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The BASS/MODEL Report on Trophic Models of the Subarctic Pacific Basin Ecosystems

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INTRODUCTION

Project scope

The PICES Carrying Capacity and Climate Change (CCCC) BAsin Scale Studies (BASS) Task Team was established to facilitate studies of the impacts of climate change and climate variability on the physical and biological processes in the gyres of the western and eastern subarctic Pacific Ocean.

In general, the oceanography and ecology of the eastern (ESA) and western (WSA) basins of the subarctic Pacific (Fig. 1) are poorly understood relative to the coastal areas. It is known that the central subarctic Pacific is productive as indicated by the large abundance of Pacific salmon, squid and other important fishes. Recent studies also suggest that the oceanography of the gyres is closely linked to the decadal scale changes in climate. Therefore, it is important that there is a co-ordinated effort to focus on the priority research issues, and to exchange scientific information on a timely basis.

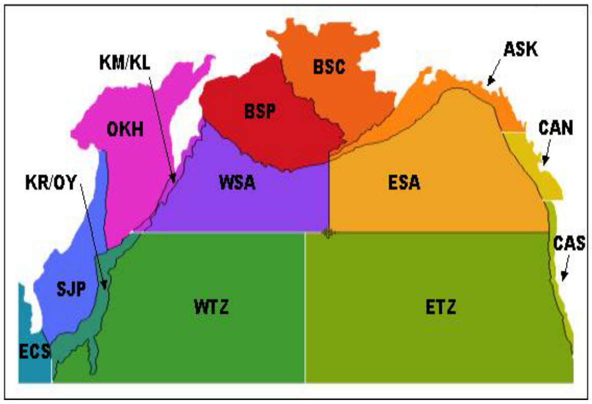


Fig. 1 Sub-regions in the PICES area (north of 30°N and including the marginal seas) of the N. Pacific Ocean. ASK - Gulf of Alaska Continental Shelf; BSC - Bering Sea Continental Shelf; BSP - Bering Sea Pelagic; CAN – California Current North; CAS – California Current South; ECS - East China Sea; ESA - Eastern Subarctic; ETZ - Eastern Tropical Zone; KM/KL - Kurile Islands Region; KR/OY - Kuroshio/Oyashio Region; OKH - Sea of Okhotsk; JP - Sea of Japan; WSA - Western Subarctic; WTZ - Western Tropical Zone.

At the PICES Sixth Annual Meeting, the BASS Task Team sponsored a symposium on the *Ecosystem dynamics of the Eastern and Western Gyres of the Subarctic Pacific*. The purpose was to bring together available information on the two gyres in a comparative framework. Topics included:

1. ocean responses to climate forcing,
2. nutrients and primary production,
3. structure of the lower trophic levels, the mesozooplankton communities, and the epipelagic nekton,
4. the role of midwater fishes, and
5. the importance of these areas to marine birds and mammals.

Papers presented at the meeting were published in a special issue (Beamish *et al.* 1999a) of *Progress in Oceanography* (Guest Editors: R.J. Beamish, S. Kim, M. Terazaki and W.S. Wooster).

A follow-up workshop was convened in Hakodate, Japan (October 2000), to identify potential models which might have utility for examining gyre systems (McFarlane *et al.* 2001). Trophodynamic linkages that were likely to be common, as well as those that were model-specific, were identified, and shortcomings were highlighted. Discussions included identifying data groups and potential data sources, incorporating climate and oceanographic change in models, and linking models of the oceanic gyre to models of coastal regions.

Participants recognized that modelling would play an increasingly prominent role in examining the dynamics of the gyres, and recommended the BASS and MODEL Task Teams examine the feasibility of using the ECOPATH/ECOSIM modelling approach as a means to organize our understanding of ecosystems of the subarctic gyres. Specific objectives were to: (a) synthesize all trophic level data in a common format, (b) examine trophic relations in both gyres using ECOPATH/ECOSIM, and (c) examine methods of incorporating the PICES NEMURO lower trophic level model into the analysis.

Three workshops followed in Honolulu, U.S.A. (March 2001), then Victoria, Canada (October 2001), and finally in La Paz, Mexico (April 2002), where the ECOPATH/ECOSIM baseline models were developed, linked to the NEMURO model, and a number of hypotheses tested (see Appendices C to F for workshop reports).

The purpose of this approach was to provide a "picture" of the two subarctic gyres, and to facilitate our understanding of how these systems respond to natural and anthropogenic change. This report presents our current understanding of the dynamics of these systems. Further, this report should serve as an outline for data availability and more critically, gaps in upper trophic level biological data as they affect our understanding of the function and variation in the subarctic gyres' food webs. Finally, it is hoped that the report will form the basis of future work to link the subarctic gyre system to coastal systems.

Climate change, carrying capacity and food web models of the subarctic Pacific Ocean

The subarctic Pacific consists of a major cyclonic gyre surrounded on the north by coastline and boundary currents, and on the south by the Subarctic Current, which isolates the gyres from subtropical waters. The main gyre is pinched at its longitudinal center by the Aleutian Islands, which causes re-circulation of its waters into two sub-gyres: the Western Subarctic and Eastern (Alaskan) Subarctic Gyres (Fig. 2). The two subarctic gyres are biologically distinct, supporting different species and production patterns from plankton through predatory marine mammals (Beamish 1999). As such, the two separate ecosystems are the primary subjects for comparison in this report.

The biological production, carrying capacity, and food webs of the Eastern and Western Gyres have been subjects of considerable speculation, especially given difficulty of access, and the relatively limited data collection performed in these high seas areas (Pearcy *et al.* 1999). This interest has been driven in part by the fact that the gyres are a "rearing and growth" area for Pacific salmon (*Oncorhynchus* spp.), and are therefore production areas for important commercial fisheries. Additionally, the link between climate and fisheries on decadal (regime shift) scales points to important ecosystem interactions occurring within the gyres and in synchrony with Pacific-wide events (*e.g.*, the Pacific Decadal Oscillation, Mantua *et al.* 1997).

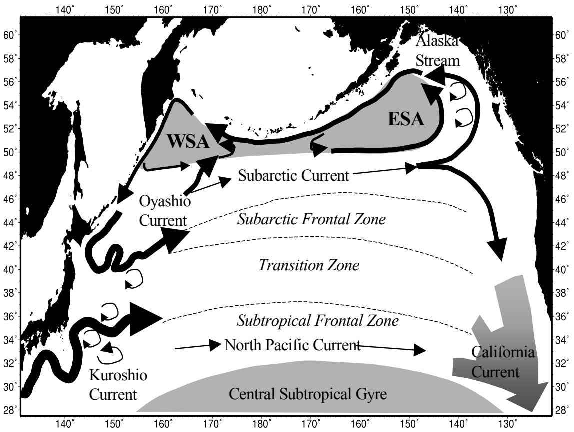


Fig. 2 Western and Eastern Subarctic Gyres (WSA and ESA, shaded gray areas), boundary currents (arrows), and subarctic/subtropical frontal zones (dotted lines). Oceanographic features are approximate and may change on interannual time scales.

Attempts to quantify the carrying capacity and/or maximum production rates of fish in the gyres have revealed a fundamental paradox. Calculations of zooplankton biomass and production, when compared to demands made by foraging salmon, the dominant fish, invariably indicated a surplus of available food. Models constructed in the 1970s (Favorite and Laevastu 1979) concluded that the North Pacific could sustain ten times the 1970s standing stock of salmon.

