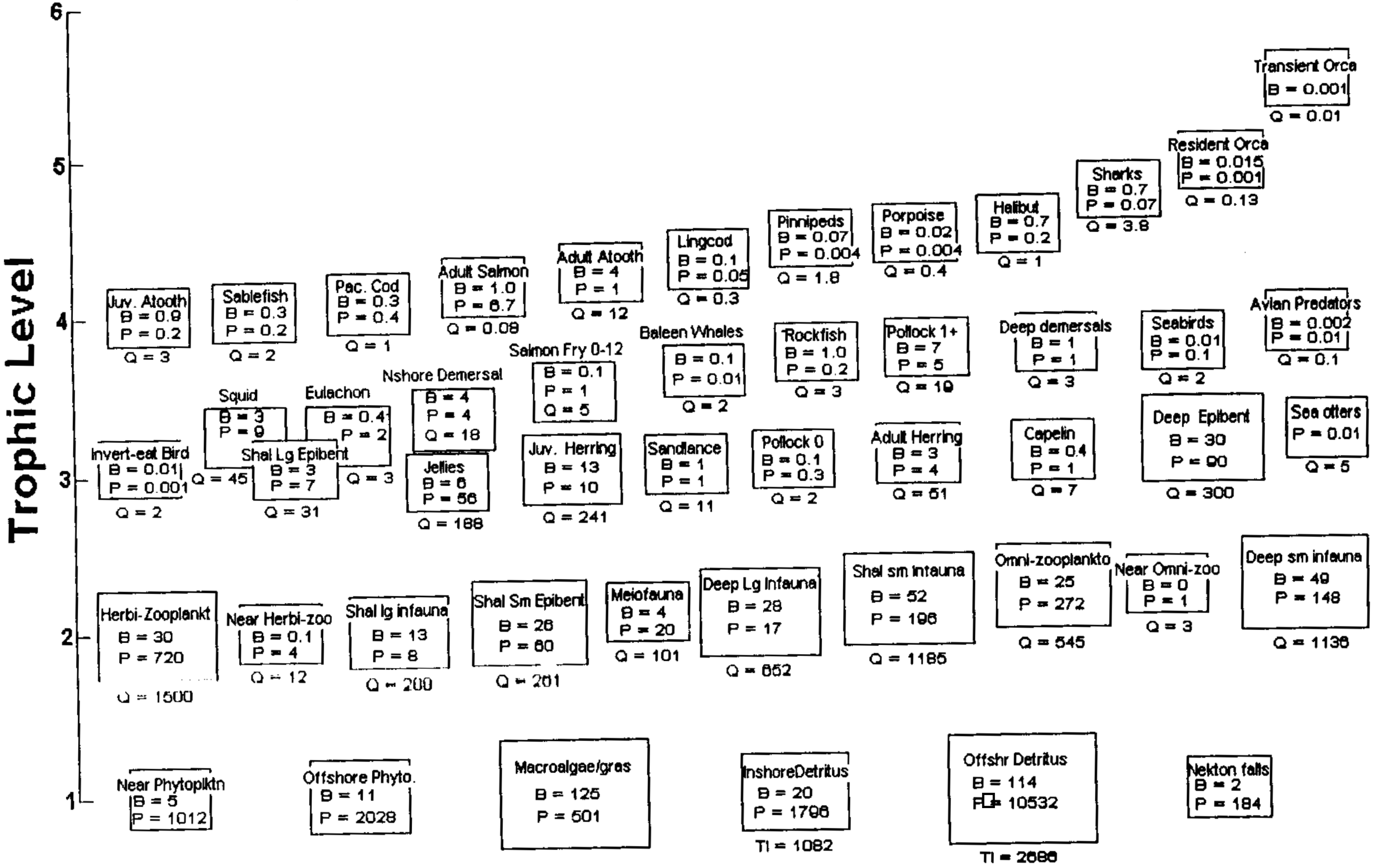

Figure 6. Biotic components of the balanced trophic model of Prince William Sound, Alaska displayed on a trophic level scale (vertical axis). Biomass (B) is displayed for each component in t·km^{-2}; production (P), consumption (Q), and total input (TI) are expressed in t·km^{-2}·year^{-1}. Trophic flows are not displayed here, as there are too many connections for this format.

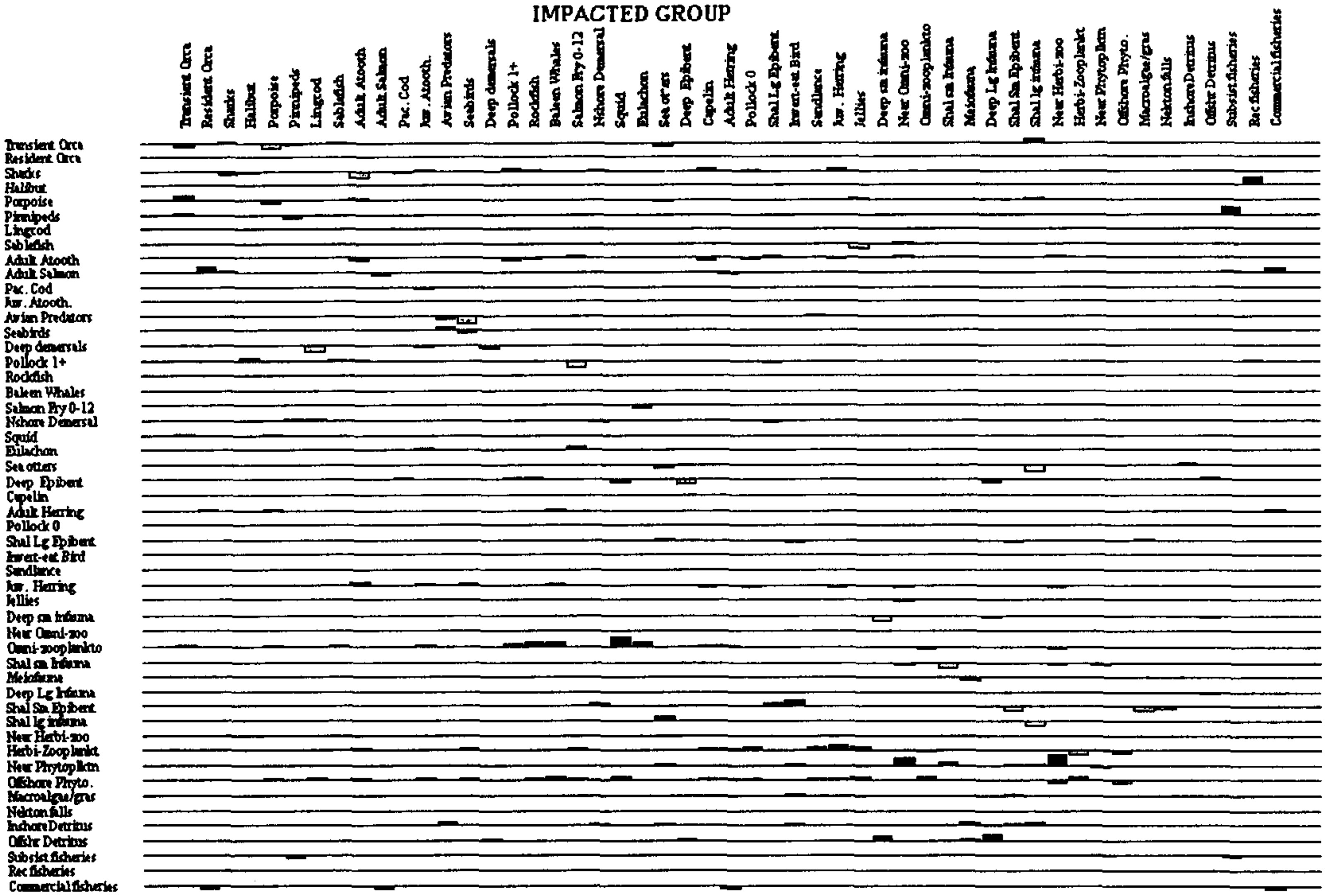

Figure 7. Mixed trophic impacts of groups in the PWS ecosystem model, representing the direct and indirect impacts that a small increase of the groups on the vertical axis would have on those on the horizontal axis. The black bars above the lines are positive impacts (facilitation) whereas the shaded bars extending below the lines are negative impacts (inhibition). The routine that generated this graph was adapted from the input-output analysis of Leontief (1951).

One of the main uses of a balanced trophic model approach, like Ecopath, is the insight it can provide into indirect effects of known, or predicted, changes in certain parts of the system (Gaedke 1995, *also see* Wootton 1994 and Menge 1995), and thus, it is a way to gain understanding of the functioning of parts of the defined ecosystem, within the connected system. Both the description by Ecopath and the prediction by Ecosim and Ecospace can be useful in any part of the scientific process, from synthesis and summary to research design and hypothesis formulation. An obvious direct application of this approach is resource management and planning.

Construction of the Ecopath model can also highlight groups in the ecosystem for which little information is known. These 'weak links' in the model limit our understanding of the system even though they get more refined through the modelling exercise. These can then be a focus of future research.

Temporal simulations of perturbations

The Ecosim routine can be used to simulate perturbations, which could be stated as 'what if' scenarios, like as those provided during the collaborative model development and shown previously. The approach can be used to simulate of changes in the relative biomass trajectories of ecosystem components over a specified time horizon in response to specified changes in mortality rates for one or more components. These temporal simulations have been the feature of Ecosim, but additional simulation routines have been added to the software. Of particular note is the spatially-explicit dynamic simulation routine Ecospace.

Three caveats are useful here for understanding the output of the Ecosim runs in this section: (1) simulated responses in ecosystem components are the result of biotic interactions only, and do not include any responses of, or control by, physical forcing in the environment. Physical forcing (e.g., oceanographic regime shifts) can be simulated in Ecosim by various methods, but this was not necessarily the focus of the simulation examples herein; (2) Ecosim runs are based on one possible scenario for the PWS food web, albeit a likely scenario based on the information at hand from 1994-1996. Ecosim enables prey switching based on prey availability and other factors (see Walters et al., in press), even though the starting point of each simulation is the generalized Ecopath model of the system in which diet compositions are specified; (3) the extent to which biological forcing and subsequent cascading effects, and system destabilization, in the simulations resembles the dynamics of the real PWS depends on the degree of interactive plasticity as well as prey vulnerability, both of which can be adjusted and refined.

An unlimited variety of simulations can be conducted as researchers and other individuals explore the model food web. Only a few simulations are provided below as examples of the different ways that the approach can be used.

Example 1: Removing sharks

This example illustrates how the ecological role of a single group can be explored. Figure 8 illustrates the output of a dynamic simulation of removing sharks from Prince William Sound. The biomass of some species increase in response to shark removal, while the biomass of other species decrease, according to the trophic relationahips specified in the Ecopath model. In this simulation, an important suite of predators (sharks) is removed from the system, and several other fish are predicted to increase in response. These are either competitors or prey of sharks, or both. The degree of importance of the types of relationships can then be explored. In addition to the species that increased in response to shark decreases, several species declined. These include juvenile and adult herring, capelin, juvelile pollock, squid, rockfishes, other shallow and deep demersal fishes, and avian raptors. These are the types of organisms that might be facilitated by the presence of sharks in the PWS system that existed between 1994 and 1996). (Note: Caution is advised when interpreting the salmon trajectory since salmon are transients in the system).

Example 2: Changes in fishing effort

The example depicted in Figure 9 illustrates how the Ecopath with Ecosim approach can be used to simulate the responses of biota to increases or decreases in the fishing mortality associated with a particular fishery. This example illustrates changes in the biomass of several species of high-trophic level predators in response to increases or decreases in fishing mortality. This simulation indicates that the fisheries of Prince William Sound not only directly influence the biomass of particular species (i.e., herring and salmon), but they also compete with other predators for food to the entent that this competition influences the biomass of these mamalian, avian, and fish predators. It was initially surprising that such strong indirect effects of the fishing in PWS was indicated by these simulations, given that the annual flow of biomass to fisheries is 0.24% of the overall flows of biomass in the system. Such simulations provide insights into the effects of diverting forage fish energy in these types of marine ecosystems. More detailed approaches can be taken to pursue the phenomenon of 'trophic interception' revealed by this broad-scale simulation.

Example 3: Catastrophic disturbances

Figure 10 depicts an analysis of broad-scale an more complex disturbances in which more than one biotic group are directly impacted and the indirect responses other organisms can be explored in addition to the more general character of the response of the biotic system as a whole. In this case, the responses of the food web to three scenarios of catastrophic disturbances were compared. These consisted of (a) the great Alaskan earthquake of 1964 (magnitude 9.2), which shook and tilted Prince William Sound causing tsunamis, and which mostly impacted lower and mid trophic level organisms; (b) Scenario #1 of the *Exxon Valdez* oil spill, based on documented impacts of the spill, which focused on impacts to upper trophic level organisms, and some lower trophic level organisms of the intertidal; and (c) Scenario #2 of the *Exxon Valdez* oil spill, also based on documented impacts of the spill, but complemented with likely impacts of the spill that were not documented, in which both upper and lower trophic level organisms were impacted.

Good information on the direct effects of these complex physical disturbances is necessary for the simulations to be meaningful. This type of analysis is, thus, less straightforward than explorations of ecosystem the roles of single species. This analysis is presented here to illustrate the types of simulations that are possible. This simulation is, in effect, an exploration of the trophic character of disturbance. It indicates that ecosystems can recover rapidly to disturbances that affect mostly lower trophic levels; they recover more slowly when disturbances affect mostly upper trophic levels; and they may well stabilize at alternate stable states when disturbances impact a mix of high and low trophic levels. This analysis indicates that the working assumption that Prince William Sound is recovering from the *Exxon Valdez* Oil Spill may be a reckless assumption. These simulations indicate that Prince William Sound, or other ecosystems, might not recover from disturbances that are severe enough across a broad range of trophic levels. Prince William Sound might 'stabilize' in an altered state.

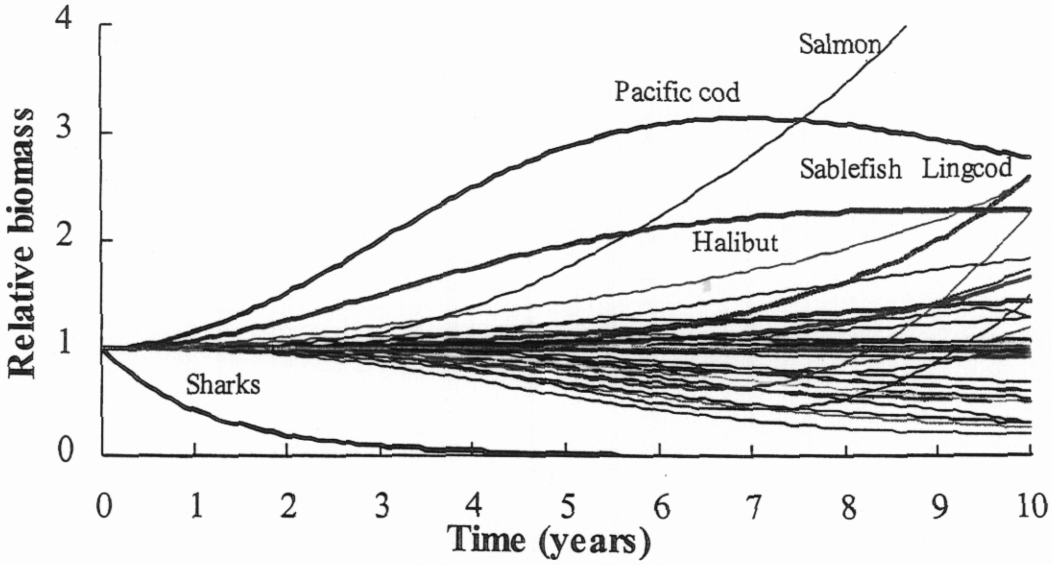

Figure 8. Simulated removal of sharks from Prince William Sound, revealing potential indirect trophic cascading effects of sharks. This figure shows increases and decreases in biomasses of various species (i.e., groups) in response to removal of sharks, based on their trophic relationships with sharks, or species affected by sharks (e.g., prey, competitors, etc.)