Yet during the 1980s and 1990s, when the system contained only twice the total salmon biomass examined by Favorite and Laevastu, salmon sizes declined (Bigler *et al.* 1996, Ishida *et al.* 1993, Ricker *et al.* 1995). Conservative production estimates, using observed 1980s and 1990s zooplankton and salmon biomass, indicate that adult salmon consume between 0.04% and 0.10% of available annual zooplankton production (Brodeur *et al.* 1999). Since salmon are a dominant pelagic nekton in the region, it seems at a first glance unlikely that this level of consumption would lead to competition for prey, and thus represent an ecosystem at its carrying capacity for salmon. However, as suggested by Pearcy *et al.* (1999), trophic and seasonal compression of salmon foraging opportunities may reveal more specific foraging limitations: calculations of the forage available for salmon and other large nekton in the gyres is re-examined here.

Further, it is clear that environmental forcing on multi-year scales, for example through the PDO and ENSO, affects the biology of higher trophic levels in these ecosystems and across the globe (Beamish 1993; Brodeur and Ware 1995; Hollowed *et al.* 1998; Francis *et al.* 1998; Beamish *et al.* 1999b). The effects of climate are not limited to the direct increase or decrease of the biomass of the entire system. Animals with longer-than-annual life histories integrate short term changes, and their biomass may not respond immediately to changes in ocean conditions. In order to move from correlative to mechanistic relationships linking climate and biology, it is necessary to construct models, either conceptual or quantitative, which account for appropriate time scales of interaction through the food web. Links may not be linear or direct, and scale is critical.

For example, the shoaling mixed layer is used by Polovina *et al.* (1995) to predict increases in zooplankton production based on the increased concentration of nutrients within the mixed layer. However, as Freeland *et al.* (1998) point out, while the mixed layer may concentrate nutrients during the spring growth of zooplankton, it may also limit resupply of nutrients later in the season. Thus, while the overall quantity of zooplankton production averaged annually may increase, the extent of the bloom throughout a season, and the resulting zooplankton community structure and transfer of energy to other portions of the food web, may increase for some species but decrease for others.

To examine such indirect and possibly unexpected interactions, food web models are a useful tool, and must be scaled to account for differences in rates across trophic levels on both seasonal and interannual scales. To accomplish this, multiple models should be examined in concert, with some models covering small or short scale dynamics (such as those associated with plankton dynamics), and some covering the annual scales of fisheries models. Finally, migration models linking gyres with coastal areas should be used to expand the view to examining synchronous changes that have been reported in marine populations across the widest possible area of the North Pacific.

Purposes of these models

The ECOPATH models presented here are based on the pooling of available data from both sides of the Pacific Ocean. Data from these ecosystems has been brought together and discussed in previous international workshop settings (Beamish *et al.* 1999a): the present work represents the first steps in an ongoing quantitative synthesis. These models provide a quantitative framework for cataloging these data and a guide for directing future data collection.

Various conceptual food web models of the gyres have been constructed (Sanger 1972; Pauly and Christensen 1996; Brodeur *et al.* 1999), usually with a combination of quantitative and qualitative data. These previous models have begun to address and assess the “carrying capacity” of the subarctic Pacific for many important species, especially Pacific salmon: this work is continued here.

More critically, in view of regime- or longer-term climatic change, and the acknowledged importance of links between climate and the production of Pacific salmon and other species, it is desirable to focus research priorities based on quantitative assessments of current notions of subarctic ecosystem sensitivities and interactions. Due to the difficulty of data collection in the open ocean, the ecological links with coastal ecosystems, and the necessity of strong international collaboration in future research of these ecosystems, it is useful to have a quantitative framework for pooling information.

ECOPATH, as a tool, is a relatively straightforward method for constructing a quantitative food web for the purposes of hypothesis exploration and data synthesis. The food webs created are similar to those created through other synthetic methods: the resulting models represent a "snapshot" of what is essentially a moving target, a changing ecosystem. By providing the snapshot as a step in continuing workshops and collaborations, we examine our view of the ecosystem's sensitivities to change as viewed and modeled through the data currently available. Moreover, we are able to use this framework as a guide to data synthesis, by providing foci for continued international collaboration and collective research.

By simultaneously presenting two models built on a similar framework for two different systems (Eastern and Western Gyres), we stress a comparative approach in examining the underlying biology and climate interactions: these comparisons are emphasized in the results of this work. This comparative approach is crucial to understanding the synchronous interactions (simultaneous species rises and collapses) reported in coastal and oceanic ecosystems throughout the world.

The dynamic simulations presented here using ECOSIM include attempts to fit or model changes in biomass as they might occur given certain types of physical forcing. In these models we attempt to take into account the dynamic nature of multiple pathways available in the food webs, and through the examination of simplified interannual patterns, to begin stretching from the correlative to the mechanistic relationship. Finally, we report on the first stages of linking a smaller-scale nutrient-phytoplankton-zooplankton model (NEMURO) with ECOSIM to partially bridge the gap between the seasonal production cycle and the longer time periods associated with regime shifts.

METHODS

Model setting

The Eastern and Western Subarctic Gyres as defined by PICES are broad and heterogeneous areas, with currents and other oceanographic boundaries ensuring that multiple ecosystem processes occur within the gyres (Fig. 2). ECOPATH, on the other hand, is a "closed system" model that assumes spatial homogeneity. However, since biological data do not exist in the gyres for explicitly separating sub-areas, it was decided that two basin models, one for each of the west and east, would be most appropriate.

The original aim was to create models that were targeted to "central gyre" rather than boundary current processes. However, in many cases data for central gyre processes was unavailable. Specifically, in the east, the plankton data and driftnet fishery data were dominated by information near the sub-arctic boundary and NEMURO model calibrated to the Station P region (Subarctic Boundary) were used. In the west, many of the surveys were dominated by both southern boundary processes (in the case of sardines and Pacific pomfret) or Kamchatka Current specific data (in the case of data provided by Russian colleagues). Finally, for species such as marine mammals for which only aggregate North Pacific biomass estimates were available, species were assumed to occur in the gyres in proportion to their area as defined by PICES sub-areas (Fig. 1, Table 1) rather than as defined by shifting oceanographic boundaries (Fig. 2).

The time period chosen for the model was to be as close to present-day as possible; however, when the project was initiated it was recognized that an oceanographic "regime shift" in the late 1990s may have occurred for which biological data was not yet available. Additionally, one of the primary sources of data for upper trophic level fish species, the Japanese squid driftnet fishery, was operative mainly during the late 1980s. Therefore, the target time period for data was chosen to be the late 1980s/early 1990s. While data outside this time period was used when necessary, data quality as reported in Appendix A was downgraded appropriately, with very little data being included from "pre-1976" regime conditions.

Table 1 Ocean surface areas of PICES sub-regions shown in Figure 1, to the nearest thousand square kilometers (Hunt *et al.* 2000).

Region name	Abbreviation	Area (km^2)	Percent
Eastern Bering Sea Shelf	BSC	1,022,000	3.9%
Western Bering Sea and Basin	BSP	1,358,000	5.1%
Gulf of Alaska	ASK	429,000	1.6%
California Current North	CAN	166,000	0.6%
Eastern Subarctic	ESA	3,622,000	13.6%
Western Subarctic	WSA	2,168,000	8.2%
Kamchatka and Kurile Islands	KM/KL	112,000	0.4%
Sea of Okhotsk	OKH	1,600,000	6.0%
California Current South	CAS	129,000	0.5%
Eastern Transition Zone	ETZ	7,809,000	29.4%
Western Transition Zone	WTZ	6,338,000	23.9%
Kuroshio/Oyashio Currents Zone	KR/OY	348,000	1.3%
Japan/East Sea	SJP	1,006,000	3.8%
East China Sea	ECS	435,000	1.6%
TOTAL		26,542,000	100.0%

While ECOPATH is a closed-system model, it does allow some scope for accounting for migrating species, provided that migration is a relatively small proportion of the biomass. However, the dominant commercial fish species in the gyres, and thus a major focus for the models, were Pacific salmon species, all of whom leave the gyres for freshwater systems during the adult phase of their life cycle. Rather than attempting to model "outside" coastal and freshwater processes, salmon data was calibrated to represent "within-system" growth and mortality processes only, and thus the dynamics of juvenile salmon were left as an input to the model (rather than a derived result).

Finally, pink salmon, a dominant upper trophic-level species in the gyres, have a two-year high/low biomass cycle which has been shown to affect the diets and distribution of other species in the subarctic Pacific (Tadokoro *et al.* 1996). Rather than attempting to capture an "average" ecosystem which might never exist, it was decided in the first stages of the project to average high years only for the base ECOPATH salmon species, and thus capture the maximum impact that pink salmon might be expected to have in the system. However, it was not possible, due to limited data, to match these cycles with other species which might have similar cycles (such as euphausiids or micronektonic squid, Aydin 2000).

Other specific data issues, which were revealed later during the modelling process, are detailed in Appendix A by functional group, and noted in the "Results and discussion" section as they might affect our perceptions of the model. In general, the results reported are those which are relatively robust to changes in the above initial assumptions. It should be noted that, at the outset, a major goal of this work was to provide a "gyre-specific" outline for one portion of the Pacific salmon life cycle to guide future research. The most important next step in examining subarctic processes will be to link these results with coastal and freshwater processes, and in doing so to examine climate/ecosystem interactions as a whole.

Base ECOPATH formulation

ECOPATH with ECOSIM (EwE) is a tool for constructing a food web model from fisheries and biological data by subjecting the data to the constraint of ecosystem-level mass-balance. The model assists in the construction of a quantitative food web by ensuring that the biomass inputs and outputs of each ecosystem component (functional group or species) provide a consistent accounting within the specified range of uncertainty in the data.

ECOPATH's strength lies in its emphasis on using data collected and analyzed in many common types of fisheries analyses (especially stock assessment and food habits studies), and its ability to combine the data into a single coherent picture. ECOPATH is a food web analysis tool that has gained broad recognition as a methodology for assembling and exploring data on marine food webs (Polovina 1985; Christensen and Pauly 1992; Christensen *et al.* 2000; see the website *www.ECOPATH.org* for the latest available software, manuals, and list of published models).

ECOPATH is a mass-balance model, built by solving a simple set of linear equations which quantify the amount of material (measured in biomass, energy or tracer elements) moving in and out of each compartment (functional group) in a modeled food web. A single functional group (food web compartment) may be a single species or a set of trophically similar species. The master ECOPATH equation is, for each functional group (i) with predators (j):

$$B_i\left(\frac{P}{B}\right)_i * EE_i + IM_i + BA_i = \sum_j \left[B_j * \left(\frac{Q}{B}\right)_j * DC_{ij} \right] + EM_i + C_i$$

The definition of the parameters in the above equation, and the general methods used to derive each parameter, are given in Table 2.

The preferred method for using the ECOPATH model is to input all parameters from independent data sources, except for ecotrophic efficiency (EE) for each functional group. ECOPATH will estimate vector EE values by solving the resulting set of linear equations, with EE as the unknown for each functional group, utilizing the generalized inverse method (Mackay 1981) to guarantee a solution. The estimation of EE is the primary tool for data calibration in ECOPATH: independent estimates of consumption and production of different species often lead to initial conclusions that species are being preyed upon more than they are produced (EE>1.0), which is impossible under the mass-balance assumption (Christensen *et al.* 2000).

By using an EE greater than 1.0 as a diagnostic tool for error, it is then possible to assess the relative quality of each piece of input data to adjust inputs to a self-consistent whole. This process is known as "balancing" the model: it does not imply that the true ecosystem is in equilibrium but rather quantifies the uncertainty contained in the estimates of supply and demand present in the system.

In cases where biomass or P/B ratio are unknown for a functional group, the EE for the group may be fixed (usually at a value between 0.8-1.0) and used to estimate the minimum biomass or production rate required to satisfy the consumption rates of the group's predators. In our study, this "minimum production" method was used only in cases where no reasonable estimate of biomass is available for a group.

The mass-balance constraints of ECOPATH do not in themselves require or assume that the modeled ecosystem is in equilibrium, but rather require that any directional component (known increase or decrease of biomass) be included in the mass-balance accounting through the biomass accumulation (BA) term. However, in practice, especially in systems with sparse data such as the subarctic gyres, the necessary averaging of data over longer (climatic regime-scale) time periods requires an added assumption of relative stability.

Within a modeled regime, it is assumed that the ecosystem lies close (within the range of short-term process noise) to an attractive and relatively stable equilibrium for all modeled biomass components. The system is not assumed to exist in this state in any given instant; rather, like a carrying capacity for an individual species, it is the state towards which the ecosystem would tend in the absence of driving perturbations (changes in fishing rates, climate, or other process-related noise).

Table 2 Parameters and parameter calculation methods for the ECOPATH master equation.

Parameter	**Abbreviation and units**	**Calculation methods used**
Biomass	B (t/km^2)	Survey estimates, sampling programs, stock assessments
Production/Biomass	P/B (1/year)	Mortality rates, growth rates, bioenergetics models
Consumption/Biomass	Q/B (1/year)	Bioenergetics models, gut content analysis
Diet composition	DC (proportion by biomass)	Gut content analysis
Fisheries Catch	C (t/km^2)	Fisheries statistics
Biomass Accumulation	BA (t/km^2)	Biomass trend data
Immigration and Emigration	IM and EM (t/km^2)	Migration studies
Ecotrophic Efficiency	EE (proportion)	Estimated by ECOPATH or set at standard level to estimate biomass

ECOPATH model building and balancing

The construction of an ECOPATH model for each of the two regions shown in Figure 1 was an iterative process of data gathering and examination. Data were collected and/or contributed by Task Team members and workshop participants, and graded by quality as fully documented in Appendix A.

During this initial data gathering and preparation, no attempt was made to adjust or balance the input parameters based on mass-balance concerns. The results of this initial phase was an unbalanced model; that is, a quantitative food web for which many of the functional groups' EEs were far greater than 1.0, indicating potential errors in the input data or incorrect/incomplete model formulation. These unbalanced models were presented at the initial three-day workshop in Honolulu, U.S.A. (Appendix D) and, based on discussion of data quality and sources, adjustments were made to balance the model (reduce all EEs below 1.0) as discussed in Appendix A.

After conducting this initial balancing exercise, varied metrics of ecosystem structure, such as community respiration, production, trophic level, and niche habitat were calculated from the balanced models of the two ecosystems. Further, initial ECOSIM runs (perturbation analyses) were performed as described below. The results of these runs with the initial balanced models often highlighted connections in the model which were felt by workshop participants to be inaccurate, represent model pathologies, or not accord with limited historical data and/or experience. After this workshop, additional data sources were targeted and provided which helped to clarify many of these data gaps (see Appendix A).

Thus, several generations of balanced models were produced and subjected to the similar tests before the final workshop in La Paz, Mexico (Appendix F). The two models presented here, one for each of the Eastern and Western Gyres, represent the final iteration of these models. In several cases documented in Appendix A, data did not exist to clarify perceived model errors and thus recommendations for future data collection are provided.