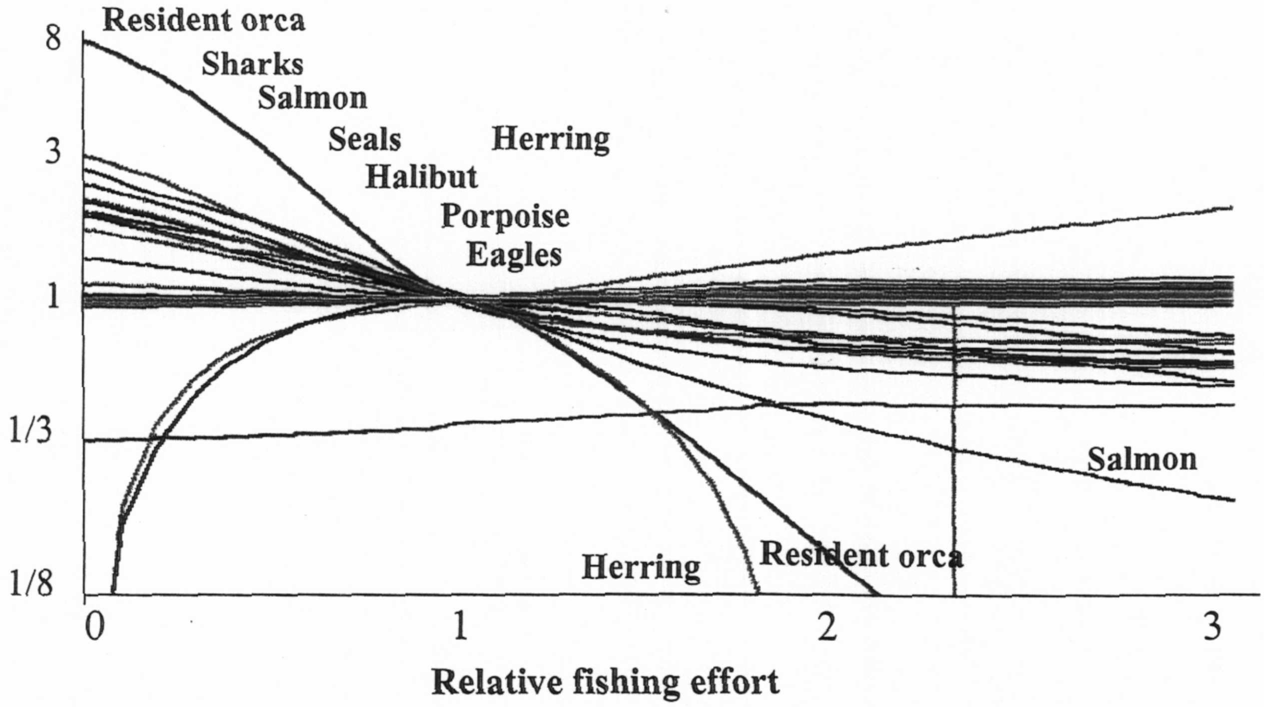

Figure 9. Simulation of changes in the biomass of Prince William Sound biota along a continuum of change in commercial fishing effort. Current commercial fishing effort corresponds with the '1' on the horizontal axis. The simulation indicates that several predators would be more abundant if less fish were commercially caught; these same species would be less abundant at higher levels of fishing. Two species are predicted to go below 1/8 the current abundance at twice the current levels of fishing.

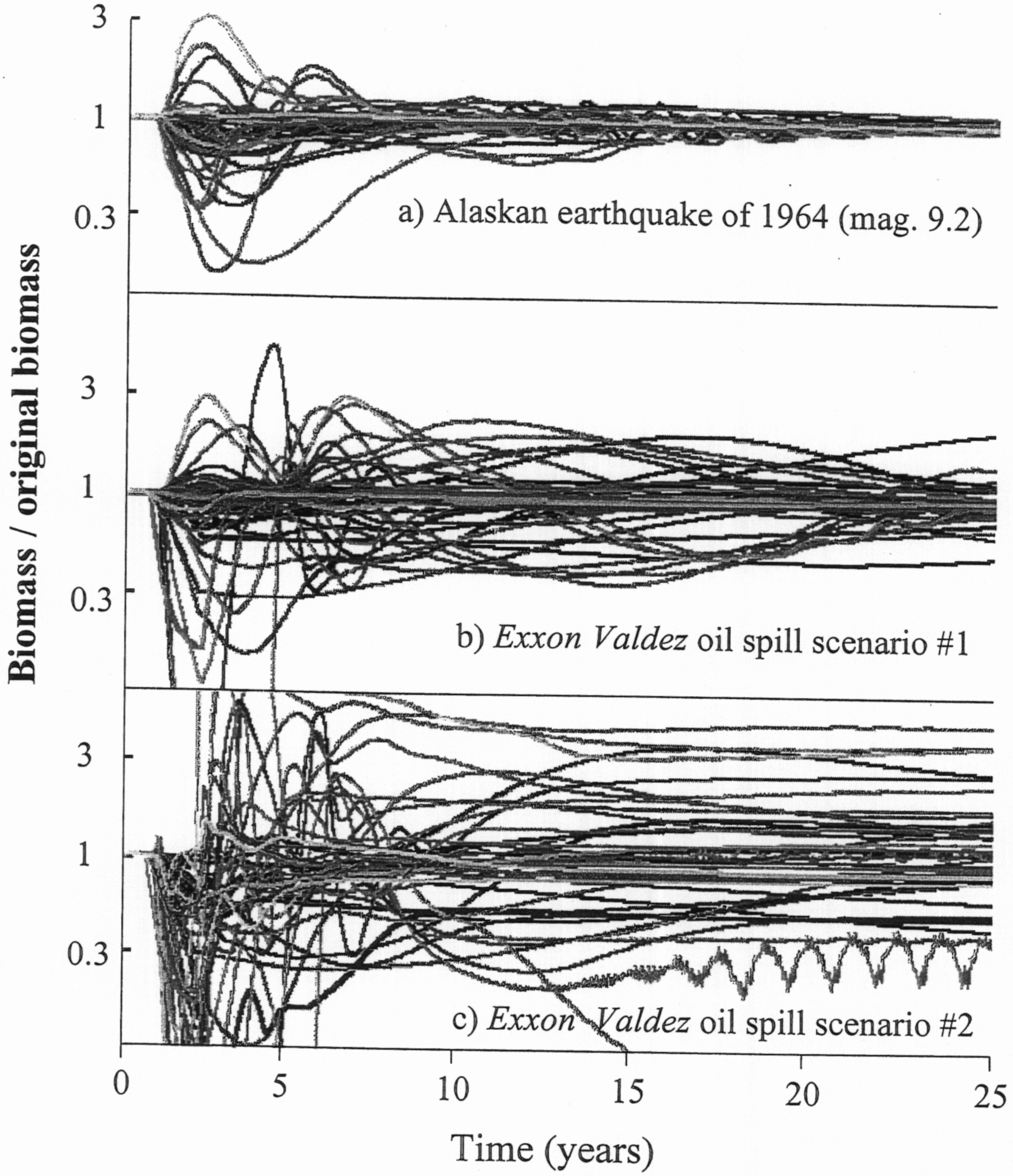

Figure 10. Simulations of three catastrophic disturbances in Prince William Sound, Alaska: (a) the great Alaskan earthquake of 1964 (magnitude 9.2), which shook and tilted Prince William Sound causing tsunamis, and which mostly impacted lower and mid trophic level organisms; (b) Scenario #1 of the *Exxon Valdez* oil spill, based on documented impacts of the spill, which focused on impacts to upper trophic level organisms, and some lower trophic level organisms of the intertidal; and (c) Scenario #2 of the *Exxon Valdez* oil spill, also based on documented impacts of the spill, but complemented with likely impacts of the spill that were not documented, and in which both upper and lower trophic level organisms were impacted.

Spatially explicit simulations

The Ecopath with Ecosim software now includes a routine that enables temporal simulation of biomass trajectories in a spatially-explicit context (Walters et al., in press). Biomasses of the various components in a food web redistribute themselves spatially according to the interface between habitat characteristics and trophic interactions. Furthermore, spatially-explicit questions or management options can be explored. A simulation using the Prince William sound model is presented here only for the purpose of providing an example of how the Ecospace routine can be used. The particular simulation presented here was not intended to be precise; it was intended as an example of the general types of responses that might be encountered during such simulations.

Ecospace example : a marine protected area

Ecospace was used with the Prince William sound model to explore the effects of a large marine protected area encompassing approximately half of the 9,059 km^2 sound. The first step in preparing an Ecospace scenario is to delineate the various types of habitats in the ecosystem. The numbers and differently colored (or shaded) cells in Figure 11 correspond with the habitat types presented above. This type of information was collected during early stages of this project by inference (in the form of spatial distribution patterns of the organisms) and more directly (information about habitats). Step two involves assigning habitat preferences to each biotic component (species or guild). Preferences are defined in the form of relative movement rates, relative vulnerability to predation, and relative feeding rates in the various habitat types.

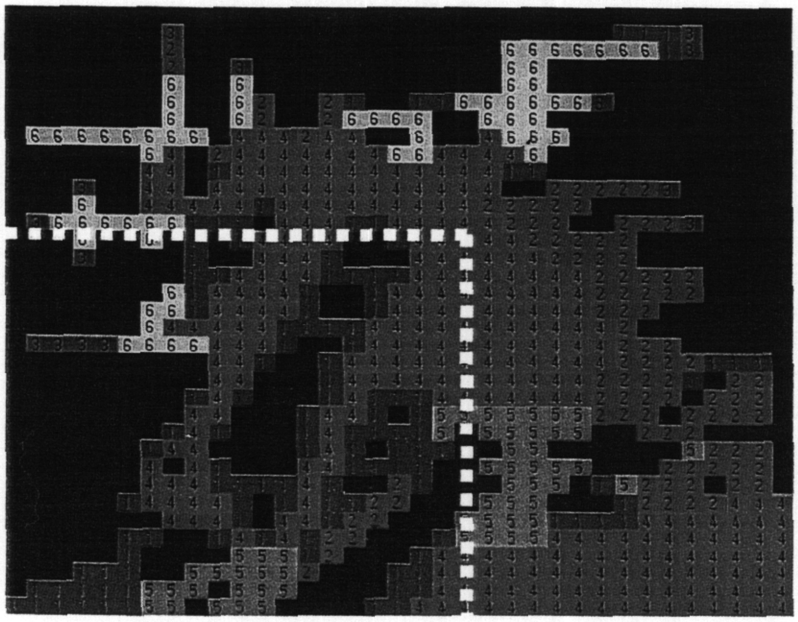

Figure 11. Diagrammatic map of Prince William Sound. Land areas are shown in black. Specified habitats are numbered and color coded. A simulated marine protected area (MPA) is delineated in the Southwestern part of PWS by the dotted white lines.

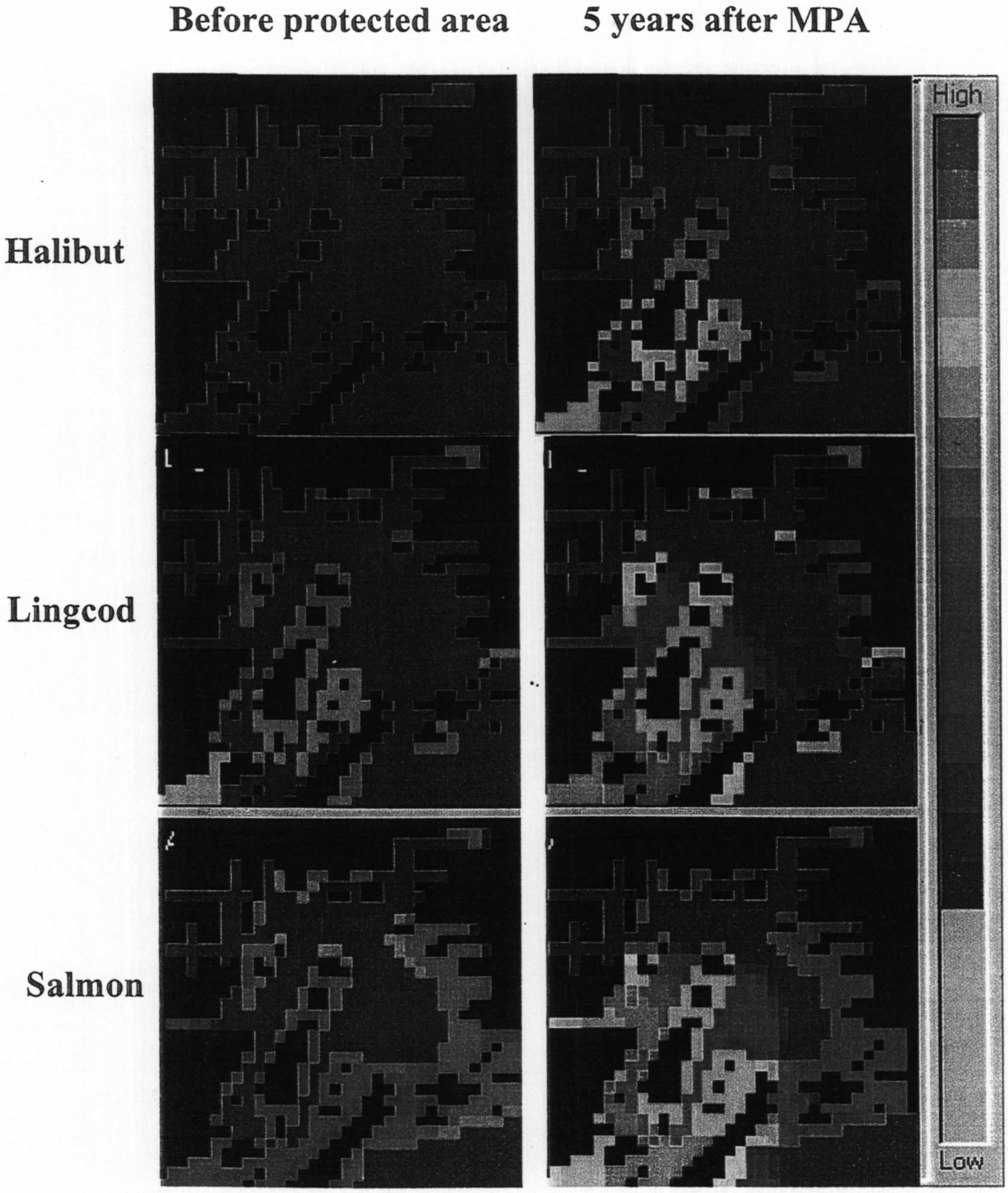

Figure 12. Simulated spatial re-distributions of three of the 48 groups in the PWS model based on trophic interactions in preferred versus non-preferred habitats; with unrestricted fishing effort (left hand column), and five years after the simulated establishment of a marine protected area (right hand column). Colors (or shadings; right panel) represent changes in biomass density, where reds are increases in biomass density, blues are decreases, and green corresponds with the biomass density of the uniformly distributed, pre-simulation model.

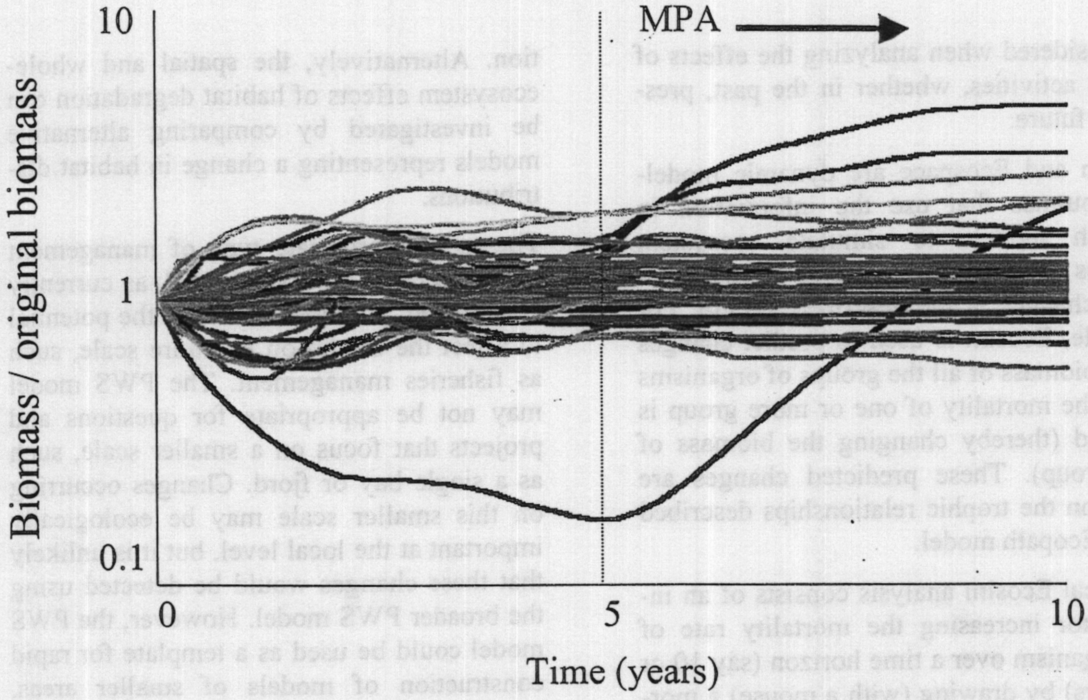

Figure 13. Temporal biomass trajectories associated with spatial re-distribution of PWS biotic components both before and after the establishment of a simulated marine protected area. Most groups equilibrate in the specified spatial arena, and some groups increase after establishment of a marine protected area in which fishing is excluded.

Some of the results of this simulation of the effects of a marine protected area are shown in Figures 12 and 13. Three of the 48 groups in the PWS model are shown to have increased five years after the establishment of this large marine protected area. For this simulation, the biota in the model were given five years to equilibrate with each other in the specified habitats before a five year establishment of the marine protected area. Not shown in these figures is the resulting spatial distribution of fishing fleets, which began congregating along the boundaries of the MPA. Also not shown in this simulation are the responses of PWS rockfish (*Sebastes*). An additional simulation is needed for meaningful spatial analysis of this group of species in PWS (which is probably declining).

Ecopath and Resource Management

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The Ecopath trophic modelling approach consists of both static and dynamic modelling in a windows-based software package. The static Ecopath model is a quantitative description of the trophic flows in an ecosystem averaged over a pre-defined area and time period. It includes all components of an ecosystem (aggregated into fifty 'boxes' or less), so it can be used as a focal point for collection of broad information about an ecosystem, including estimates of basic population, production, and consumption information, fisheries information, and other migration and trend information. The static Ecopath model is the foundation upon which effects on all components of ecosystems can be considered when analyzing the effects of human activities, whether in the past, present, or future.

Ecosim and Ecospace are dynamic modelling routines that use the information in Ecopath models to simulate ecosystem changes resulting from natural or anthropogenic changes in the described system. For example, Ecosim is used to predict changes in the biomass of all the groups of organisms when the mortality of one or more group is changed (thereby changing the biomass of that group). These predicted changes are based on the trophic relationships described in the Ecopath model.

A typical Ecosim analysis consists of an investigator increasing the mortality rate of one organism over a time horizon (say 10 or 20 years) by drawing (with a mouse) a mortality trajectory in the graphical interface for input. This increase in mortality might simulate an increase in fishing, or a possible effect of increased sediment runoff, effluent, or collecting and food gathering by visitors. The output of the simulation reveals indirect ecosystem effects by displaying the prediction of changes in other groups over time. Although a given model may not have adequate power to reveal all impacts, the simulation will reveal those that are most prominent. When a good model has been constructed, the functional responses (direction and relative magnitude of changes) of groups can be revealing indicators for managers, while the indicated magnitudes of changes are taken as indicative only.

Ecospace is a new development of the Ecopath approach that enables resource managers and scientists to simulate changes in spatial dynamics in response to trends of resource use or management actions. It is a habitat-based approach in which components of the ecosystem achieve spatial distributions according to movement rates and vulnerability to predators, which the user adjusts for each species in each habitat (default rates are provided). For example, the effects of marine protected areas on fish stocks can be simulated in a particular situation. Alternatively, the spatial and whole-ecosystem effects of habitat degradation can be investigated by comparing alternative models representing a change in habitat distributions.

The most appropriate type of management applications of the PWS model, as currently constructed, are those that have the potential to affect the Sound on its entire scale, such as fisheries management. The PWS model may not be appropriate for questions and projects that focus on a smaller scale, such as a single bay or fjord. Changes occurring on this smaller scale may be ecologically important at the local level, but it is unlikely that these changes would be detected using the broader PWS model. However, the PWS model could be used as a template for rapid construction of models of smaller areas, which could detect ecological impacts of local disturbances or protective measures.

Future restoration and planning

The general usefulness of the Ecopath approach (with Ecosim and Ecospace) for future restoration and planning is evident by Figures 8-13. We suggest that these tools can not only aid in the scoping and development of assessment programs and in the analyses of their data, but they can also play an important role in future restoration and resource planning. Beyond the useful ecosystem description using Ecopath, the specific uses of the dynamic modelling routines discussed herein are to point to functional responses of components of the ecosystem based on the biological, trophic, and habitat information used in the model. It is these functional responses, rather than particular magnitude of responses, that are useful and reliable indicators of response to simulated disturbances, trends, or management actions. Most of all, the current and future usefulness and success of this approach depends on a functional collaborative process, such as the one engaged in during this project.

Ecosystem Models as Caricatures: the case of Prince William Sound

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University of Washington, Dept. of Zoology, Seattle

It has become quite popular in ecological circles to decry the lost opportunity of effectively studying the Exxon Valdez oil spill. We worry that in the rush to point fingers and bill for damages, we failed to gather data that would allow any assessment of dynamic responses to the spill and cleanup. Still, enormous efforts were expended in studies, many of which recorded abundance-- precisely the sort of data that Ecopath requires. This Ecopath project has collated an encyclopedic amount of information in one easily accessible form. At its best, it reveals not only point estimates of biomass, births, and deaths, but also their variability and uncertainty.

The Ecopath model of Prince William Sound is a caricature, as are all models. But of course caricatures can be revealing, even though they are wrong. The values in this model are almost certainly incorrect: as an example, density estimates of intertidal epifauna varied by three orders of magnitude, even in a single habitat, and once these are averaged and corrected for Sound-wide habitat availability (for which there must be error in estimation, nor will it all have equivalent epifauna), the true tonnage cannot be known with any more certainty. The mechanisms in this model are likely to be incorrect as well, since the only mechanism presently used to represent interactions is direct consumption. It ignores the fact that consumers often do more than skim production off of their prey; they can shift composition to species with lower productivity and actually alter the production/biomass (P/B) of the group. Interactions also occur through direct competition or through habitat alteration; for instance, the organic structure of kelp and eelgrass beds is known to influence juvenile fish growth and mortality risk[a]. Some of these mechanisms may occur within Ecopath 'boxes' and therefore their effects could be incorporated over short time frames. In a general sense, however, these errors in accuracy and mechanism only matter if questions are asked that draw on aspects of the model that are importantly wrong. It would be fooling, for instance, to use this caricature to set fishery quotas, or to predict all the effects of dredging a seagrass bed.

The sort of question that can be asked of Ecopath models is, essentially, in which portion of the food web are dynamics most unknown? They may be unknown because no data exist (P/B and Q/B in particular were often copied from similar groups in other systems); or because confidence limits are large; or because it is unclear how details within groups should be expressed as an aggregate (although combined in a single group, many of the rockfish had essentially no diet or spatial overlap. Presumably consumption rates, conversion efficiencies, and productivities might also differ among species. What should the food web connections with this box be?); or because the ecotrophic efficiency is unlikely (way more is produced than used by the next trophic level, or vice versa). These unknown, uncertain, or unlikely portions of the food web bear additional scrutiny. If more energy appears to be used than is available, for instance, further study of this nexus of interactions might reveal new connections, resources, and unrecognized imports, not simply errors in estimation.

In fact, it may prove more illuminating to leave these models unbalanced-- after all, there's no clear evidence that biomass and P/B are more poorly known than any other parameters, yet these tend to be adjusted because they cause fewer unwanted changes elsewhere in the model. Balancing Ecopath models solves the puzzle one way out of a

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[a] A routine called "mediation" has recently been added to Ecosim which allows for non-feeding interactions between groups (see www.ecopath.org) (Editors).

multidimensional space of possible ways, and we may be tempted to breathe a sigh of relief and say "Yes, that's how it must be." Complacent, we may be less inclined to search for biologically-based parameter revisions and empirical evidence of what's actually going on in these interactions.

It is possible to imagine that the system would indeed be 'out of balance' in the Ecopath sense for any number of reasons.

1. It is well-known that being spatially-explicit can change the outcome of interactions, even to the extent of whether or not a species persist. This issue may be remedied at a coarse scale in Ecospace.

2. Biomasses and productivities of PWS biota change dramatically on a seasonal basis. In the current model, such fluctuations are simply averaged out-- 1 duck present for 3 winter months is just 0.25 ducks annually. On the other hand, the season of its residence could coincide with a time when mussels are newly-settled and therefore not particularly energetically valuable, but extremely vulnerable to predation. Major changes also happen cyclically or catastrophically on long time scales, but several models could be built to represent different conditions.

3. With some notable exceptions (salmon, bird predators), PWS is assumed to be a closed system, but many imbalances could be redressed through supplies or export of energy from outside the Sound.

4. There are no microbes in the model, despite recent recognition that the 'microbial loop' in pelagic systems can provide large proportions of energy to higher trophic levels. Even in benthic systems, much of the decomposition of macrophyte drift occurs by bacteria; and many benthic species consume bacterial films that grow on rock, soft sediment, or detritus. Including these food sources could substantially shift the basal production available to the system. On the other hand, including microbes might not have much effect on the relative strength of links currently incorporated in the model. Certainly, the issue could be explored.

5. Production is an amalgamation of processes, including growth of surviving individuals and recruitment of new individuals. It is fairly easy to accept that biomass growth will be a function of existing biomass (assuming constant size structure), but the relationship to recruitment is less clear--fisheries biologists have been struggling with stock-recruitment curves for decades, and they are if nothing else exceedingly variable. One cohort of herring can dominate biomass for 10 years, because recruitment is so intermittent; there appears to be no way for Ecopath to link the fates of larvae in the zooplankton box to eventual recruitment events and adult populations.

All that said, Ecopath is still a way to frame the question of whether these issues of scale, taxonomic focus, and parameterization actually influence trophic flows. Incorporating these issues may not be necessary to understand trophic flows (though they should not be assumed unimportant), and certainly it complicates the model.

The advantage of Ecopath over Ecosim is that mass-balance is a relatively simple matter of solving simultaneous algebraic equations. It is possible to determine exactly why the program gives the 'answer' it does. Ecosim is less transparent, but it is dynamic and therefore able to generate predictions about the food web effects of perturbations. It would be interesting to know if these predictions are robust to assumptions about prey vulnerability. It would also be interesting to know if the predictions are testable; for instance, are any groups expected to move outside their range of natural variation in a time frame that would allow the change to be attributed to a particular event?

Caricatures are wrong but useful as long as they're not asked to perform tasks involving portions that are importantly wrong. This Ecopath exercise has clearly been useful in pulling together disparate data about PWS. It has also usefully focussed attention on uncertainties, variation, and trophic imbalances that may only be resolved by better studying and understanding the roles of species embedded within complicated webs of interaction.

An annotated list of Alutiiq words relevant to modeling the Prince William Sound ecosystem

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The incorporation of traditional environmental knowledge (TEK) into environmental science has recently become a subject of great interest. The cross fertilisation of TEK and western science could enrich both intellectual traditions. In the Alaskan context of rehabilitation efforts that have followed the Exxon Valdez oil spill in Prince William Sound (PWS) a large scientific research effort has begun in an area rich with TEK. To begin incorporating TEK into the scientific study of the PWS ecosystem (while also allowing natives to use scientific knowledge) a logical first step is to catalogue local terms for the flora and fauna of PWS. This approach has been successfully applied to the Strait of Georgia ecosystem (Pauly et al. 1998) by using a catalogue of Saanich words for various fish species to help validate models of its potential historic state. In the PWS area a similar approach was deemed useful since TEK is often a valuable source of *qualitative* information as to the behaviour, location, and diet, of organisms. Johannes (1981) provides a wonderful example of the intimacy of knowledge that can be possessed by a traditional sea faring people of the aquatic environment and its organisms.

Practitioners of the ecological sciences have usually drawn the vast majority of their conclusions on the investigation of *quantitative* information. This has led to many notable achievements in the study of aquatic ecology, especially for modelling the population dynamics of single species. A relatively new approach however, has been to model whole ecosystems using approaches such as Ecopath (Christensen and Pauly 1993, and see other contributions in this volume). For general ecosystem modelling significant advances may be achieved by including native knowledge holders in the scientific process. This is because many of the questions addressed by ecosystem modelling are *qualitative*. TEK is also particularly helpful in the novel practice of modelling historic ecosystems. Often the TEK of the local community contains precise knowledge of species present (in both contemporary and historic contexts), their diets and the seasonal fluctuations of populations.

A particularly valuable aspect of such information could be the determination of species that may have been present long ago, but have since been extirpated. By constructing organism name inventories from different locales modelled ecosystems we may gain some insight as to distributions in time and space, population variations, and changes in diet. Such information may also be incorporated into relational databases such as Fishbase (Froese and Pauly 1998) to facilitate the determination of patterns. By such mechanisms local knowledge can be integrated into traditional scientific analysis. These databases should also help translate science into terms understandable by the local people themselves, since they allow the linking of biological concepts.

An example of information on historical populations is the existence of a word for 'mammoth' in several languages of Arctic peoples from western Alaska through northern Canada and Greenland (Fortescue et al. 1994). The fact that so many languages have an established word, not a recent loan word, for this long since vanished animal suggests these languages have other valuable ecological information.

Equally interesting is the information that may be obtained from stories and oral history. Although the Inuit from Greenland have no word for mammoth they do have one for a legendary six legged animal, the pronunciation of which is close to the word for mammoth in other Arctic languages (Fortescue et al. 1994). This is probably a construct from a cultural recollection of the mammoth. It would not be surprising for the trunk of the beast to be later described as a leg. The inuit can be forgiven for thinking the creature had an even number of appendages like most others, therefore describing it as six legged instead of possessing five major appendages.

The language from which words for aquatic flora and fauna, and associated words were derived for this study was Alutiiq Alaskan Yupik (AAY), "...spoken in Alaska on the Shores of Prince William Sound, at the tip of the Kenai Peninsula, on Kodiak Island, and on the Alaska Peninsula." (Fortescue et al. 1994). The language is, however, generally referred to simply as Alutiiq (Leer 1978).

A few words must be said about the languages of Arctic people. Generally these languages are referred to as 'Eskimo' languages, although we recognise that some consider the use of the word Eskimo somewhat inappropriate. This set of languages can be broken into three major groups; Inuit, spoken from the Seward Peninsula to Greenland; Yupik, spoken from the South shore of Norton Sound to PWS; Aleut, spoken in the Aleutian Islands. These languages are coastal, the interior of Alaska being dominated by Athabaskan languages. Other works have attempted to catalogue terms for aquatic species, such as McAllister et al. (1987) in their List of Inuktitut (Eskimo), French, English, and scientific names of marine fishes of Arctic Canada. Such works, however, are not directly applicable to either the specifics of the language and ecosystem of PWS, and were therefore not used here. It will be necessary in the future to compare words in the languages of other studies like McAllister et al. (1987) to synthesise the knowledge of what are closely related languages.

Leer (1978) and Fortescue et al. (1994) split AAY into two dialects, Chugach (C) and Koniag (K). C was further split into two sub dialects: 'Prince William Sound', found in the eastern portion of the geographic distribution of the C dialect (CE) and 'Kenai Peninsula' found in the west (CW). The K dialect was also split into two sub dialects; Kodiak, found in the eastern portion of its geographic distribution of K (KE), and Alaska Peninsula (KW), found in the west. Whenever possible the word from the CE subdialect was used for this study as it would be from people living closest to the ecosystem being modelled. If the CE term was not available then words were used in the following order of preference C>CW>K>KE>KW>AAY. See Figure 14, derived from Fortescue et al. (1994), for a guide to the locations of these dialects.

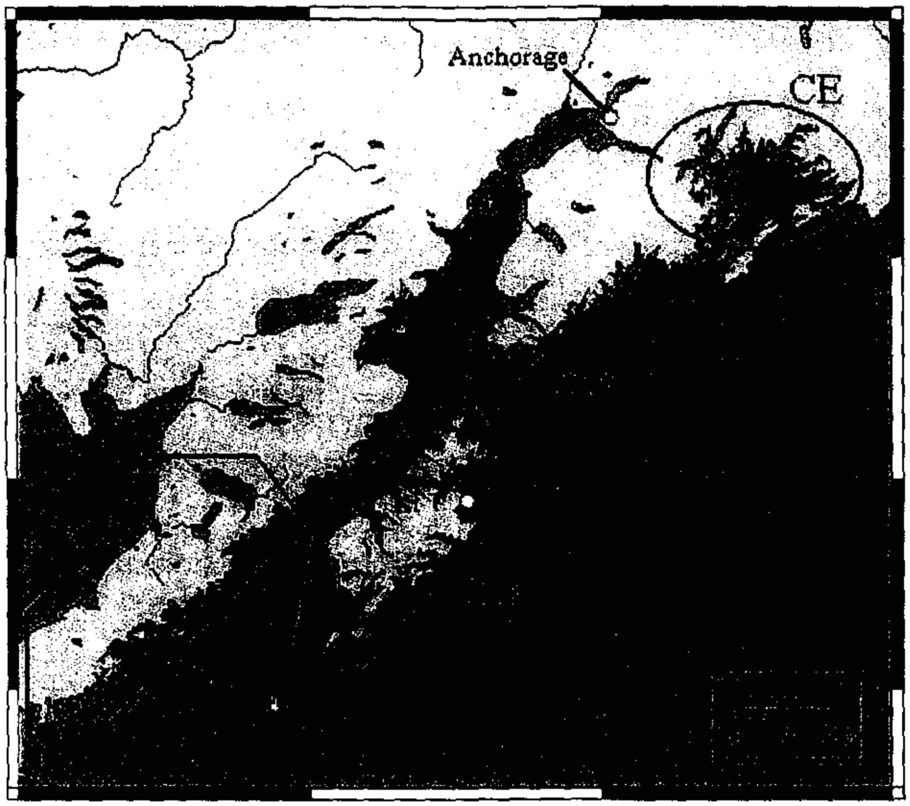

Figure 14. Geographic range of Alutiiq Alaskan Yupik, its dialects and subdialects: CE is the Prince William Sound subdialect and CW is the Kenai Peninsula subdialect of Chugach. For the Koniag dialect KE represent the subdialect spoken in and around Kodiak while KW is the subdialect spoken on the Alaskan Peninsula.

Due to limitations of the fonts available through the word processor used in this project many phonemes listed by Fortescue et al. (1994) have been approximated. This was not a difficulty with words from the list in Leer (1978) since he used phonemes with simple typewritten approximations. Following information from Pullum and Ladusaw (1986) the definitions of symbols were obtained so that a suitable symbol from the fonts available to the author could be used. The replacement symbols are as follows:

- An upside down lower case e, or schwa, meaning pronouncing the letter as a short e was denoted as ‘e’;
- An l with a belt around it meaning slight aspiration on either side of the tongue when pronouncing l was denoted as ‘✖’;
- An m with a small circle below the right hand arch, meaning slight aspiration through the nose when pronouncing the m was denoted as ‘m_0’;
- An n with a small circle underneath, meaning slight aspiration through the nose when pronouncing the n was denoted as ‘n_0’;
- An n with a small circle on the tip of the tail, meaning slight aspiration through the nose when pronouncing ‘ng’ was denoted as $✱_0$;
- A small capital r, as high as a lower case r, meaning heavy rolling of the letter when pronouncing r was denoted as ‘R’;
- Verbs, which must be conjugated can be recognised by the Alutiiq transliteration having a dash on the end, thus ‘-’.