The comparative ecosystem metrics of energy flow and niche habitat reported in the "Results and Discussion" section are from these two final models. Most of the calculation methods for these metrics are documented in the ECOPATH literature, specifically in the User's Manual (Christensen *et al.* 2000); cases where our calculations differed are indicated in the section.

Dynamic simulations using ECOSIM

This assumption of relative stability becomes a formal constraint in the extension of the ECOPATH model to dynamic predictions through the use of ECOSIM. ECOSIM uses the mass-balance solution to the ECOPATH master equations to calibrate the following biomass dynamics model:

$$\frac{dB_i}{dt} = GE_i \sum_{j \in prey} \left[f_{ij}(\overline{B}) \right] - \sum_{k \in pred} \left[f_{ki}(\overline{B}) \right] + PP(B_i) + IM(B_i) + BA(B_i) - EM(B_i) - F_{i,}B_i - M_{0i}B_i$$

More specific information on each of the above functions, and their calculation from ECOPATH parameters, is given in Table 3.

This general model as written does not automatically assume that an equilibrium state exists for all functional groups in the ecosystem. In particular, the predator/prey interaction functions f(B) are set from consumption, production, and diet parameters plus an additional term, vulnerability, which represents the relative strength of top-down (Lotka-Volterra) interactions and bottom-up (density-dependent ratio) interactions. Further, the relative importance of foraging time limitation or handling time may be included as tunable parameters. In theory the use of these functions does not guarantee that the system has an equilibrium state, and the above formulae may include oscillatory or chaotic dynamics.

However, as coded and used in practice as a transition between ECOPATH and ECOSIM, the parameter M_0 ("other" mortality) for each functional group is set after all of the other parameters in the rate equation have been calculated. It is set from EE values so that, in the

Table 3 Terms in the ECOSIM dynamic equations.

Parameter	Abbreviation	Notes
Growth efficiency	GE	Constant for each predator, calculated as (P/B)/(Q/B) from ECOPATH balance; may be subject to time forcing.
Consumption equation	*f(B)*	As documented in Walters *et al.* (1997), independent terms for each predator/prey link include predator density dependence. Calibrated from ECOPATH Q/B and diet composition. Handling time (dependent on sum of prey) and other adjustments or forcing are possible as documented in the EwE manual.
Primary production rate	PP	Simple density-dependent half-saturation curve for all primary producers.
Immigration	IM	Constant yearly rate independent of biomass (assumed determined by outside dynamics). Determined from input ECOPATH immigration.
Emigration	EM	Per-biomass rate determined from input ECOPATH emigration.
Biomass Accumulation	BA	Per-biomass rate determined from input ECOPATH biomass accumulation.
Fishing mortality	F	Per-biomass rate determined from input ECOPATH fisheries catch and biomass.
"Other" (not predation) natural mortality	M_o	Determined by ECOPATH ecotrophic efficiency and used to ensure equilibrium in the absence of biomass accumulation.

absence of a non-zero biomass accumulation (BA), the ECOPATH system of mass-balance equations also represents the equilibrium state of the dynamic equations for all functional groups. The fact that other parameters were adjusted in the ECOPATH stage to ensure that all EEs<1.0 guarantees that a stable equilibrium exists in the model, although this equilibrium may approach an oscillatory or chaotic state if vulnerability is set for strong top-down (Lotka-Volterra) interactions.

The practice also guarantees that only a single equilibrium state exists: it is not possible for "state flips" or multiple equilibria to exist as emergent properties of changes in state space. Regime shifts are thus only modellable as input (hypothesized) changes in external forcing parameters that persist throughout the regime, and not as internal ecosystem re-organizations. While diet switching occurs in a modelled predator as differing prey species change in biomass, "preferences" remain constant and thus overall transitions remain smooth and reversible.

Thus the EE term performs a "double duty" in the EwE approach as it represents model uncertainty in ECOPATH, yet is used as a dynamic equilibrium-creating term in ECOSIM. The relative stability of this equilibrium is determined by all of the parameters in the system, but in particular, by adjusting the vulnerability parameter for each predator prey link. Additionally, a "low but positive" threshold is assumed for each biomass that ensures that no biomass may permanently be removed from the ecosystem.

The resulting set of differential equations is run forward in time using standard numerical integration routines (Runge-Kutta order 4 or Adams-Basforth) which allow for the input of time varying forcing functions in fishing mortality rates (F's) or primary production rate (PP's). Other possible forcing functions, such as time-varying growth efficiencies (GE's) as an interaction between temperature and biology, were not explored in these experiments.

Discussion of the uncertainty, and in particular the overstability of ECOSIM under the above default assumptions, is discussed elsewhere (Aydin and Friday 2001). In practice, it is quite possible to tune ECOSIM with historical data to remove overstability from the model. By allowing the model to "spin-up" from a hypothetical stable state to a far-from-equilibrium state, large-scale changes and the effect of permanent decline of component functional groups may be considered. However, the limited historical data available in the subarctic gyres proved to be insufficient to fully calibrate these particular simulations.

Given the limitations of historical data available for the gyres, the ECOSIM results presented here should be considered first-order perturbation analyses. These are perturbations of ecosystems as they exist within a regime, and do not represent regime shifts except in cases where the mechanism of regime shift (such as increased primary production) is hypothesized separately and input to (rather than derived from) the model. Even given this limitation, it is possible to test effects, for example, of assuming that a regime shift is the result of an increase in primary production input into the model. Again, while it is possible to tune a version of the ECOSIM equations to model regime scale "switches" in habitat or predator/prey interactions, in the case of the gyres the data was insufficient to pursue this route.

Perturbation-style projections

While the lack of historical data for the gyres prevents the calibration of ECOSIM equations to create truly "predictive" models, the results may be used as a general first-order perturbation analyses. That is, large external forcing events may be applied to the ECOSIM equations to determine what species and/or functional groups will tend to respond the most to particular types of ecosystem changes. The interest here is primarily in the comparative approach between systems.

Two basic types of perturbation analyses were carried out. The first was to change primary production rates by increasing and/or decreasing the constant parameters of the PP function. The second was to remove specific functional groups by drastically increasing fishing (F). For each of these perturbations, the change was made at the beginning of the simulation and remained in place for 50 simulated years. The biomass differences at the end of the 50 years are reported.

In order to estimate errors that might arise from assuming a single equilibrium state, simulations were repeated for 10,000 Monte Carlo estimates of equilibrium states. Each separate state was determined by drawing a subset of the ECOPATH parameters (B, P/B, Q/B, and DC vectors) from distributions based on their error ranges listed in Appendix A, and re-balancing each model to determine EE values. These multiple states are reported as 95% confidence intervals for each base simulation.

This type of error analysis does not account for systematic bias; specifically, the error that might occur from assuming an incorrect functional response, or incorrectly accounting for relative degrees of top-down and bottom-up forcing (the "vulnerability" and passive respiration parameters indicated above). With extremely limited data for historical fitting, we were unable to accurately tune the models to account for these biases. For some simulations, the effects of assuming increased or decreased vulnerabilities are reported. However, without the ability to accurately tune these models, the results presented here should be considered to provide simple directional (up or down) relationships between components of the ecosystem and should not be used as quantitative predictions.

Regime-fitting style projections

As described in Appendix A, outputs from NEMURO, a detailed nutrient-phytoplankton-zooplankton (NPZ) model calibrated with Eastern Gyre (Station P) zooplankton data, were used to calibrate seasonal dynamics in ECOSIM lower trophic level functional groups. This allowed

ECOSIM to be run in two modes: with and without seasonal forcing; the latter assumes that seasonal processes are time-smoothed to an annual average.