The following table was adapted from entries in Leer (1978), Fortescue et al. (1994), and the personal research notes of Jeff Leer. Entries that were taken from Leer (1978) and Fortescue et al. (1994) are cited as such. Entries from Jeff Leer's research notes are denoted as 'Leer notes'. In Fortescue et al. (1994) all phonemes were ordered alphabetically, as in a dictionary. The structure of phonemes in Leer (1978) was different from Fortescue et al. (1994) and no typographical modifications were needed. Lastly, the words in Leer (1978) refer to C in general and are cited as such. Since this paper seeks to add terms from Alutiiq to a scientific data base it is sensible to order the terms into functional groups and then to alphabetise according to their English equivalents, thus making the list accessible to the largest possible audience. The functional groups the terms were separated into are: general animal terms, general bird terms, bird names, general fish terms, fish names, general mammal terms, mammal names, invertebrates, and plants. The words are each described using the following format:

Format: English name / *Alutiiq name* / Language, Dialect, Subdialect / Remarks, if any

Animals, general

animal / *u✱u✱siq* / KW / (Fortescue et al. 1994).
animal / *ungu'alaaq* / CE / (Leer notes).
animal, to take as game / *pit'e-* / C / (Leer notes).
egg / *pelisuq* / C / (Leer notes).
female / *arnaqiitak* / C / (Leer notes).
game, caught / *pitaq* / C / (Leer notes).
male / *angusaluq* / KW / (Leer notes).
male / *erilek* / C / (Leer 1978).
monster / *cacalaa'ak* / CE / (Leer notes).
monster, lake / *arwalaayak, ar'ulaayak* / CW / (Leer notes).
oil, from animals or plants / *uquq* / C / (Leer 1978).
rib / *cakia<R>aq* / AAY / (Fortescue et al. 1994). The K subdialect also uses this word to refer to the rib of a boat.
stomach / *aqsaquq* / C / (Fortescue et al. 1994).
tusk , canine tooth / *tuluRyaq, tuluRneq* / AAY / (Fortescue et al. 1994).

Birds, general

backbone, upper part of / *atankuyuk* / CE / Leer notes.
beak, bill / *cugg'eq* / C / (Leer 1978).
breastbone / *qatek* / CE / (Leer notes).
crop / *uniirwik* / CE / (Leer notes).
down feather / *tenga'uk* / CE / (Leer notes).
egg, to lay / *peksu-* / C / (Leer notes).
eggs, a complete set of, or batch, in a nest / *naaneq* / AAY / (Fortescue et al. 1994).
eggs, to sit on / *waa-* / C / (Leer notes).
feather / *culuk* / C / (Leer 1978).
feather, tail / *kingumik* / CE / (Leer notes).
feather, tail, long / *culugpak* / CE / (Leer notes).
fledging bird / *tengnerraq* / C / (Leer notes).
gizzard / *aqsaqullnaa* / CW / (Leer notes).
nest / *ungluq* / C / (Leer notes).
ptarmigan, crop of / *pukuyaq* / KW / (Leer notes).
taking off and flapping wings against water surface / *paa-* / AAY / (Fortescue et al. 1994).
to peck / *pu'uγ*/ AAY / (Fortescue et al. 1994).
wing / *saqeq* / C / (Leer notes).
wings, to flap / *saqiur-* / C / (Leer notes).
wishbone / *agaq* / CE / (Leer notes).

Bird names

albatross, black footed / *iklliyayuusiq* / CE / (Leer notes). i.e., *Diomedea nigripes* (Griggs 1997).
albatross, short tailed / *ungusarpak* / CE / (Leer notes). i.e., *Diomedea albatrus* (Griggs 1997).
auklet / *akllegaq* / CE / (Leer notes). There are four species of auklet in the PWS area; the rhinoceros auklet (*Cerorhinca monocerata*), Cassin's auklet, (*Ptychoramphus aleuticus*) and the parakeet auktet (*Cyclorrhynchus psittacula*) and the crested auklet (*Aethia cristatella*) (Griggs 1997).
brant / *kam̥uk* / CE / (Fortescue et al. 1994). i.e., *Branta bernicula.*
chicken hawk / *qecuwaliq* / C / (Leer 1978). No synonym for 'chicken hawk' was found. There are four species of hawk which can be found in PWS; the red-tailed hawk (*Buteo jamaicensis*), rough-legged hawk (*B. lagopus*), goshawk (*Accipiter gentilis*), and sharp-shinned hawk (*A. striatus*) (Griggs 1997).
coot / *tekicehnquaq* / CE / (Leer notes). i.e., *Fulica americana.*
cormorant / *agayuuq* / C / (Leer notes). It seems unlikely that there is only one word for cormorant, since four species; the double crested cormorant (*Phalacrocorax auritus*), pelagic cormorant (*P. pelagicus*), Brandt's cormorant (*P. penicillatus*), and the red faced cormorant (*P. urile*) are all found in PWS (Griggs 1997).
cormorant, double breasted / *agayuurpak* / C / (Leer notes). Likely the double crested cormorant, *Phalacrocorax auritus.*
cormorant, pelagic / *uyalek* / AAY / (Leer notes). i.e., *Phalacrocorax pelagicus.*
cormorant, summer / *plaatuugualek* / CE / (Leer notes). Litrally means 'one that has a kerchief' and therefore may refer to Brandt's cormorant (*Phalacrocorax penicillatus*) which has a prominent blue chin or the red faced cormorant (*P. urile*) which has a red 'mask' on its face (Griggs, 1997).
crane / *tatellgaq* / C / (Leer notes). i.e., *Grus canadensis.*
crow / *apalngaa'aq* / CE / (Leer notes). i.e., the northwestern crow (*Corvus caurinus*), the only crow found in PWS (Griggs 1997).
dipper / *kui'im ayakutua* / C / (Leer notes). i.e., *Cinclus mexicanus.*
dowitcher, short-billed / *kukukuaq* / CW / (Leer notes), i.e., *Limnodromus griseus.* This word may also refer to the common snipe.
duck / *saquleq* / C / (Leer 1978). This is a ge-

neric word for any species of duck.

duck / *ungusaq* / CE / (Leer notes). This is a generic word for any type of duck.

duck, 'eider-like', small / *extuk* / AAY / (Fortescue et al. 1994). Whether this refers to juvenile eiders of either species found in PWS, the common eider (*Somateria mollissima*) or the king eider (*S. spectabilis*), or other small duck like birds is unclear. This could refer to species such as scaups (*Aythya*), buffleheads and goldeneyes (*Bucephala*), or scoters (*Melanitta*) (Griggs 1997). There is also potential for steller's eider (*Polysticta stelleri*) to be found in the PWS area. Note that *extuk* is the same word as that for a repeated sharp noise.

duck, all white / *nasqurtuli'aq* / CE / (Leer notes). Perhaps a word for domesticated white ducks.

duck, American widgeon / *qacaaq* / KW / (Leer notes). i.e., *Anas americana*. Note that this word may also be identified as the teal.

duck, black scoter / *sukumyaaq* / CE / (Leer notes). i.e., *Melanitta nigra*.

duck, bufflehead / *nacallngaayak* / C / (Leer notes). i.e., *Bucephala albeola*

duck, canvasback / *tengyuq* / CE / (Leer notes). i.e., *Aythya valisineria*. This creature has also been identified as the 'blue-billed' duck by locals and has the synonym of *egtuk*.

duck, eider / qayarriq / C / (Leer notes). There are two species of eider duck which frequent the waters of PWS; the king eider (*Somateria spectabilis*) and the common eider (*S. mollissima*) (Griggs 1997). This word is used in the KW sub-dialect to refer to the spectacled eider (*S. fischeri*).

duck, eider, brown / *qaanillqaacak* / C / (Leer notes). May refer to the common eider (*Somateria mollissima*), but may also refer to the female eiders in general which are brown as in many species of duck.

duck, falcated teal / *kau'utaaq* / CE / (Leer notes). i.e., *Anas falcata*.

duck, gadwall / *tengyunguaq* / KW / (Leer notes). i.e., *Anas strepera*. Note that this word may also be identified as the green-winged teal (*Anas crecca*).

duck, goldeneye / *nasqurtuliq* / CW / (Leer notes). There are two species of goldeneyes found in PWS; the common goldeneye (*Bucephala clangula*) and Barrow's goldeneye (*B. islandica*).

duck, goldeneye / *qapugnaq* / C / (Leer notes). There are two species of goldeneyes found in PWS; the common goldeneye (*Bucephala clangula*) and Barrow's goldeneye (*B. islandica*).

duck, green-winged teal / *apa'ariilnguq* / CE / (Leer notes). i.e., *Anas crecca*.

duck, green-winged teal / *tengyunguaq* / KW / (Leer notes). i.e., *Anas crecca*. Note that this word may also be identified as the gadwall (*Anas strepera*).

duck, harlequin / *qaingiaq* / CE / (Leer notes). i.e., *Histrionicus histrionicus*.

duck, king eider / *qe[illegible]a[illegible]ek* / AAY / (Fortescue et al. 1994). i.e., *Somateria spectabilis*.

duck, mallard / *ngillqitaq, nillqitaq* / C / (Fortescue et al. 1994). i.e., *Anas platyrhynchos*.

duck, mallard / *seqtaq* / CE / (Leer notes). i.e., *Anas platyrhynchos*.

duck, oldsquaw / *arrangkiluk* / C / (Leer notes). i.e., *Clangula hyemalis*.

duck, pintail / *amutaarualek* / C / (Leer notes). i.e., *Anas acuta*.

duck, ring-necked / *nasqurtuliq* / KW / (Leer notes). i.e., *Aythya collaris*.

duck, rock / *ungunguasaaq* / C / (Leer 1978). No synonym has been found for this word.

duck, surf-scoter / *tunuculek* / CW / (Leer notes). i.e., *Melanitta perspicillata*..

duck, teal / *qacaaq* / KW / (Leer notes). There are two species of teal found in PWS; the green winged teal (*Anas crecca*), and blue-winged teal (*Anas discors*) (Griggs 1997). Note that this word may also be identified as the American widgeon (*Anas americana*).

duck, white-winged scoter / *gaalerualek* / CE / (Leer notes). i.e., *Melanitta fusca*.

eagle, bald / *quckalaq* / CE / (Leer notes). i.e., *Haliaeetus leucocephalus*.

eagle, golden / *anglluayuq* / (Leer notes). i.e., *Aquila chrysaetos*.

goose / *tengmiaq* / CE / (Leer notes). There is no distinction as to whether this word means the white fronted goose (*Anser albifrons*), the Canada goose (*Branta canadensis*), the brant (*B. bernicula*), or any two, or all of these species of goose which could be found in PWS (Griggs 1997). Note, too that the emperor goose (*Chen canagica*) could also be sighted in PWS.

goose, Canada / *laɣiq* / KW / (Fortescue et al. 1994). i.e., *Branta canadensis*.

goose, white fronted / *neqlleq* / KE / (Leer notes). i.e *Anser albifrons*.

goshawk / *ulualek* / CW / (Leer notes). i.e., *Ac-*

cipiter gentilis.

grebe, large / *atatarpak* / CE / (Leer notes). The red-necked grebe (*Podiceps grisegena*) is the largest of the two species of grebe found in PWS (Griggs 1997).

grebe, red-necked / *atatak* / CW / (Leer notes). i.e., *Podiceps grisegena.*

grebe, small / *atataa'aq* / CE / (Leer notes). The horned grebe (*Podiceps auritus*) is the smallest of the two species of grebe found in PWS (Griggs 1997).

guillemot / cugaq / CE / (Leer notes). i.e., the pigeon guillemot (*Cepphus grylle*).

gull, Bonaparte's / *marayaaq* / CW / (Leer notes). i.e., *Larus philadelphia.* This name is also used to refer to the long-tailed jaeger (*Stercorarius longicaudus*) and arctic tern (*Sterna paradisaea*).

gull, glaucus / *kukiswak* / KW / (Fortescue et al. 1994). i.e., *Larus hyperboreus.*

gull, herring / egyaaq / C / (Leer notes). i.e., *Larus argentatus.*

gull, sea / *naru'aq* / CE / (Leer notes). The mew gull (*Larus canus*), glaucus gull (*L. hyperboreus*), herring gull (*L. argentatus*), glaucus winged gull (*L. glaucescens*) and Bonaparte's gull (*L. philadelphia*) are all found in PWS (Griggs 1997).

gyrfalcon / *nerusicuulek* / C / (Leer notes). i.e., *Falco rusticolus.*

hawk, red-tailed / *aarruliq* / CE / (Leer notes). i.e., *Buteo jamaicensis.*

hawk, rough-legged / *qill'iq* / CE / (Leer notes). i.e., *Buteo lagopus.*

hawk, sharp-shinned / *qecu'alia'aq* / C / (Leer notes). i.e., *Accipiter striatus.* May also refer to the red-tailed hawk *Buteo jamaicensis.*

heron / *yuaqurtuliq* / CE / (Leer notes). i.e., great blue heron (*Ardea herodias*).

jaeger, long-tailed / *maraayaq* / CW / (Leer notes). i.e., *Stercorarius longicaudus.* This word has also been identified as refering to Bonapartes's gull (*Larus philadelphia*) and arctic tern (*Sterna paradisaea*).

kingfisher, belted / *nalu'alia'aq* / CE / (Leer notes). i.e., *Ceryle alcyon.*

kittiwake / *qay'aqaaq* / CE / (Leer notes). This probably refers to the black-legged kittiwake) *Rissa tridactyla*).

kittiwake, red-legged / *kiuksaa'aq* / CW / (Leer notes). i.e., *Rissa brevirostris.* This word literally means 'red-legged duck' so there may be some confusion in the translation.

loon / *tuullek* / C / (Leer notes). There are five species of loon in the PWS area: the red throated loon (*Gavia stellata*), the Pacific loon (*G. pacifica*), the common loon (*G. immer*), the yellow billed loon (*G. adamsii*), and the arctic loon (*G. arctica*) (Griggs 1997). Informants on Kodiak island identified this as the word for the arctic loon (Leer notes).

loon, red throated / *qaqaaqaaq* / K / (Fortescue et al. 1994). i.e., *Gavia stellata.*

loon, small / *quiriiq* / CE / (Leer notes). Of the loon species found in PWS the two smallest are the red-throated loon (*Gavia stellata*) and the Pacific loon (*G. pacifica*) (Griggs 1997).

magpie, summer / *qallqanayuumiq* / CE / (Leer notes). i.e., *Pica pica.*

magpie, winter / *man ★skia'aq* / CE / (Leer notes). i.e., *Pica pica.*

merganser, red-breasted / *iisuuteklek* / CE / (Leer notes). i.e., *Mergus serrator.*

merganser, sawbill / *paiq* / C / (Leer notes). Probably refers to the common merganser (*Mergus merganser*), the merganser most seen in PWS (Griggs 1997).

murre / *allpaq* / C / (Leer notes). Two species of murre are found in the PWS area; the common murre (*Uria aalge*) and the thick billed murre (*U. lomvia*) (Griggs 1997).

murre, common / *quanaaq* / CE / (Leer notes). i.e., *Uria aalge.* The word literally means 'thank-you' and is a reference to the friendly demeanor of these birds.

murrelet, marbled / *taitui'aq* / C / (Leer notes). i.e., *Brachyramphus marmoratus.*

owl, great grey / *eyiik* / C / (Leer notes). i.e., *Strix nebulosa.*

owl, great horned / *yartuliiq* / CE / (Leer notes). i.e., *Bubo viginianus.*

owl, snowy / *anipaq* / CE / (Leer notes). i.e., *Nyctea scandiaca.*

oystercatcher, black / *kiggwikiaq* / CE / (Leer notes). i.e., *Haematopus bachmani.*

phalarope, northern / *uqui'aq* / CE / (Leer notes). There are two species of phalarope in PWS; the red necked phalarope (*Phalaropus lobatus*) and the red phalarope (*P. fulicaria*) (Griggs 1997). 'Northern' phalarope may be an Alaskan term for one of the two.

puffin, horned / *qilangaak* / CE / (Leer notes). i.e., *Fratercula corniculata.*

puffin, sea parrot / *tun ★aq* / KE / (Fortescue et al. 1994). It is unclear whether this refers to the horned puffin (*Fratercula corniculata*) or the the tufted puffin (*F. cirrhata*).

puffin, tufted / *ngaq'ngaaq* / C / (Leer 1978). i.e., *Fratercula cirrhata*.

raven / *apalngaaq* / CE / (Leer notes). i.e., *Corvus corax*.

sandpiper / *ayakutaq* / C / (Leer 1978). May also be called *kui'im ayakutaa*. There are several species of sandpiper native to PWS; the rock sandpiper (*Calidris ptilocnemis*), purple sandpiper (*C. maritima*), pectoral sandpiper (*C. melanotos*), Baird's sandpiper (*C. baidii*), western sandpiper (*C. mauri*), least sandpiper (*C. minutilla*), sanderling (*C. alba*), dunlin (*C. alpina*), solitary sandpiper (*Tringa solitaris*), and spotted sandpiper (*Actitis macularia*) (Greer 1997).

sawbill duck / *paiq* / C / (Leer 1978). This may refer to either of two mergansers; red-breasted (*Mergus serrator*) or common (*M. merganser*) found in PWS. These ducks have obvious serations on their bills.

snipe / *kulickiiq* / CE / (Leer 1978). i.e., the common snipe (*Gallinago gallinago*). Derived from Russian.

swan / *uquirpak* / CE / (Leer notes). It is not specified whether this refers to the trumpeter swan (*Cygnus buccinator*) or the tundra swan (*C. columbianus*) both of which occur in PWS. It may also refer to the whooper swan (*C. cygnus*) although it is now an extremely rare species (Griggs 1997).

swan / *saqulegpak* / KW / (Leer notes). May refer to the whooper swan (*Cygnus cygnus*).

tern, arctic / *ayusaq* / C / (Leer 1978). i.e., *Sterna paradisaea*.

tern, common / *teki'aq* / KW / (Leer notes). i.e., *Sterna hirundo*, which does not normally extend as far northwest as PWS (Griggs 1997).

Fish, general

cod egg / *mac'utak* / CE / (Leer notes).

fish / *iqalluk* / C / (Leer 1978).

fish cloaca / *qurwikusaaq* / KW / (Leer notes).

fish pew for tossing fish / *ipuun* / AAY / (Fortescue et al. 1994).

fish eggs / *lluu'ak* / CE / (Leer notes).

fish eggs soaked in fresh water / *qaRmit* / AAY / (Fortescue et al. 1994). This word also means 'to be crunchy', a textural phenomenon occuring when fish eggs are put in fresh water.

fish eggs, aged, added to cooked salmon eggs (fish-egg cheese) / *piinaq* / C / (Fortescue et al. 1994).

fish eggs, membrane containing / *puŋneq* / AAY / (Fortescue et al. 1994).

fish eggs, mixed with oil, mashed potatoes and other ingredients / *akutaq* / C / (Leer 1978).

fish fin / *suluksuk* / KW / (Leer notes).

fish fin, anal / *pamyursuun* / C / (Leer notes).

fish fin, caudal, paddle, oar / *angua'un* / AAY / (Leer notes). Note the overlap of fin and oar.

fish fin, dorsal / *culugsuun* / C / (Leer notes).

fish fin, pelvic / saqiu'um / CW / (Leer notes).

fish gill / *pacik* / C / (Leer notes).

fish head, aged / *uqsuq* / CE / (Fortescue et al. 1994).

fish head, bones in bioled / *mat'ruat* / CE / (Leer notes).

fish head, cod / *iicumaaq* / CE / (Leer notes).

fish meat, drying / *kinertaq* / AAY / (Leer notes).

fish milt / *napasaaq* / CE / (Leer notes).

fish pie / *piłuk, piluk* / C / (Leer 1978). From the Russian word *pirok*.

fish rack / *initaarwik* / C / (Leer 1978).

fish scale / *qugleq* / CE / (Leer notes).

fish skin, / *ami'aq* / C / (Leer notes). May also refer to dried fish skin.

fish slime / *nuayaaq* / C / (Leer notes).

fish tip / *tuqlluq* / C / (Leer notes).

fish trap / *taluyaq* / AAY / (Fortescue et al. 1994).

fish, a cut piece of / *kep'aq* / KW / (Leer notes).

fish, aged / *cin'aq* / AAY / (Leer notes).

fish, aged, aged fish eggs / *qulunguaq* / CE / (Leer notes).

fish, boiled / *egaapiaq* / C / (Leer 1978).

fish, boiled, half dry / *uumataq* / C / (Leer 1978).

fish, cut / *sege-* / C / (Leer notes).

fish, dark meat under skin, fish kidney / *qet'aq* / CE / (Leer notes).

fish, dead, found along a river after spawning / *urullciq* / CE / (Leer notes).

fish, dried / *mingciq* / CE / (Leer notes).

fish, dried / *tamuuq* / AAY / (Fortescue et al. 1994).

fish, head cartilage / *tatangquq* / AAY / (Leer notes).

fish, old / *aakanaq* / C / (Leer 1978).

fish, raw / *qasaq* / AAY / (Fortescue et al. 1994).

fish, raw, to eat / *qasaR-* / AAY / (Fortescue et al. 1994).

fish, salt / *sulunaq* / C / (Leer 1978).

fish, salted, smoked / *palik* / CW / (Leer 1978). cf the AAY term 'to smoke fish', *puyuqe-*.

fish, skeleton cut for drying / *ataneq* / C / (Leer 1978).

fish, swim bladder / *pagaaciq* / CE (Leer notes).

fish, to smoke / *puyuqe-* / AAY / (Fortescue et al. 1994).

fish, to spawn / *qarya-* / CW / (Leer notes).

minnow / *napi'aq* / CE / (Leer notes).

salmon, rear half / *taggwi* / ? / (Leer notes).

salmon, male pink with hump on back / *amaqataq* / KW / (Leer notes).

salmon, moldy and dying after spawning / uukanaqicuk / CE / (Leer notes).

salmon, turned red after entering fresh water / *nariqaaq* / CE (Leer notes).

salmon, with hump after entering fresh water / *qutnguq* / C / (Leer notes).

tom cod egg / *arhmaasuuk* / C / (Leer notes).

Fish names

bass, black / *tukuq* / C / (Leer 1978). Clemens and Wilby (1961) state that 'black bass' is a term used to refer to two different species of rockfish (genus *Sebastes*) on the West Coast of North America, the blue rockfish (*Sebastes mystinus*) and the black rockfish (*Sebastes melanops*).

bass, sea / *tilpuuk* / CW / (Leer notes). i.e., white sea bass (*Atractoscion nobilis*).

capelin / *cikeq* / AAY / (Fortescue et al. 1994). i.e., *Mallotus villosus*.

cod / *amutaq* / C / (Leer 1978) i.e., Pacific cod (*Gadus macrocephalus*).

cod, arctic / *atgiaq* / CW / (Leer notes). i.e., *Boreogadus saida*.

cod, kelp / *culugpua'ak* / CE / (Leer notes). No scientific name could be associated with this fish.

cod, white / quuguuk / CW / (Leer notes). No scientific name could be associated with this fish.

cod-like fish, long with big eyes / *iituliq* / ? / (Leer notes). No scientific name could be associated with this fish.

eel / *quguutnaq* / C / (Leer notes). It is not specified what type of eel this refers to. It may also refer to any eel like fish.

eulachon / *cikeq* / KW / (Leer notes). i.e., *Thaleichthys pacificus*.

flounder, rough-skinned / *ggagtuliq* / C / (Leer 1978). i.e., the starry flounder (*Platichthys stellatus*), which has rough scales.

flounder, smooth-skinned / *matuqulluk* / CE / (Leer notes). Many species of flounders and flounder like fish (family Pleuronectidae) have smooth skin. It is uncertain whether this word refers to one in particular, or all non rough-skinned flounders in general.

flounder, starry / *ur'auk* / CE / (Leer notes). i.e., *Platichthys stellatus*.

hake, Pacific / *rririliq* / C / (Leer notes). i.e., *Merluccius productus*. This word may also refer to the whiting (*Theragra chalcogrammus*), which is closely related to Pacific hake

halibut / *sagiq* / C / (Leer notes). i.e., *Hippoglossus stenolepis*.

herring / *iqalluarpak* / C / (Leer 1978). i.e., *Clupea pallasi*.

Irish lord / *nyangtaaq* / CE / (Leer notes). i.e., the red Irish lord (*Hemilepidotus hemilepidotus*). The brown Irish lord (*H. spinosus*) does not normally range as far north as Alaska (Clemens and Wilby 1961). An English synonym for this fish is bullhead. It should, however, be noted that the word *el'ista* in the CE subdialect is the name for a larger variety of bullhead (Leer notes). Therefore, *nyangtaaq* may refer to the brown Irish lord and *el'ista* may refer to the red Irish lord since the latter is usually much larger than the former.

lumpfish / *amrruq* / C / (Leer notes). i.e., the spiny lumpsucker (*Eumicrotremus orbis*).

pike / *qalru* / KW / (Leer notes). i.e., *Esox lucius*.

salmon / *iqa*[illegible]*uk* / AAY / (Fortescue et al. 1994). Note that this word may also be used to refer to other fish.

salmon or trout fry / *ilaRnaq* / KE / (Fortescue et al. 1994).

salmon, chinook (king) / *iqallugpak* / CE / (Leer notes). i.e., *Oncorhynchus tshawytscha*.

salmon, chum (dog) / *alngartuliq* / CE / (Leer notes) i.e., *Oncorhynchus keta*.

salmon, chum (dog), old, after spawning / *ka*[illegible]*itn*$_{o}$*eq* / K / (Fortescue et al. 1994). i.e., *Oncorhynchus keta*.

salmon, cutthroat trout / *talaa'ik* / CE / (Fortescue et al. 1994). i.e., *Oncorhynchus clarki*.

salmon, pink / *amarturpiaq* / CE / (Leer notes). i.e., *Oncorhynchus. gorbuscha*.

salmon, red (sockeye) / *niklliq* / C / (Leer 1978). i.e., *Oncorhynchus nerka*.

salmon, silver (coho) / *caayuaq* / CE / (Fortescue et al. 1994). i.e., *Oncorhynchus kisutch*.

salmon, steelhead / *mayu'artaq* / C / (Leer notes). i.e., *Oncorhynchus mykiss*.

sculpin, red-bellied / asirnaq / CW / (Leer notes). Refers to a species locally known as the red-bellied sculpin. No scientific name could be found for this fish. There are many sculpin species (family Cottidae) in PWS.

sculpin, yellow / *kala'aq* / CW / (Leer notes). Refers to a species locally known as the 'yellow sculpin'. No scientific name could be found for this fish. There are many sculpin species (family Cottidae) in PWS.

shark / *qaacaq* / C / (Leer 1978). The three most commonly observed sharks in PWS are; the spiny dogfish (*Squalus acanthias*), salmon shark (*Lamna ditropis*), and sixgill shark (*Hexanchus griseus*) (see Hulbert, this vol.)

skate / sagirniilnguq / C / (Leer notes). This could refer to any of the skate species (family rajidae) found in PWS

smelt, boreal / *iqalluaq* / KW / (Leer notes). Presumably refers to capelin (*Mallotus villosus*), although other smelt (Osmeridae) do reside in PWS.

snapper, red / *ushmaq* / CE / (Leer notes). i.e., *Sebastodes ruberrimus*.

sole / *tasaayaq* / KW / (Leer notes) / This could refer to any of the numerous species of sole and flounder (family Pleuronectidae) inhabiting PWS.

stickleback / *cukilrua'ak* / CE / (Leer notes). i.e., *Gasterosteus aculeatus*.

tomcod / *taaqatak* / CE / (Leer notes). i.e., *Microgadus proximus*.

trout / *saagua'aq* / CE / (Leer notes). Any member of the family Salmonidae.

trout, hook-nosed / *curlluk* / KE / (Leer notes). No scientific names has been associated as of yet with this fish.

trout, spotted / *giigaq* / KW / (Leer notes). Both the Dolly Varden (*Salvelinus malma*) and brook trout (*S. fontinalis*) have prominent spots.

whiting / *rririliq* / C / (Leer notes). i.e.. *Theragra chalcogrammus*. This word might also refer to the Pacific hake (*Merluccius productus*), a close relation of whiting.

Mammals, general

ambergris / kulamiim miryaa, kulamiim qulaq'aa / CE / (Leer notes). Literally, 'whale vomit'.

baleen / *negarkaq* / C / (Leer notes).

fin, dorsal / *puguun* / CE / (Leer notes).

flipper, front / *it'ga'aq* / KW / (Leer notes).

flipper, tail / *it'alaq* / C / (Leer notes).

food in stomach or intestines / *imanaq* / AAY / (Fortescue et al. 1994). This word is related to similar words in other Eskimo languages for a species of mollusk eaten by walrus.

fur / *amiq* / C / (Leer 1978).

gut, blown up / *suplluaq* / CE / (Leer notes). Usually from a bear or sea lion.

meat, between ribs and fat of a seal / *qiak* / KW / (Leer notes).

membrane, covering seal gut / *katu'arneq* / CE / (Leer notes).

oil, rendered / *egneq* / AAY / (Leer notes). Mostly derived from seals.

oil, to fry in, render oil by frying blubber / *cuataaR* / C / (Fortescue et al. 1994). Mostly derived from seals.

oil, to render / *ege-* / C / (Leer notes).

pelt, skin side / *cata* / CW / (Fortescue et al. 1994).

porpoise skin / *mangtak* / C / (Leer notes).

sea lion flipper, gristly layer underneath / *maunak* / C / (Leer notes).

seal bladder / *meq'artaq* / CE / (Leer notes). Used as a buoy, or to carry fresh water.

seal fat / *usulkiiq* / AAY / (Fortescue et al. 1994).

seal fetus / *imlauq* / KW / (Fortescue et al. 1994).

seal head / aalisuuk / KW / (Leer notes).

seal hide, dehaired by hanging over hot rocks in a sauna / *ulikuq* / CW / (Leer notes).

seal hide, dehaired by stretching and scraping, used for a kayak cover / *nengugtaq* / C / (Leer notes).

seal hide, old, used for various purposes / *cimyaq* / C / Leer notes).

seal meat between ribs and fat / *qiak* / KW / (Leer notes).

seal oil / *blubber* / uquq / AAY / (Fortescue et al. 1994).

seal, pelvis bone / *mak'atestaaq* / C / (Leer notes). Used to play a kind of divining game

sealskin float / *awataq* / KW / (Fortescue et al. 1994).

sealskin, to take blubber off of / *qapagte-* / AAY / (Leer notes).

sinews / qikarlluk / KW / (Leer notes). Usually derived from caribou and sea lion and used for sewing.

skin, tanned, from young aninmal / *qatgwiaq* / CW / (Leer notes). Used as underwear.

walrus tusk, ivory / *tugka'aq* / KW / (Leer notes). i.e., the tusk of *Odobenus rosmarus*.

whale tail / *caqrwik* / K / (Leer notes).

Mammal names

bear, black / *tan'erliq* / C / (Leer notes). i.e., *Ursus americanus*.

bear, brown / *laqlaq* / C / (Leer notes). i.e., the grizzly bear (*Ursus arctos*).

bear, grizzly / *taquka'aq* / K / (Leer notes). i.e., *Ursus arctos*.

dolphin / *qaaniq* / C / (Leer 1978) i.e., Pacific white sided dolphin (*Lagenorhynchus obliquidens*).

fur seal / *aataak* / C / (Leer 1978). i.e., *Callorhinus ursinus*.

otter, sea / *ikam'aq* / C / (Leer 1978). i.e., *Enhydra lutris*.

porpoise / *cilpiq* / C / (Leer notes). This word refers to a porpoise with a long (dorsal?) fin. When diving four points from its body break the surface.

porpoise / *mangaq* / C / (Leer notes). It is not specified whether this refers to the harbor porpoise (*Phocoena phocoena*) or Dall's porpoise (*Phocoenoides dalli*) both of which are found in PWS (Hill et al. 1997).

sea lion / *wiinaq* / C / (Leer notes). There is no distinction whether this word refers to the steller sea lion (*Eumetopias jubatus*) or the northern fur seal (*Callorhinus ursinus*) both of which may be found in PWS (Hill et al. 1996).

seal / *qaigyaq* / C / (Leer notes). It seems most likely that this word refers to the harbor seal (*Phoca vitulina*), but it can also refer to other seals. The northern elephant seal (*Mirounga angustirostris*) is the only other likely to be seen in PWS (Hill et al. 1997).

seal, small that does not grow / *nainguaq* / KW / (Leer notes). No scientific name was founf for this animal.

seal, spotted / *alngalck* / C / (Leer notes). i.e., *Phoca largha*. Not now resident in PWS (Hill et al. 1997).

walrus / *asguq* / CE / (Leer notes). i.e., *Odobenus rosmarus*.

whale, bowhead / *ar'uq* / CW / (Leer notes). i.e., *Balaena mysticetus*, a species not resident in PWS (Hill et al. 1997).

whale, humpback / *qen ✱ulek* / CE / (Fortescue et al. 1994). i.e., *Megaptera novaeagliae*. Fortescue et al. (1994) note that this might also refer to whales in general, as they only cite one author for the humpback whale definition.

whale, killer / *arlluk* / C / (Leer notes). i.e., *Orcinus orca*.

whale, large type / *taksugpak* / CE / (Leer notes). The most common large whales that would be seen in or around PWS are the gray whale (*Eschrichtius robustus*), the humpback whale (*Megaptera novaeangliae*), the fin whale (*Balaenoptera physalis*), and the northern right whale (*Eubalaena glacialis*) (Hill et al. 1997). The fin whale is the largest and the term may refer specifically to it, but this is not specified. The whale is said to be narow and long, one informant said sixty feet (twenty meters) long, with teeth, suggesting it may be the sperm whale (*Physeter catodon*).

whale, minke / *mangarniiq* / C / (Leer notes). i.e., *Balaenoptera acutorostrata*.

whale, sperm / *kulamak* / CE / (Leer notes). i.e., *Physeter catodon*. This word can also refer to any whale.

whale, white / *asi'arnaq, anaqarnaq* / C / (Leer notes). i.e., the beluga whale (*Delphinapterus leucas*).

whale, with 'carved' breast / uniinalek / CE / (Leer notes). No scientific name was found for this whale.