EwE includes simple non-linear data fitting routines that allow forcing functions to be input and shaped so as to minimize error between ECOSIM time trends and input historical data: this method may be used to tune the model or explore hypotheses on climate forcing as they explain historical data.

After the literature review and workshops detailed in Appendices C-F, a limited number of biological time series were available for the purposes of such fitting. While some data existed from high seas cruises over several years (Appendix A), these data were limited in coverage and noisy, and generally were collected over time periods too short to allow for fitting.

Adult abundance data for Pacific salmon (*Oncorhynchus* spp.) were available for longer periods (40 years or more), but these data were specific to freshwater stock or country rather than ocean feeding areas (coastal areas and gyres). However, tagging information (*e.g.* Myers *et al.* 1996) provides qualitative descriptions of stock distribution within the gyres.

It was felt, on balance, that using these data to construct some "back-of-the-envelope" time trends for salmon in the gyres, as described in Appendix A, could be a useful starting point for comparing salmon trends to possible trends in lower trophic-level production in the gyres. These estimates do assume some degree of mixing of Asian and North American stocks in both gyres, and unlike maturing adult net-sampling programs, take into account the presence of immature feeding fish. However, it should be emphasized that, while the results presented below provide a starting point for examining the relationship between gyre production and salmon, extensions of data through new time series, and modeling techniques through explicit gyre/shelf linkage considerations, are strongly encouraged for future pursuit.

RESULTS AND DISCUSSION

Food web structure

Energy flow

The results discussed in this section are based on the "final" 1990s food webs of the Western Subarctic Pacific (WSA) and the Eastern Subarctic Pacific (ESA) ECOPATH models. The data used to construct the final models, adjustments made to create mass-balance, all final input parameters, and the assessed data quality of input parameters, may be found in Appendices A and B.

For comparative purposes, individual functional groups ("boxes") were chosen to be as similar as possible between the WSA and ESA models. In the end, 55 functional groups were chosen to reflect the similarities in species composition between the two systems, with differences being assumed to occur in biomass and diet compositions of the common functional groups (Fig. 3). Species occurring on one side of the Pacific were assumed to have a biomass of zero on the other side. In some broad functional groups, such as mesopelagic fish or micronektonic squid,

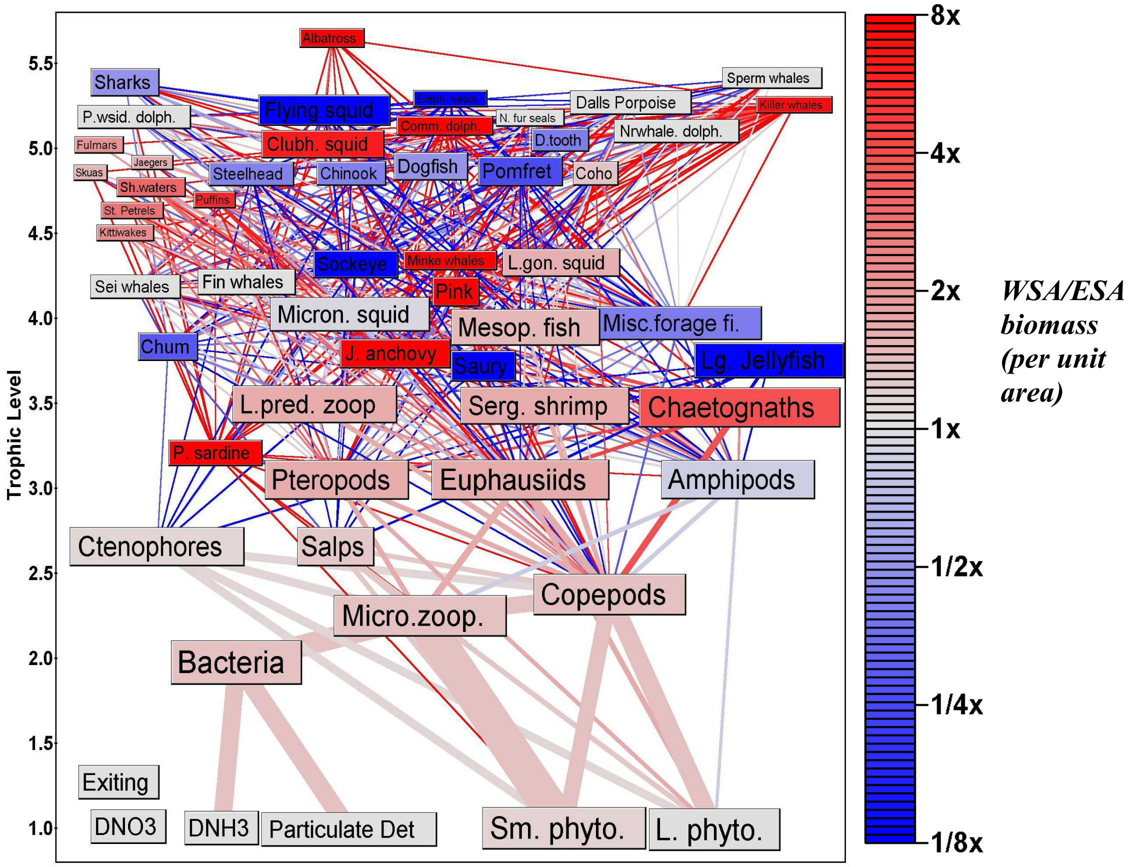


Fig. 3 Food webs of the Western and Eastern Subarctic Pacific Gyres (WSA and ESA) combined to show differences in biomass (boxes) and flow rates (lines between boxes). Red indicates higher biomasses or rates in the WSA; blue indicates higher biomasses or rates in the ESA. Box areas and flow widths are proportional to log (biomass or flow rate).

the species making up the groups may differ between the two sides. Due to data limitations and assumed low variation in comparison to biomass, it was assumed that functional groups' life-history and bioenergetics parameters (P/B and Q/B) were identical between the two systems.

The WSA was estimated to possess a higher biomass across the board for lower trophic level species (phytoplankton and zooplankton). In trophic levels 3+, the biomass of sardine, anchovy, chaetognath, pink salmon, minke whale, clubhook squid, common dolphin, tufted puffin and albatross were higher in the WSA. The ESA has higher biomass levels of large jellyfish, saury, Pacific pomfret and flying squid, and all species of salmon except pink.

The high estimated biomass of flying squid in the east versus pink salmon in the west highlights an issue with data collection in the two gyres: much of the data in the east is from more southerly regions. It is unclear if the difference between salmon and flying squid is due to an east/west difference or a north/south difference. The effects of east/west versus north/south may also be real since the influence of the Subarctic Current is more limited in the west than in the east (Fig. 2).

The WSA has a higher biomass (per unit area) for all trophic levels, and this difference increases with increasing trophic level. Trophic level 1 biomass is approximately 5% higher in the WSA while trophic level 5 biomass is 25% higher in the WSA (Table 4; trophic levels denoted by Roman numerals are "transformed" trophic levels as per Ulanowitz 1983).

The lower trophic levels (1 and 2) have throughputs that are extremely high in comparison to other ECOPATH models, for example the Eastern Bering Sea (Aydin *et al*. 2002). This is probably due to the inclusion of an explicit bacterial group as an intermediate detrital recycler (on trophic level 2). This also has the effect of lengthening the assumed pathways between lower and upper trophic levels. Further, the assumed high efficiency of bacterial metabolism leads to the high transfer efficiencies measured on trophic level 2 (Table 4). In general, detrital turnover times and bacterial recycling are some of the least understood processes in these or other models; for example, the NEMURO NPZ model reported different seasonal results depending on whether a bacterial loop was explicitly present. Instead of explicitly including the bacteria as was done in the ESA and WSA models, it is probably sufficient to assume that bacterial processes occur within the detritus functional groups and that cycling rates and turnover times can be controlled within the models by varying the size of the detrital pool.