Invertebrates

anemone, sea / *sanaqusak* / C / (Leer 1978). i.e., members of the class Anthozoa.

barnacle / *qauq* / C / (Leer notes). i.e., a species of either genus *Semibalanus* or *Balanus*.

chiton, gumboot / *urriitaq* / C / (Leer 1978). i.e., *Cryptochiton stelleri*.

chiton, ladyslipper / *uriitarpak* / C / (Leer 1978). i.e., an unidentified member of the class Polyplacophora.

clam / *salaq* / C / (Leer 1978) i.e., members of the class Bivalvia.

clam, geoduck / *salarpak* / CE / (Leer notes). i.e., *Panope abrupta*.

clam, razor / *cingtaataq* / C / (Leer notes). i.e., *Siliqua patula*.

clam, red neck / *tuuqaatiq* / CE / (Leer notes). No scientific name was found for this species.

clam, long-necked / *alirualek* / CE / (Leer notes). No scientific name was found for this species.

clam, small high water / *set'alek* / CE / (Leer notes). No scientific name was found for this species.

cockle / *taugtaaq* / C / (Leer notes). i.e., *Clinocardium nuttalli.*

crab / *yual'aak* / CE / (Leer notes) i.e.. members of the order Decapoda, infraorder Brachyura.

crab, dungeness / *canipgaq* / CE / (Leer notes). i.e. *Cancer magister.*

crab, tanner / *pupsuleryu'alq, pupsuleryua'ak* / CE / (Leer notes). i.e., *Chionoecetes bairdi.*

cucumber, sea / *kingugpak* / CE / (Leer notes). i.e., members of the class Holothuroidea.

tusk shell / *iwiluryaaq* / C / (Leer notes). i.e., *Dentalium pretiosum.*

flea, sand / *petgeryaaq* / AAY / (Fortescue et al. 1994). i.e., *Orchestia traskiana.*

invertebrate, marine / *imaam kingua* / CW / (Leer notes). Literally means 'sea bug'.

jellyfish / *qaacek* / C / (Leer 1978). i.e., members of class Scyphozoa, order Semaeostomeae.

limpet, Chinaman's hat / *melungqucak* / CE / (Leer notes). i.e., belongs to the family Acmaeidae.

mussel / *amyak* / C / (Leer notes). Since there is no further clarification, the word might refer to large individuals of either or both species, *Mytilus edulis* and *M. trossulus*, found in Alaska (Foster 1997).

mussel, big brown / *melugyaq* / KW / (Leer notes). Apparently refers to the genus *Modiolus.*

octopus / *amikuk* / C / (Leer notes). i.e., members of the family Octopodidae.

oyster / *qailim matutii* / CE / (Leer notes). i.e. members of the genus *Crassostrea.*

sand flea / *qumitgaq* / c / (Leer 1978). i.e., members of the order Amphipoda

sea star / *agsiq* / C / 'Starfish' in Fortescue et al. (1994). i.e., members of the class Asteroidea.

sea star / *agyaruaq* / CW / (Leer 1978). Note the difference with the word in Fortescue et al. (1994); both are used in CW. This one is a newly coined word meaning 'something like a star'.

sea urchin / *uutuk* / AAY / (Fortescue et al. 1994). i.e., members of the class Echinoidea.

sea worm, black / *anaqiitak* / C / (Leer notes). No scientific name was found for this species.

shrimp / *petgeryaarpak* / CE / (Leer notes). i.e. a member of the class Decapoda.

snail / *ipuk* / CW / (Leer notes). i.e., members of either order Mesogastropoda or order Neogastropoda.

snail, large / *ipuullquq* / C / (Leer notes).

snail, coffee / *kauglaq* / C / (Leer notes). No scientific name was found for this snail.

squid / *amikurniilnguq* / CE / (Leer notes). i.e., members of the family Loliginidae.

Plants / Protists

algae / *aqayak* / KE / (Fortescue et al. 1994).

driftwood / *pukilaaq* / C / (Leer 1978).

driftwood, bark used for fire / *ketaq* / C / (Leer 1978).

driftwood, small piece / *camRu(q)* / AAY / (Fortescue et al. 1994).

eelgrass / *cuula'ik* / CE / (Leer notes).

kelp, brown / *set'alek* / CE / (Leer notes). A brown kelp with pencil-like marks and two leaves on each side of the stem. The stem is eaten.

kelp, brown, heavy, flat, wide / *cimyaruaq* / CE / (Leer notes). Perhaps a member of the family Laminariaceae.

kelp, bulb / *aqlluurteshnaq* / CE / (Leer notes). No synonym was found for this species.

kelp, bull / *qalinguq* / C / (Leer notes) i.e., *Nereocystis leutkeana.*

kelp, bull, head / *nasquluk* / CW / (Leer notes).

kelp, bull, tail (whip) of / *nuakataq* / C / (Leer notes). Often used for fishing line.

kelp, green, large round head / *meq'artaq* / CE / (Leer notes). No synonym was found for this species.

kelp, long stringy / *arlluguaq* / CE / (Leer notes). Has gas bladders strung out like buoys at intervals.

kelp, sheet / *kapuustaaruaq* / C / (Leer notes). A large, green coloured species, the name of which was derived from the Russian word for cabbage. Perhaps a member of the family Laminariaceae.

kelp, streamer of / *sel'aq* / CW / (Leer notes).

log, drift / *tep'aq* / AAY / (Leer notes).

plant, eaten by swans from lake bottoms / *qerqaq, rrertaq* / AAY / (Leer notes).

seaweed, branched in fingers / *ata'ik* / CE / (Leer notes). Possibly refers to members of the family Codiaceae.

seaweed, bulbous / *iituq* / C / (Leer notes). A kelp with hole in the blade, perhaps a reference to the appearannce of the blade of reproducing *Nereocystis luetkeana* individuals.

seaweed, edible (dulse) / *caqallqaq* / C / (Leer 1978).

seaweed, edible (dulse), large / *caqallqarpak* / CE / (Leer notes).

seaweed, fucus / *ellquaq* / CW / (Leer notes). i.e., *Fucus gardneri.*

seaweed, long, fishline / *nemeRyaq* / AAY / (Fortescue et al. 1994).

seaweed, hair / *nuaruaq* / CE / (Leer notes). No synonym was found for this species.

seaweed, red / *nepuaq* / CE / (Leer notes).

weeds, water / *ney'aq* / CE / (Leer notes).

DISCUSSION

One of the most striking features of this word list is the contrast between the groups of organisms for which names appear. For instance the coverage of names for mammals and birds is comparatively rich whereas the detail of names for invertebrates, and plants is less informative. Such varying detail can be explained by two processes, the first a result of the linguists who recorded Alutiiq terms, the second a result of the Alutiiq people who acted as informants.

In obtaining terms for a species linguists must know something of the classification of those animals they are seeking to define. It is not surprising, therefore, that there is more details for bird and mammal species. These are the most familiar aquatic species to lay people and non-specialists and the easiest to observe from land. It should also be noted that of the fish named, the most detailed information relates to economically important species, which, again would be more familiar to someone lacking a specialists' knowledge of local organisms.

Problems may also arise in translating some terms. For example, Fortescue et al. (1994) base their dictionary on many sources which originally sought to translate 'Eskimo' terms to European languages other than English, including Danish, Russian, German, and French. This implies a larger scope for confusion in obtaining common names for animal species than in English alone, an already rich language for common names. For example, *Oncorhynchus tshawytscha* can be referred to as 'king salmon', 'tyee salmon', 'spring salmon', 'quinnat salmon', or 'chinook salmon' depending solely on the locale on the west coast of North America. Therefore, in the final unification of all the sources to the dictionary there is much room for confusion between common European names.

Problems of ascribing too much detail may occur such as in the popular myth of 'Eskimo' languages having many terms for snow. This myth has been effectively refuted by Martin (1986). However, as Pullum (1991) points out the story is still held to be true by many, including linguists and scientists. The story has its basis in the Worfian hypothesis that a people's environment helped shape the richness of their language. Therefore, for northern peoples it was logical that there must be many words for snow. Numbers of words for snow in Eskimo languages have been variously reported as high as 400 (see Pullum 1991). The myth was also fed by paternalistic urban views of the type of society Inuit peoples must have and has been magnified through time.

As for the informants, they too act as a filter of information. As Berlin (1992) points out that informants quickly become aware of the level of expertise of the person studying their language. Given this understanding, informants will provide more detail where they believe the greater understanding lay. So if the informants felt the linguist was unfamiliar with invertebrates of the area, they may quite logically omit detail that might be wasted on an observer incapable of distinguishing the different species.

A further layer of filtering may occur in cases where people having knowledge of certain types of animals were simply not questioned. For example the division of labour in traditional societies may be according to class, family or sex. Often the upper class may have exclusive rights to hunt large game animals. Another common phenomenon is women being the people most often responsible for collecting invertebrates and plants from the nearshore environment. It is easy to imagine that linguists studying a given community may in all likelihood spend the majority of their time with male hunters. By this mechanism there would be an increased likelihood of informant-driven filtering occurring. Members of the less talked to groups would likely see the linguist as having very little knowledge or interest in the species they may be asked to give information on. Berlin (1992) gives an example of such a mechanism for women of the Aguaruna who were unwilling to provide knowledge they had of manioc species (a plant) since male questioners were felt to be 'ignorant' on the topic.

We can see from these issues a need to bridge the gap between TEK and traditional science. Most important to bridgeing this gap is a clear understanding of what different people mean when they use a particular word. This paper represents such a step for PWS by cross referencing animals and concepts with their scientific equivalents. We have attempted to minimise difficulties, confusion and assumptions by the long term contact Jeff Leer has had with communities of Alutiiq speakers throughout his career as a linguist. His continuing contact with speakers in the communities from which the words in this study were used allows for a greater degree of precision and accuracy than could be achieved by simply consulting a dictionary.

Without such interpretation local TEK could be misrepresented, as either not specific or overly specific. For example, a people who fish will have much to say about the habits of the species they target. However, they may have somewhat less to say about the habits of other organisms which they do not use. Such distinctions are useful in determining what knowledge TEK and science can most effectively exchange. Cultures do classify organisms in roughly similar fashion, but these classifications reflect the relative abundance of the organisms they encounter (Berlin 1992). Thus, by accurately identifying the words in two languages and the organisms they refer to, we can begin to establish the bridges required for cross validation of TEK and science.

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Appendices

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Appendix 2. Workshop Agendas

Fridays Lunch Meeting Agenda

Preparation of March Food Web Workshop

12:15 - 1 pm, January 30, 1998
Quadrant Room, Hotel Captain Cook
Anchorage, Alaska

This is an informal lunch meeting during which data-weak components of a straw-man PWS ecosystem will be identified for refinement by EVOS-funded investigators, and during which participants can help plan a collaborative food web workshop to be held in March

Lunch for that day (sandwiches, salads, and drinks) will be served in the room for the participants of the meeting.

1. Introduction of Ecopath project managers and EVOS researchers (10 min)
    a. Stuart Pimm
    b. Bob Powell
    c. Daniel Pauly
    d. Tom Okey
    e. Name, affiliation, and interest of other EVOS researchers

2. Presentation of UBC/Tennessee near-term project aims (materials) (15 min)
    a. Preliminary Ecopath model of PWS (report)
    b. Poster outlining key elements of project
        * *including list of ecosystem components for which information is needed*
    c. Guidelines for describing functional groups in PWS ecosystem

3. Planning the March workshop (15 min)
    a. Suggestions for items to consider
    b. Suggestions for meeting participants
    c. Other matters

4. Further discussion (guided small groups as desired)

Please contact Tom Okey at UBC with questions about the agenda, or the lunch meeting.
Fisheries Centre, 2204 Main Mall, Vancouver B.C. Canada V6T 1Z4 604.822-1950, tokey@fisheries.com

Food Web Workshop Agenda

Constructing an ECOPATH model of Prince William Sound

March 2-4, 1998
EVOS Restoration Office
245 G Street, Suite 401, Anchorage

Monday 2 **Workshop Day 1** in restoration office conference room
0915 - 0920 Welcome to EVOS office .... *Stan Senner*
0920 - 1925 EVOS program context--ecosystem synthesis .... *Andy Gunther*
0925 - 0945 Round-table introductions
0945 - 1000 About this workshop .... *Daniel Pauly*
1000 - 1015 Coffee break
1015 - 1100 **Presentation 1** - Introduction and orientation to ECOPATH modelling-*D. P.*
1100 - 1140 **Presentation 2** - Demonstration of preliminary ECOPATH model of Prince William Sound prior to the EVOS .... *Tom Okey*
1140 - 1200 Questions and discussion
1200 - 1330 Optional sandwich lunch provided in room, or lunch on your own
1330 - 1430 **Workshop Session 1:** Review of period and area to be covered. Moderator: *D. Pauly*
1430 - 1700 **Workshop Session 2:** Definition of ecosystem components ("boxes") to be included in the models, assignment of components, and discussion of completeness. Moderator: *D. Pauly*

Tuesday 3 **Workshop Day 2**
0900 - 1000 **Presentation 3:** From static to dynamic models .... *Stuart Pimm*
1000 - 1020 Coffee break
1020 - 1200 **Workshop Session 3:** Participants assemble key parameter estimates (Biomass, consumption, etc.) for their group.
1200 - 1330 Optional sandwich lunch provided in room, or lunch on your own
1330 - 1500 **Workshop Session 4:** Assembling a diet matrix. Mod.: *D. Pauly*
1500 - 1520 Coffee break
1520 - 1700 **Workshop Session 5:** Data entry and balancing model. Moderator: *D. Pauly*

Wednesday 4 **Workshop Day 3**
0900 - 1030 **Workshop Session 6:** Definition of major habitat types and species or group affinities to these habitats. Moderator: *T. Okey*
1030 - 1050 Coffee break
1050 - 1200 **Session 6 (continued):** Data entry using ECOPATH IV.
1200 - 1330 Optional sandwich lunch provided in room, or lunch on your own
1330 - 1500 **Workshop Session 7:**Discussion of flow networks and ancillary statistics of balanced models. Moderator: *D. Pauly*
1500 - 1520 Coffee break
1500 - 1700 **Workshop Session 8:** Wrapping Up -
(a) What have we learned, and what have we accomplished?
(b) Future Actions--applied uses/identified weaknesses, Moderator: *D. Pauly*

Ecopath Workshop Agenda

A balanced trophic model of PWS: presentation and refinement

October 5, 1998
EVOS Restoration office conference room
645 G Street, Suite 401, Anchorage

0915 - 1920 EVOS program context--ecosystem synthesis .... *Bob Spies*
0925 - 0935 Round-table introductions (whole room)
0935 - 0950 About this workshop, about ECOPATH modelling .... *Daniel Pauly*

0945 - 1015 Presentation of ECOPATH model of Prince William Sound, 1994-1996 .... *Tom Okey*
  a) Process of model construction
  b) Trophic structure and collaboration
  c) Balancing the PWS trophic model

1015 - 1030 Coffee break

1030 – 1130 Analysis if the PWS food web ... *Stuart Pimm*
1130 – 1200 "What if" scenarios and spatial simulations ... *Tom Okey*

1200 - 1330 Lunch on your own in downtown Anchorage

1330 - 1430 Questions and discussion about the simulations and their implications, including suggested improvements to the approach.

1430 - 1445 Plans for the coming year ... *Daniel Pauly*

1445 - 1500 Comments from the Chief Scientist and Peer Reviewers

Close

1600 Informal demonstrations of Ecopath and Alaska FishBase (if desired)

Workshop Agenda

Ecosystem-based stewardship of PWS living resources by local communities and students:

uses of a food web model

September 27, 1999, 1 - 5 pm
EVOS Restoration office conference room
645 G Street, Suite 401, Anchorage

1:05 – 1:15 Welcoming remarks .... *Hugh Short and Helen Morris*
1:15 – 1:30 Brief round-table introductions (whole room)
1:30 – 1:35 About this workshop ... *Tom Okey*
1:35 – 2:00 ECOPATH modeling and its uses .... *Daniel Pauly*

2:00 – 2:30 **Presentation 1** – The ECOPATH model of Prince William Sound, ... *Tom Okey*

a) Building the model
b) Animals, plants, and energy flow in PWS
c) Description, simulated playing, and virtual experiments

2:30 – 2:45 Coffee break

2:45 – 3:30 **Presentation 2** – Managing resources and learning through simulation .... *Daniel Pauly and Tom Okey*

3:30 – 4:00 Playing the 'what if' game ... (whole room)

4:00 – 5:00 Questions and discussion in casual format

Ecopath Workshop Agenda

A balanced trophic model of PWS: applications for ecosystem-based management

September 28, 1999 9 am
Alaska Dept. of Fish and Game
Division of Commercial Fisheries
333 Raspberry Road, Anchorage

0910 - 1920	Welcoming remarks and description of fisheries management in PWS .... *Stephen Fried*
0920 - 0930	Round-table introductions (whole room)
0930 - 1000	About this workshop: ECOPATH modeling and its applications .... *Daniel Pauly*
1000 - 1030	**Presentation 1 -** Presentation of ECOPATH model of Prince William Sound, 1994-1996 .... *Tom Okey* d) Process of model construction e) Description of food web structure f) From description to dynamic modeling to management
1030 - 1045	Coffee break
1045 - 1115	**Presentation 1 (continued):** d) Ecosim - dynamic temporal simulation e) Ecospace - dynamic spatial simulation
1115 - 1200	Questions and discussion
1200 - 1330	Lunch on your own
1330 - 1430	**Presentation 2:** Management applications of the PWS model: complimenting existing tools ... *Daniel Pauly and Tom Okey*
1430 - 1530	Group discussion about the approach, the PWS model, and potential management applications
1530 - 1545	Summary comments ... *any participants or presenters*
1545 - 1550	Closing comments .... *Stephen Fried*
1550	Informal demonstrations if desired

Appendix 3

Monthly Estimates for PWS Zooplankton Parameters (R.T. Cooney, *unpublished data*; depth of integration = 300 m; PWS area used = 8800 km^2)

Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Biomass (g·m^{-3})												
Total Zooplankton	0.03613	0.00805	0.04589	0.23862	0.43135	0.60514	0.35001	0.22229	0.09457	0.09573	0.07997	0.06420
Zoops <= 1 mg wet wt	0.01881	0.00700	0.02113	0.13613	0.23933	0.41893	0.29484	0.17179	0.04874	0.06520	0.04791	0.03062
Zoops >1 mg wet wt	0.01747	0.00135	0.02448	0.10249	0.19202	0.18621	0.05517	0.05050	0.04583	0.03053	0.03206	0.03358
Copepoda	0.01716	0.00433	0.02894	0.18237	0.34731	0.35525	0.18937	0.12095	0.05252	0.05809	0.04404	0.02999
Pteropoda	0.00086	0.00014	0.00018	0.00110	0.00781	0.12087	0.06825	0.03485	0.00144	0.00010	0.00084	0.00158
Amphipoda	0.00437	0.00008	0.00539	0.00475	0.00541	0.00677	0.00449	0.00456	0.00464	0.00704	0.00785	0.00866
Larvacea	0.00028	0.00022	0.00034	0.00234	0.02484	0.03391	0.06993	0.03600	0.00208	0.01097	0.00566	0.00035
Euphausiacea	0.00826	0.00055	0.00402	0.00904	0.01913	0.00905	0.00690	0.00687	0.00683	0.00472	0.01035	0.01597
Other	0.00520	0.00274	0.00701	0.03902	0.02685	0.07929	0.01107	0.01907	0.02707	0.01481	0.01124	0.00766
(t·km^{-2})												
Total Zooplankton	10.84	2.42	13.77	71.59	129.41	181.54	105.00	66.69	28.37	28.72	23.99	19.26
Zoops <= 1 mg wet wt	5.64	2.10	6.34	40.84	71.80	125.68	88.45	51.54	14.62	19.56	14.37	3.06
Zoops >1 mg wet wt	5.24	0.41	7.34	30.75	57.61	55.86	16.55	15.15	13.75	9.16	9.62	10.07
Copepoda	5.15	1.30	8.68	54.71	104.19	106.58	56.81	36.28	15.76	17.43	13.21	3.00
Pteropoda	0.26	0.04	0.05	0.33	2.34	36.26	20.48	10.45	0.43	0.03	0.25	0.16
Amphipoda	1.31	0.02	1.62	1.43	1.62	2.03	1.35	1.37	1.39	2.11	2.35	0.87
Larvacea	0.08	0.06	0.10	0.70	7.45	10.17	20.98	10.80	0.62	3.29	1.70	0.03
Euphausiacea	2.48	0.17	1.21	2.71	5.74	2.72	2.07	2.06	2.05	1.42	3.10	1.60
Other	1.56	0.82	2.10	11.71	8.06	23.79	3.32	5.72	8.12	4.44	3.37	0.77
t in PWS												
Total Zooplankton	95370	21252	121150	629957	1138764	1597570	924026	586846	249665	252727	211108	169488
Zoops <= 1 mg wet wt	49656	18475	55773	359394	631839	1105980	778383	453534	128684	172125	126481	26946
Zoops >1 mg wet wt	46113	3567	64617	270574	506938	491581	145638	133315	120991	80610	84634	88659
Copepoda	45302	11431	76402	481457	916898	937860	499937	319295	138653	153358	116266	26391
Pteropoda	2270	370	475	2904	20618	319097	180180	91991	3802	264	2218	1390
Amphipoda	11525	201	14238	12543	14288	17875	11851	12045	12239	18575	20712	7616
Larvacea	742	570	908	6178	65572	89528	184618	95049	5481	28963	14938	304
Euphausiacea	21806	1452	10613	23866	50503	23892	18216	18124	18031	12461	27311	14054
Other	13724	7228	18514	103010	70884	209318	29225	50342	71460	39106	29663	6740

Continued on next page...

P/B Ratios (monthly)												
Total Zooplankton	0.40	0.30	0.40	0.80	1.50	2.30	1.60	0.80	0.70	0.40	0.40	0.40
Zoops <= 1 mg wet wt	0.50	0.30	0.50	1.00	3.00	4.50	2.00	1.00	0.70	0.50	0.50	0.50
Zoops >1 mg wet wt	0.10	0.20	0.40	1.00	1.50	0.50	0.40	0.30	0.20	0.20	0.10	0.10
Copepoda	0.30	0.15	0.25	0.40	1.20	1.60	1.40	1.20	0.50	0.40	0.30	0.30
Pteropoda	0.05	0.02	0.10	0.40	0.80	0.40	0.30	0.30	0.20	0.20	0.15	0.08
Amphipoda	0.10	0.10	0.10	0.10	0.20	0.30	0.40	0.20	0.20	0.10	0.10	0.10
Larvacea	0.10	0.10	0.20	0.30	0.40	0.40	0.30	0.30	0.30	0.20	0.20	0.20
Euphausiacea	0.05	0.08	0.10	0.15	0.25	0.30	0.25	0.20	0.20	0.20	0.12	0.10
Other	0.10	0.05	0.15	0.25	0.30	0.30	0.30	0.20	0.10	0.10	0.10	0.05
Production (t·month^{-1})												
Total Zooplankton	38148	6376	48460	503965	1708146	3674410	1478442	469476	174765	101091	84443	67795
Zoops <= 1 mg wet wt	24828	5542	27886	359394	1895517	4976912	1556766	453534	90079	86063	63241	13473
Zoops >1 mg wet wt	4611	713	25847	270574	760407	245791	58255	39994	24198	16122	8463	8866
Copepoda	13591	1715	19100	192583	1100278	1500576	699912	383154	69326	61343	34880	7917
Pteropoda	114	7	48	1162	16495	127639	54054	27597	760	53	333	111
Amphipoda	1152	20	1424	1254	2858	5363	4740	2409	2448	1858	2071	762
Larvacea	74	57	182	1853	26229	35811	55385	28515	1644	5793	2988	61
Euphausiacea	1090	116	1061	3580	12626	7168	4554	3625	3606	2492	3277	1405
Other	1372	361	2777	25753	21265	62795	8767	10068	7146	3911	2966	337
Q/B (Ingest·month^{-1}/ biomass)												
Total Zooplankton	1.33	1.00	1.33	2.67	5.00	7.67	5.33	2.67	2.33	1.33	1.33	1.33
Zoops <= 1 mg wet wt	1.67	1.00	1.67	3.33	10.00	15.00	6.67	3.33	2.33	1.67	1.67	1.67
Zoops >1 mg wet wt	0.33	0.67	1.33	3.33	5.00	1.67	1.33	1.00	0.67	0.67	0.33	0.33
Copepoda	1.00	0.50	0.83	1.33	4.00	5.33	4.67	4.00	1.67	1.33	1.00	1.00
Pteropoda	0.17	0.07	0.33	1.33	2.67	1.33	1.00	1.00	0.67	0.67	0.50	0.27
Amphipoda	0.33	0.33	0.33	0.33	0.67	1.00	1.33	0.67	0.67	0.33	0.33	0.33
Larvacea	0.33	0.33	0.67	1.00	1.33	1.33	1.00	1.00	1.00	0.67	0.67	0.67
Euphausiacea	0.17	0.27	0.33	0.50	0.83	1.00	0.83	0.67	0.67	0.67	0.40	0.33
Other	0.33	0.17	0.50	0.83	1.00	1.00	1.00	0.67	0.33	0.33	0.33	0.17

Appendix 3 (cont.) Monthly Estimates for PWS Nearshore Zooplankton Parameters (inshore of 20 m isobath)
(R. Foy, *unpublished data*)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	mean
Biomass (g·m^{-3})													
Carnivorous jellies	0.06	0.00	0.01	0.10	0.20	1.11	0.61	0.44	0.36	0.28	0.07	0.12	0.2
Omnivorous zooplankton	0.02	0.00	0.03	0.04	0.05	0.13	0.13	0.10	0.06	0.02	0.01	0.01	0.0
Herbivorous zooplankton	0.07	0.00	0.06	0.09	0.13	0.14	0.06	0.11	0.06	0.01	0.00	0.01	0.0
Biomass (t·km^{-2})													
Carnivorous jellies	0.55	0.01	0.06	1.02	1.98	11.13	6.08	4.36	3.59	2.82	0.65	1.21	2.78
Omnivorous zooplankton	0.16	0.04	0.28	0.40	0.52	1.28	1.26	1.01	0.61	0.22	0.12	0.08	0.49
Herbivorous zooplankton	0.66	0.03	0.58	0.93	1.29	1.42	0.57	1.09	0.58	0.06	0.04	0.12	0.61
Biomass (t·km^{-2}; PWS-wide)													
Carnivorous jellies	0.09	0.00	0.01	0.16	0.31	1.76	0.96	0.69	0.57	0.45	0.10	0.19	0.44
Omnivorous zooplankton	0.025	0.006	0.044	0.063	0.082	0.204	0.199	0.160	0.097	0.034	0.019	0.012	0.07
Herbivorous zooplankton	0.105	0.005	0.092	0.148	0.204	0.225	0.090	0.174	0.092	0.010	0.006	0.019	0.09
total mt (0-20m stratum)													
Carnivorous *jellies*	780	21	79	1446	2813	15780	8617	6187	5093	3999	927	1710	3954.2
Omnivorous zooplankton	227	52	395	563	731	1820	1783	1431	868	305	170	109	704.4
Herbivorous zooplankton	935	41	826	1325	1824	2013	803	1552	820	88	57	171	871.2
P/B ratio (year^{-1})													
Carnivorous jellies	0.15	0.04	0.04	0.28	0.52	2.98	1.46	1.12	0.94	0.77	0.21	0.33	8.8
Omnivorous zooplankton	0.71	0.07	0.72	1.01	1.30	1.50	0.58	1.17	0.62	0.07	0.02	0.13	7.9
Herbivorous zooplankton	0.66	0.30	2.90	2.45	2.01	5.19	4.96	4.15	2.52	0.89	0.64	0.32	27.0
Q/B ratio (year^{-1})													
Carnivorous jellies	0.50	0.13	0.13	0.93	1.72	9.94	4.85	3.73	3.15	2.56	0.69	1.09	29.4
Omnivorous zooplankton	2.37	0.23	2.39	3.36	4.34	5.01	1.93	3.90	2.06	0.22	0.08	0.43	26.3
Herbivorous zooplankton	2.22	1.01	9.67	8.18	6.69	17.29	16.54	13.82	8.40	2.98	2.14	1.06	90.0

Appendix 4

Derivation of diet compositions of forage fish, 1994-1996
(data are from APEX-SEA program, provided by M. Sturdevant)

Tables A4-1 to A4-7 (inside the following boxes) show proportions and percentages of prey categories (defined for the PWS model) for seven species of forage fishes. Diets were derived from the APEX-SEA project data contained in each box (data provided by M. Sturdevant).

Table A4-8 shows seasonal changes in the diet composition of juvenile Pacific herring (R. J. Foy, UAF Institute of Marine Sciences, *unpublished* data).

Box A4-1. Pacific Herring diet data

Prey	May-94	Jun-94	Jul-94	Aug-94	Sep-94	Nov-94	Jul-95	Oct-95	Jul-96	Mean
Large calanoids	48.8	37.1	36.5	75.4	14.3	6.2	8.4	47.7	33.3	34.2
Small calanoids	0.2	10.1	4.1	2.8	29.3	17.5	80.2	8.2	24.1	19.6
Larvaceans	0.0	1.1	2.8	1.1	5.2	7.8	1.5	16.1	11.5	5.2
Cladocerans	0.0	0.2	0.0	0.0	0.1	0.0	0.9	0.0	0.2	0.2
Malacostracans	44.8	25.0	0.7	2.9	19.3	0.2	0.3	0.8	3.0	10.8
Euphausiids	0.0	1.8	13.1	0.0	13.3	51.1	0.1	13.3	0.5	10.4
Hyperiid amphipods	0.9	3.4	6.1	13.8	7.5	4.7	0.6	8.6	5.7	5.7
Zoeae	0.1	4.3	1.6	2.9	1.2	0.0	0.0	0.0	0.0	1.1
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.4	0.1	0.1
Fish	4.5	10.3	19.9	0.5	5.1	0.0	0.0	0.0	0.1	4.5
Decapods	0.6	0.3	2.6	0.0	2.6	0.0	1.6	0.6	20.3	3.2
Gastropods	0.0	4.5	9.5	0.0	0.6	2.7	1.0	0.3	0.6	2.1
Invertebrate eggs	0.0	1.5	0.1	0.4	1.4	0.0	0.0	0.0	0.0	0.4
Barnacles	0.1	0.2	1.1	0.0	0.1	0.0	0.1	0.0	0.3	0.2
Others	0.0	0.2	0.1	0.0	0.1	9.4	5.4	3.9	0.4	2.2
Polychaetes	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2

Table A4-1. Derivation of Pacific Herring diet based on above data from APEX-SEA program.

Prey category	proportion	% in diet
Herbivorous Zooplankton	0.592	59.2
Omnivorous Zooplankton	0.326	32.6
Shallow Sm. Epifauna	0.082	8.2

Box A4-2. Capelin diet data

Prey	May-94	Jun-94	Jul-94	Jul-95	Oct-95	Mean
Euphausiids	1.3	5.6	55.6	0.0	92.6	31.0
Fish	60.3	24.7	0.0	0.0	0.0	17.0
Hyperiid amphipods	17.5	1.0	0.0	0.0	0.0	3.7
Malacostracans	4.4	3.8	0.1	0.0	0.0	1.7
Zoeae	0.6	3.7	3.8	0.0	0.0	1.6
Small calanoids	0.2	5.0	0.0	88.6	7.0	20.2
Large calanoids	13.8	55.8	0.0	0.0	0.0	13.9
Larvaceans	0.0	0.0	37.2	0.0	0.0	7.5
Other	0.0	0.1	3.3	4.6	0.4	1.7
Gastropods	1.3	0.2	0.0	6.7	0.0	1.6
Gammarid amphipods	0.4	0.0	0.0	0.0	0.0	0.1
Decapods	0.3	0.0	0.0	0.0	0.0	0.1

Table A4-2. Derivation of capelin diet based on above data from APEX-SEA program.

Prey category	proportion	% in diet
Omnivorous Zooplankton	0.5	55.0
Herbivorous Zooplankton	0.4	41.6
Shallow Sm. Epifauna	0.0	3.4

Box A4-3. Sandlance diet data

Prey	May-94	Jun-94	Jul-94	Sep-94	Jul-95	Jul-96	mean
Small calanoids	11.5	12.7	60.5	23.0	62.7	66.7	39.5
Large calanoids	82.0	6.0	16.4	32.1	10.8	12.2	26.6
Larvaceans	0.0	2.1	6.7	2.4	18.3	8.5	6.3
Cladocerans	0.0	0.6	0.3	0.0	0.3	0.5	0.3
Fish	2.5	73.2	2.2	0.0	0.0	0.7	13.1
Malacostracans	2.6	1.8	1.0	27.2	0.0	0.0	5.4
Euphausiids	0.5	0.5	0.5	5.0	0.1	0.1	1.1
Zoeae	0.1	0.2	0.6	3.7	0.0	0.0	0.8
Hyperiid amphipods	0.0	0.3	2.2	0.6	0.5	0.2	0.6
Barnacles	0.0	0.3	1.8	0.2	1.3	5.8	1.6
Invertebrate eggs	0.7	1.2	5.4	1.4	0.0	0.0	1.5
Others	0.0	0.1	0.1	0.0	4.9	2.0	1.2
Decapods	0.0	0.4	0.1	2.4	0.3	2.5	1.0
Gastropods	0.0	0.4	1.4	1.4	0.7	0.8	0.8
Polychaetes	0.0	0.1	0.6	0.0	0.0	0.0	0.1
Bivalves	0.0	0.0	0.0	0.7	0.0	0.0	0.1

Table A4-3. Derivation of sandlance diet based on above data from APEX-SEA program.

Prey category	Proportion	% in diet
Herbivorous Zooplankton	0.727	72.7
Omnivorous Zooplankton	0.210	21.0
Shallow Sm. Epifauna	0.062	6.2

Box A4-4. Pink Salmon fry diet data

Prey	May-94	Jun-94	Jul-94	Aug-94	Sep-94	Jul-95	Jul-96	Mean
Fish	24.0	28.2	32.4	35.6	34.3	22.2	79.1	36.5
Large calanoids	36.1	6.9	11.8	31.1	42.7	13.3	2.7	20.7
Small calanoids	7.9	17.1	10.0	0.0	0.0	0.6	0.2	5.1
Larvaceans	0.1	5.4	8.3	3.7	3.1	1.0	6.5	4.0
Cladocerans	0.0	3.2	0.1	0.0	0.0	0.4	0.0	0.5
Gastropods	1.1	21.2	28.3	0.1	0.0	33.7	0.6	12.1
Decapods	0.0	0.4	1.0	17.1	1.8	1.3	4.2	3.7
Harpact. Copepods	0.9	0.3	0.1	0.0	0.0	0.0	0.0	0.2
Polychaetes	0.8	0.2	0.1	0.0	0.0	0.0	0.0	0.2
Gammarid amphipods	0.6	0.3	0.1	0.0	0.7	0.0	0.0	0.2
Euphausiids	23.1	9.8	1.1	3.5	4.2	14.9	0.2	8.1
Hyperiid amphipods	1.1	0.5	3.2	7.9	11.0	7.9	3.7	5.0
Barnacles	1.6	1.3	0.5	0.1	0.3	0.1	0.6	0.6
Malacostracans	0.0	1.7	0.3	0.6	0.9	0.1	0.8	0.6
Chaetognaths	0.0	0.0	0.0	0.0	0.0	4.2	0.2	0.6
Zoeae	0.8	0.9	1.3	0.2	0.7	0.0	0.0	0.6
Invertebrate eggs	0.3	0.6	0.5	0.0	0.0	0.0	0.0	0.2
Others	1.7	1.8	1.0	0.1	0.2	0.1	0.2	0.7
Insects	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.1

Table A4-4. Derivation of pink salmon fry diet based on above data from APEX-SEA program.