Table 4 Throughput ($t/km^2/year$), biomass (t/km^2), throughput/biomass (1/year) and transfer efficiency (percentage) by trophic level in the ESA and WSA models.

Trophic Level	Throughput		Biomass		Throughput/Biomass		Transfer Efficiency	
	WSA	ESA	WSA	ESA	WSA	ESA	WSA	ESA
7	0.082	0.232	0.031	0.070	2.64	3.31	9.7%	22.8%
6	0.825	1.11	0.615	0.565	1.34	1.96	5.5%	11.4%
5	15.3	11.3	8.0	5.3	1.91	2.13	5.0%	5.8%
4	317	210	34	23	9.32	9.13	12.3%	11.4%
3	2,458	1,803	95	64	25.9	28.2	16.9%	16.6%
2	12,704	9,595	254	191	50.0	50.2	30.8%	30.3%
1	14,115	12,798	155	146	91.1	87.7	-	-

To show how the production in each trophic level is distributed among broad categories of species, functional groups in the original models were summed into 17 larger groups shown in Figure 4.

These groups show the surprising importance of large zooplankton (greater than copepods in body size) in middle trophic levels (4-6), relative to forage fish. The zooplankton are on a high trophic level as chains such as detritus -> bacteria -> copepods -> amphipods -> chaetognaths are possible. On trophic levels 7-8, large squid are the most productive species in both systems; in the WSA zooplanktivorous salmon (pink, sockeye and chum) are additionally important. Sharks dominate production at the top trophic level in both systems.

Connections

In the WSA, a total of 404 predator/prey links were included for the 51 functional groups in the model, while in the ESA model, a total of 363 predator/prey links were included for 48 functional groups. Since the number of links in a random web might be expected to increase with the square of the number of groups, these values indicate a similar level of connectivity modeled in the two food webs.

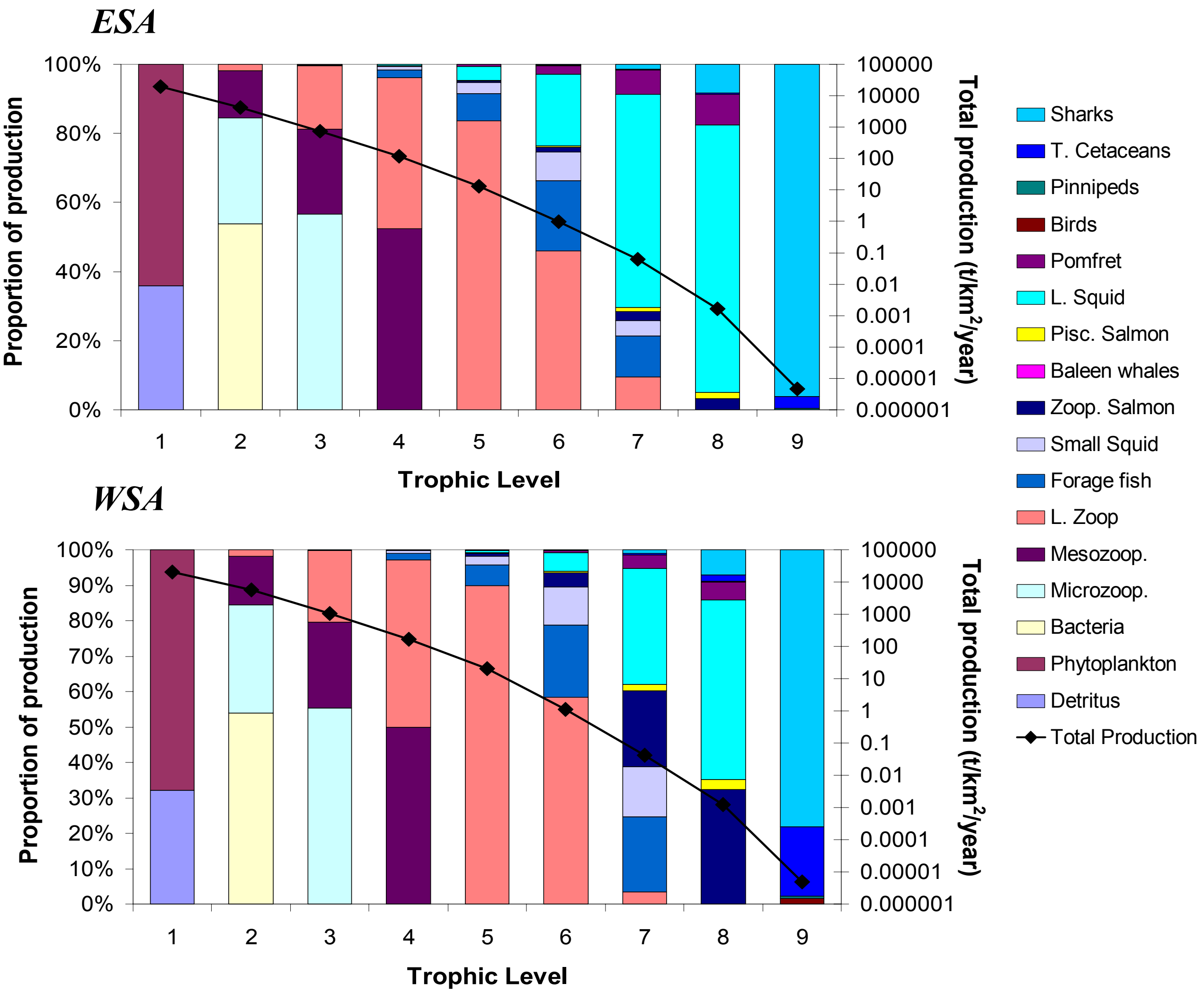


Fig. 4 Proportion of production of each trophic level attributable to each of 17 broad functional groups. Solid line shows the total production of each trophic level (t/km^2/year, log scale).

To investigate differences in connections in detail, a similarity matrix was constructed for each model by computing a measure of dietary (niche) overlap between each pair of functional groups (Christensen *et al.* 2000). This matrix was transformed into a cladogram of diet relatedness for the ESA and WSA (Figs. 5-6). The branching of the tree shows relatedness of successively more similar functional groups in terms of diets. A cutoff similarity of 0.70 (on a scale of 0 to 1) was chosen as it tends to divide functional groups into larger collections with several major diet items in common.

As seen in Figures 5-6, functional grouping with a similarity of 0.70 reveals 17 distinct feeding types in the ESA and 18 in the WSA: four of these are phytoplankton and detritus in each model. These groups, sorted by trophic level, show a progression from large squid eaters to micronektonic squid eaters, forage fish eaters, and zooplanktivores in both systems.

Some key differences in dietary niches between the ESA and WSA include sharks, which in the ESA are modeled as feeding primarily on squid, while in the west are modeled as feeding on fish, especially pink salmon. In the west, sockeye salmon are shown on a higher trophic level than pink salmon due to consumption of micronektonic squid; the two have closely related zooplankton diets in the east (Figs. 5-6). In both systems, chum salmon specialize on gelatinous zooplankton and are the only species for which such food consumption was measured.

In both systems, baleen whales consume primarily zooplankton rather than forage fish, causing them to be closer in diets to forage fish than to larger fish. This suggests their role with respect to forage fish may be more as competitor than predator in the open subarctic gyres. The lower trophic level dietary matrices were taken from the NEMURO model linkages in both models and are thus identical.