Prey category	Proportion	% in diet
Fish	0.365	36.5
Herbivorous zooplankton	0.303	30.3
Carnivorous zooplankton	0.156	15.6
Shal. Sm. Epibenthos	0.164	16.4

Box A4-5. Chum salmon fry diet data

Prey	May-94	Jun-94	Jul-94	Aug-94	Sep-94	Jul-95	Jul-96	Mean
Fish	83.1	72.2	86.5	3.5	37.6	29.6	12.1	46.4
Large calanoids	14.1	5.6	0.3	69.1	12.9	3.8	0.0	15.1
Larvaceans	0.4	0.6	2.2	11.0	8.6	5.9	5.4	4.9
Small calanoids	0.1	1.6	0.0	0.3	0.0	0.3	0.1	0.3
Cladocerans	0.0	1.4	0.0	0.1	0.0	0.0	0.0	0.2
Decapods	0.0	0.9	0.0	0.4	2.1	2.5	24.8	4.4
Gastropods	0.0	8.8	11.0	0.1	0.1	0.1	0.9	3.0
Barnacles	0.0	1.5	0.0	6.6	0.1	0.0	12.1	2.9
Gammarid amphipods	0.3	0.2	0.0	0.0	1.2	0.0	0.0	0.2
Polychaetes	0.1	0.5	0.0	0.0	0.0	0.0	0.0	0.1
Hyperiid amphipods	0.0	0.4	0.0	2.1	8.4	41.3	41.7	13.4
Malacostracans	0.0	0.5	0.0	0.0	17.9	0.0	1.0	2.8
Chaetegnaths	0.0	0.0	0.0	0.0	0.0	16.4	0.9	2.5
Gelatenous zooplankton	0.0	0.0	0.0	6.3	2.7	0.0	0.0	1.3
Euphausiids	0.1	1.2	0.0	0.0	7.2	0.1	0.0	1.2
Others	1.7	2.2	0.0	0.0	0.1	0.0	0.6	0.7
Zoeae	0.0	2.0	0.0	0.3	0.1	0.0	0.0	0.3
Invertebrate eggs	0.0	0.1	0.0	0.0	1.0	0.0	0.0	0.2
Insect	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.1

Table A4-5. Derivation of chum salmon fry diet based on above data from APEX-SEA program.

Prey category	Proportion	% in diet
Fish	0.464	46.4
Herbivorous zooplankton	0.206	20.6
Carnivorous zooplankton	0.222	22.2
Shallow Sm. Epibenthos	0.106	10.6

Box A4-6. Eulachon diet data

Prey	Nov-94	Oct-95	mean
Euphausiids	46.9	97.8	72.3
Malacostracans	53.1	1.1	27.1
Small calanoids	0.0	0.6	0.3
Gastropods	0.0	0.5	0.2

Table A4-6. Derivation of eulachon diet based on above data from APEX-SEA program.

Prey category	Proportion	% in diet
Omnivorous Zooplankton	0.994	99.4
Herbivorous Zooplankton	0.003	0.3
Shallow Sm. Epifauna	0.002	0.2

Box A4-7. Small Pacific cod diet data

Prey Category	May-94	Jun-94	Jul-94	Sep-94	mean
Large calanoids	97.9	32.0	18.5	0.2	37.2
Small calanoids	1.9	16.6	10.5	0.4	7.3
Larvaceans	0.0	0.7	1.5	0.0	0.6
Cladocerans	0.0	1.8	0.1	0.0	0.5
Euphausiids	0.0	1.5	9.4	35.0	11.4
Others	0.0	0.7	2.6	28.5	8.0
Malacostracans	0.0	2.7	2.1	23.1	7.0
Hyperiid amphipods	0.0	0.6	4.1	0.6	1.3
Zoeae	0.1	1.7	1.8	1.6	1.3
Gastropods	0.0	5.1	30.2	0.0	8.8
Gammarid amphipods	0.0	12.7	4.7	3.1	5.1
Decapods	0.0	2.9	7.2	1.7	3.0
Harpacticoid copepods	0.0	3.1	1.2	2.2	1.6
Barnacles	0.0	0.9	0.6	0.0	0.4
Polychaetes	0.0	0.5	0.0	0.2	0.2
Invertebrate eggs	0.1	0.7	0.4	0.0	0.3
Fish	0.0	15.7	5.1	3.4	6.1

Table A4-7. Derivation of Pacific cod diet based on above data from APEX-SEA program[a].

Prey category	Proportion	% in diet
Herbivorous Zooplankton	0.455	45.5
Carnivorous Zooplankton	0.290	29.0
Shal. Sm. Epibenthos	0.194	19.4
Small Pelagic Fishes	0.061	6.1

a) Not used in model because data applied only to small individuals; data from Table 2-1 in Yang (1993) were used instead.

Juvenile Pacific Herring

Table A4-8. Seasonal dietary changes in juvenile Pacific herring (Robert J. Foy, UAF Institute of Marine Sciences, unpublished data).

Prey category	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	mean
omnivorous zooplankton	0.75	0.14	0.21	0.20	0.04	0.27	0.37	0.50	0.60	0.56	0.61	0.78	**0.42**
herbivorous zooplankton	0.25	0.85	0.77	0.80	0.95	0.57	0.60	0.50	0.40	0.44	0.39	0.22	**0.56**
fish eggs	0.00	0.01	0.02	0.00	0.01	0.16	0.03	0.00	0.00	0.00	0.00	0.00	**0.02**

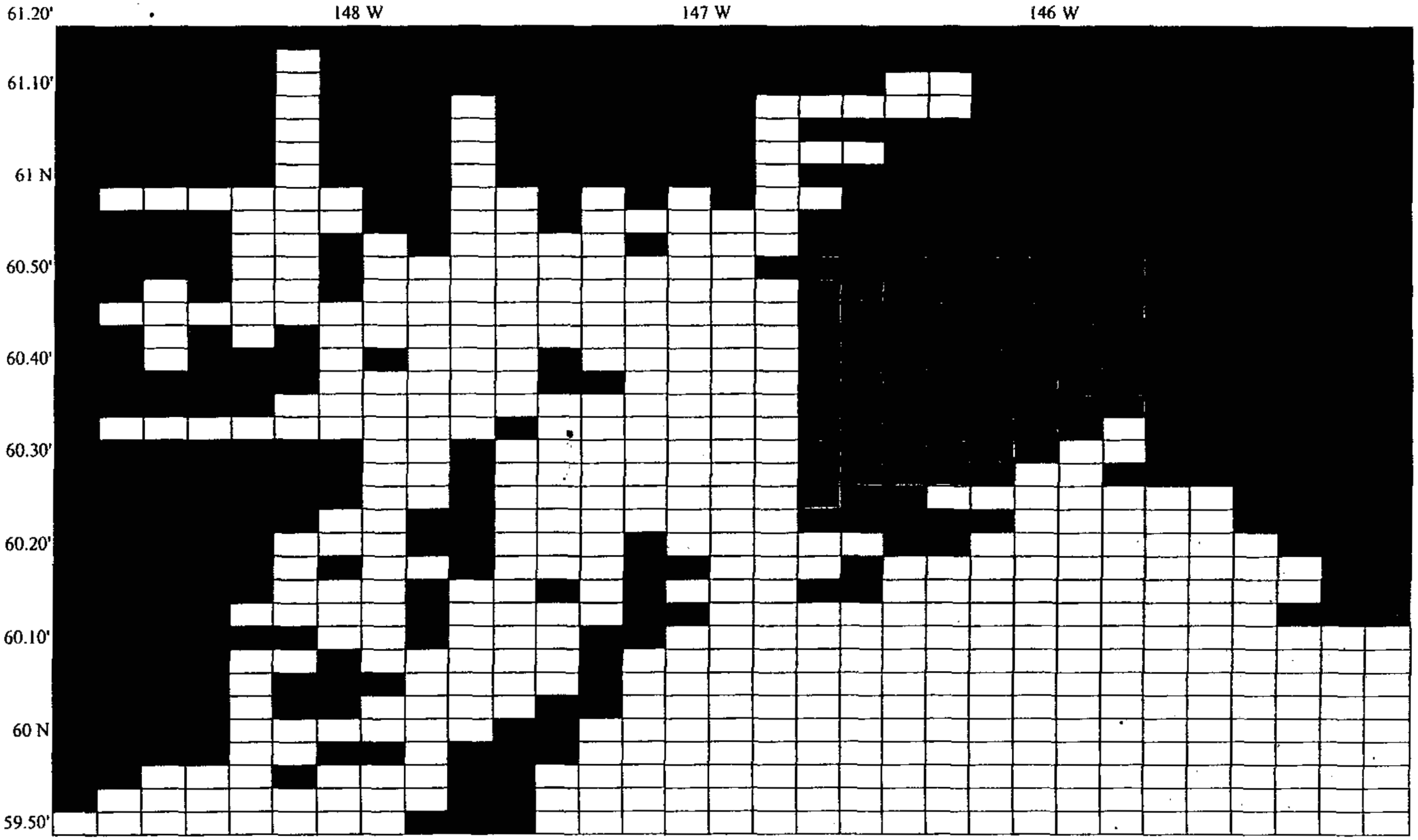
Appendix 5. Input diet compositions (% weight) of animals in Prince William Sound, Alaska, from 1994-1996.

Prey	Predator																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 Transient Orca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Resident Orca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Sharks	-	-	0.3	-	5.0	-	3.8	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Halibut	0.5	0.5	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Porpoise	59.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Pinnipeds	38.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Lingcod	-	-	-	-	-	0.1	0.5	-	-	-	-	-	-	-	1.0	-	-	-	-	-
8 Sablefish	0.5	0.5	1.0	-	10.0	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Adult Atooth	-	-	15.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Adult Salmon	1.5	74.0	32.3	13.3	-	14.0	13.6	-	-	-	-	-	8.0	-	-	-	-	-	-	-
11 Pac. Cod	-	0.5	3.5	1.2	14.0	1.0	-	0.7	-	-	-	-	-	-	-	-	-	-	-	-
12 Juv. Atooth.	-	-	0.2	4.0	-	-	-	-	-	-	5.0	-	-	-	2.0	-	-	-	-	-
13 Avian Predators	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14 Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	50.0	-	-	-	-	-	-	-
15 Deep demersals	-	-	0.3	3.8	-	-	-	4.8	-	-	7.9	-	-	-	17.0	-	3.1	-	-	-
16 Pollock 1+	-	0.5	5.0	37.4	-	11.9	5.1	20.8	25.2	-	7.3	3.7	-	6.0	-	2.0	-	-	-	-
17 Rockfish	-	-	0.4	-	-	3.0	3.0	-	1.0	-	-	-	-	-	3.0	-	-	-	-	-
18 Baleen Whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19 Salmon Fry 0-12	-	-	-	2.0	-	1.0	3.2	-	-	0.1	-	-	-	2.0	-	2.0	-	-	-	-
20 Nshore Demersal	-	0.5	-	1.3	5.0	23.0	23.4	-	9.0	-	8.0	-	4.0	8.7	11.0	-	0.2	-	-	4.0
21 Squid	-	-	2.0	0.2	30.0	12.0	-	8.0	-	-	2.5	1.0	-	0.7	5.0	4.9	15.8	-	-	-
22 Eulachon	-	-	-	0.2	6.0	5.3	4.8	10.7	4.7	0.1	0.9	14.7	4.0	4.7	1.0	4.3	-	-	30.0	-
23 Sea otters	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24 Deep Epibent	-	-	9.0	14.1	-	-	-	5.1	4.0	-	35.8	25.0	-	-	15.0	26.0	28.8	-	-	11.0
25 Capelin	-	-	0.5	0.1	-	5.5	-	0.1	5.7	0.1	0.2	4.0	-	1.0	0.5	0.9	0.1	-	1.0	-
26 Adult Herring	-	23.5	3.0	-	25.0	12.0	12.5	2.2	4.0	0.1	0.2	5.1	-	-	-	-	-	20.0	-	-
27 Pollock 0	-	-	-	-	-	-	-	0.3	1.0	-	0.3	1.0	-	-	-	0.2	0.1	-	-	-
28 Shal Lg Epibent	-	-	-	2.4	-	-	-	-	-	-	2.8	-	-	-	1.5	10.3	-	-	-	11.0
29 Invert-eat Bird	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30 Sandlance	-	-	-	0.1	1.0	1.0	-	0.1	1.5	0.1	0.2	4.3	-	15.0	-	0.6	1.1	8.0	1.0	0.5
31 Juv. Herring	-	-	2.5	10.3	4.0	9.2	18.6	5.6	40.9	0.1	0.8	26.2	-	36.7	0.5	6.0	3.1	22.0	5.7	0.5
32 Jellies	-	-	1.0	-	-	-	-	5.4	-	-	-	-	-	-	-	-	-	-	1.1	-
33 Deep sm infauna	-	-	-	-	-	-	-	0.4	-	-	2.8	-	-	-	10.5	-	0.3	-	-	-
34 Near Omni-zoo	-	-	-	-	-	-	-	-	-	-	-	0.1	1.0	1.0	-	0.2	0.3	0.3	0.1	-
35 Omni-zooplankto	-	-	7.0	-	-	-	7.7	6.7	3.0	-	-	14.9	1.0	6.2	2.0	35.1	40.0	49.7	16.3	-
36 Shal sm Infauna	-	-	-	-	-	-	-	-	-	-	2.8	-	-	-	0.5	-	-	-	-	1.0
37 Meiofauna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0	-	-	-	-	-
38 Deep Lg Infauna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.0	-	-	-	-	-
39 Shal Sm Epibent	-	-	2.0	2.4	-	-	-	-	-	-	10.0	-	4.0	5.3	1.5	-	4.7	-	15.7	70.0
40 Shal lg infauna	-	-	-	-	-	-	-	-	-	-	-	-	-	1.8	5.0	-	-	-	-	-
41 Near Herbi-zoo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-
42 Herbi-Zooplankt	-	-	-	-	-	-	3.8	-	-	-	-	-	-	0.1	-	7.4	2.4	-	28.9	2.0
43 Near Phytoplktn	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44 Offshore Phyto.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45 Macroalgae/grass	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46 Nekton falls	-	-	8.0	2.0	-	-	-	9.1	-	-	2.5	-	-	-	-	-	-	-	-	-
47 InshoreDetritus	-	-	-	-	-	-	-	-	-	-	-	-	28.0	10.8	1.0	-	-	-	-	-
48 Offshr Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.0	-	-	-	-	-
Import	-	-	4.5	5.2	-	-	-	20.0	-	99.4	10.0	-	-	-	-	-	-	-	-	-

Appendix 5. (continued). (Predator number corresponds with organism in 'prey' column.)

Prey	Predator																					
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1 Transient Orca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Resident Orca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Sharks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Halibut	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Porpoise	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Lingcod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8 Sablefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Adult Atooth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Adult Salmon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11 Pac. Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12 Juv. Atooth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13 Avian Predators	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14 Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15 Deep demersals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16 Pollock 1+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17 Rockfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18 Baleen Whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19 Salmon Fry 0-12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20 Nshore Demersal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21 Squid	0.3	-	-	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22 Eulachon	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23 Sea otters	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24 Deep Epibent	0.4	-	4.0	25.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25 Capelin	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26 Adult Herring	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27 Pollock 0	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28 Shal Lg Epibent	-	-	16.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29 Invert-eat Bird	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30 Sandlance	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31 Juv. Herring	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32 Jellies	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33 Deep sm infauna	-	-	-	30.0	-	-	-	-	-	-	-	-	4.0	-	-	-	-	-	-	-	-	-
34 Near Omni-zoo	0.3	0.3	-	-	0.3	0.2	0.2	-	-	0.1	0.1	0.1	-	-	-	-	-	-	-	-	-	-
35 Omni-zooplankto	96.6	49.4	-	5.0	41.3	37.7	27.4	-	-	20.9	9.9	22.9	9.0	-	-	-	-	-	-	-	-	-
36 Shal sm Infauna	0.1	-	-	-	-	-	-	19.0	10.0	-	-	-	-	-	-	15.0	-	-	-	-	-	-
37 Meiofauna	-	-	-	3.0	-	-	-	-	-	-	-	-	-	-	-	-	10.0	-	-	-	-	-
38 Deep Lg Infauna	-	-	10.0	5.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39 Shal Sm Epibent	0.3	0.1	-	-	3.4	8.3	-	79.0	90.0	6.3	-	-	-	-	-	-	-	-	5.0	-	-	-
40 Shal lg infauna	-	-	70.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41 Near Herbi-zoo	0.1	-	-	-	0.4	0.3	0.5	-	-	0.5	0.6	0.4	-	0.2	0.2	-	-	-	-	-	-	-
42 Herbi-Zooplankt	1.5	0.2	-	5.0	54.6	53.5	71.9	-	-	72.2	89.4	66.6	9.0	24.8	24.8	-	-	10.0	-	-	-	-
43 Near Phytoplktn	-	-	-	-	-	-	-	-	-	-	-	0.7	-	75.0	-	60.0	-	-	35.0	50.0	100	-
44 Offshore Phyto.	-	-	-	-	-	-	-	-	-	-	-	9.3	-	-	75.0	-	-	-	-	-	-	100
45 Macroalgae/grass	-	-	-	5.0	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	20.0	-	-	-
46 Nekton falls	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
47 InshoreDetritus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25.0	45.0	-	39.7	50.0	-	-
48 Offshr Detritus	-	-	-	20.0	-	-	-	-	-	-	-	-	78.0	-	-	-	45.0	90.0	-	-	-	-
Import	-	50.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 6. Diagram of the spatial distribution of arrowtooth founder in Prince William Sound (Mark Willette, Alaska Dept. of Fish and Game, personal communication; *also see* Arrowtooth flounder section). Approximately 56% of the juvenile biomass and 80% of the adult biomass of arrowtooth flounder occurs in southwestern PWS (yellow). The remainder of the juvenile biomass is found in Orca Bay and Port Fidalgo (blue). This diagram is presented here as an example of the types of spatial distribution and habitat information contributed by collaborators for specification of habitat-based Ecospace modelling (see sections on Ecosim and Ecospace).



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