Carrying capacity

The issue of "control" in the upper trophic levels, especially with regard to the carrying capacity of salmon and other large nekton, cannot be fully addressed with a static model. However, a few conclusions on general energy availability may be drawn from these food webs. (Carrying capacity as applied to salmon refers to the energy available for somatic growth, as the abundance of salmon is thought to be determined by coastal processes not included in these models).

As seen in Figure 4, the more complex assumptions about lower trophic levels (including microzooplankton and bacterial groups) effectively raises the trophic level of large (predatory) zooplankton so they function as prey and competitors for zooplanktivorous species such as salmon. A great deal of the variation in their role is expected to be seasonal.

NEMURO (as filtered through ECOPATH) predicts that, when totaled throughout the seasonal cycle of a year, 67% of large phytoplankton and 77% of small phytoplankton is consumed by zooplankton, the remainder being unaccounted for or flowing to detritus in the ESA. Of this flow to detritus, 42% must be recycled to fuel the estimated bacterial production (from the EE values in Table B6). As NEMURO results for the WSA were not available at the time of model construction, these calculations were not performed for the Western Gyre except to note that an overall greater level of primary production is required to fuel the WSA system. Since seasonal variation is greater in the WSA (Harrison *et al.* 1999; Appendix A), it is possible that a greater percentage of energy from phytoplankton blooms is not directly consumed by zooplankton in the WSA, but rather, lost or filtered through bacterial processes.

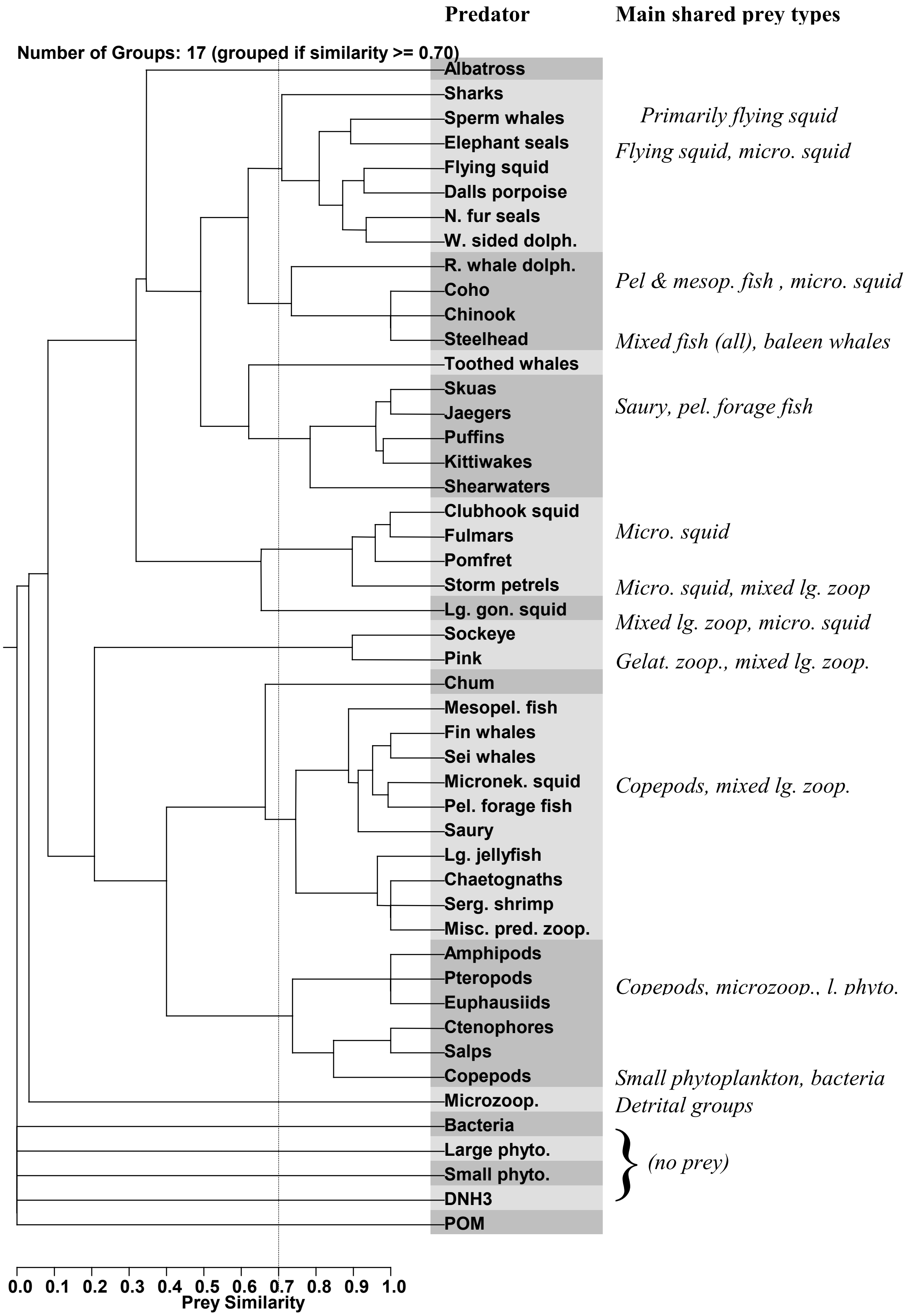


Fig. 5 Dietary niche cladogram based on pairwise diet similarity values for the ESA. Italicized text indicates main prey items in common for species within each grouping. Dotted line shows the cutoff for showing groupings (diet similarity = 0.70); cutoff is arbitrary.

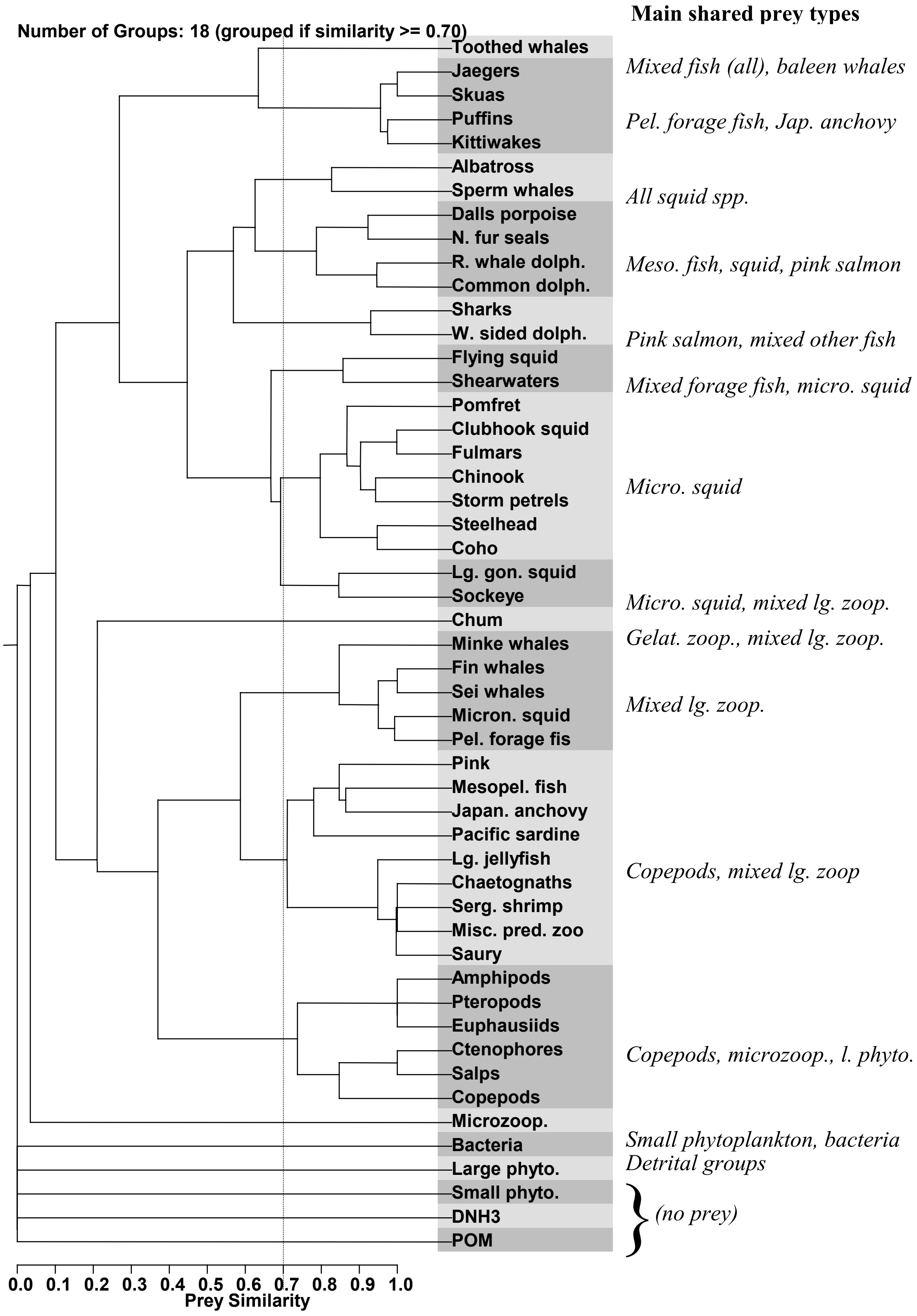


Fig. 6 Dietary niche cladogram based on pairwise diet similarity values for the WSA. Italicized text indicates main prey items in common for species within each grouping. Dotted line shows the cutoff for showing groupings (diet similarity = 0.70); cutoff is arbitrary.

If multiple zooplankton species are pooled and the destination of energy consumed by zooplankton is tracked, the difficulty of using bottom-up estimations of energy flow to project increases in nekton carrying capacity becomes evident (Table 5). Of the energy, 78% is used in respiration and 14-15% used in "internal" consumption between zooplankton species. Consumption by gelatinous species (large jellyfish and salps) accounts for 4-5% of the energy flow, while consumption by all other species amounts to less than 0.5% combined.

Accordingly, small amounts of process noise in zooplankton respiration rates may result in large changes in the estimates of forage available for large species. Since 80-90% of zooplankton consumption is lost to internal processes, a small change in respiration rates (*e.g.*, through climate-driven changes in water temperature) or efficiency of foraging opportunities (*e.g.*, through changes in seasonal timing) could lead to a substantial change in estimates of energy available throughout the food web.

However, the dominance of respirative processes in zooplankton does not remove the possibility of top-down control, or competition of large nekton through zooplankton species. While consumption represents only 5-6% of the total energy leaving the zooplankton (Table 5), this flow tends to be from the "top" of the zooplankton food web; that is from species such as euphausiids rather than microzooplankton. A small change in mortality on euphausiids, for example, may affect the "internal" consumption rates by 1-2% which would effectively double or halve the forage available for all fish species. When mortality processes are isolated, gelatinous species (large jellyfish and salps) are seen to have the largest potential for impacting zooplankton.

Overall, the possible variation in energy flow between large and small zooplankton, based on changes in seasonality or other aspects of climate, limits our ability to predict changes in gyre carrying capacity through energetic calculations of lower trophic levels alone. However, this limitation does not remove the possibility of top-down control being a factor for zooplankton in the gyres.

Perturbation-style ECOSIM projections

Initial exploratory analysis

The ECOSIM interface built into EwE allows for a quick deterministic projection of multispecies interactions resulting from basic manipulations in ecosystems; for example, the software allows users to investigate the effects of removing or reducing a species or functional group through fishing. This graphical simulation tool was used in the workshop setting in an exploratory manner (Appendix F). During the workshop, several perturbation scenarios were explored and the initial results were discussed; in some cases, this

Table 5 Destination of energy consumed by zooplanton (combined microzooplankton, copepods, eupahusiids, pteropods, amphipods, predatory zooplankton, sergestid shrimp and chaetognaths).

	ESA zooplankton			WSA zooplankton		
	T/km^2/year	% of output	% of mortality	t/km^2/year	% of output	% of mortality
Respiration	10,133	78.97%		13,765	78.97%	
Internal consumption	1,816	14.15%		2,703	15.51%	
Micronekton cons.	34	0.27%	3.87%	35	0.20%	3.60%
Gelatinous cons.	657	5.12%	74.50%	704	4.04%	73.20%
Salmon cons.	1.50	0.0117%	0.17%	2.77	0.0159%	0.29%
Squid cons.	0.14	0.0011%	0.02%	0.23	0.0013%	0.02%
Bird and mammal cons.	0.14	0.0011%	0.02%	0.17	0.0010%	0.02%
Unaccounted	189	1.47%	21.43%	220	1.26%	22.87%
Total	12,831	100%	100%	17,431	100%	100%

initial work revealed potential weaknesses in the current models or data, and resulting adjustments are noted in Appendix A. However, it was not immediately clear in the workshop how uncertainty in either model structure or input parameters would affect the results in a general sense. A subset of these scenarios was selected for further examination, specifically through sensitivity analysis.

As reviewed by Givens (1994), "simple" sensitivity analyses in deterministic models may involve setting critical input parameters too high or low, and investigating which inputs within these ranges created a large change in projected outputs. This approach was not used for several reasons. First of all, testing combinations of high and low values for a reasonable subset of input parameters would require excessive computer time. Moreover, even without requiring an equilibrium assumption, such testing of input parameters would throw away much of the constraining covariance in input parameters that were appropriate to include to continue to satisfy the overall thermodynamic bounds of the ecosystems. At the same time, it was desired to allow exploration of initial non-equilibrium states in a manner not permitted by the exploratory sensitivity analyses such as EcoRanger included in the EwE package.

To incorporate both the information in the input data (initial model state and parameters) and model information gained by thermodynamic bounding, the following procedure was used. This procedure is a simplified form of the Bayesian Synthesis approach (Givens *et al.* 1993), where the simplification arises since there is no informative prior information on model outputs, only inputs, and the only added information comes from model structure rather than from fitting to new (time series) data. Several iterations and variations of this procedure were performed, and the selected method was chosen to minimize problems such as "Borel's Paradox" associated with mapping and updating probability distributions with deterministic models (Givens 1994), although aspects of the problem may still exist. The final procedure used is outlined as follows:

1. For each of the ESA and WSA, 20,000 simulated ecosystems were created using a Monte Carlo process [see Box A]. Each ecosystem consisted of a set of parameters for the ECOSIM dynamic equations and a vector of initial biomass values and was not necessarily in initial equilibrium. Ranges of parameters were based on confidence ranges of ECOPATH inputs in Appendix A. The parameters chosen for drawing were picked based on which parameters might be expected to be relatively independent within a single functional group.

2. Each generated ecosystem was tested for relative thermodynamic consistency, to discard perceived "impossible" states and to impose the likely existence of an equilibrium state containing positive biomass for all functional groups without explicitly specifying the equilibrium as in EwE [see Box A(3)]. This constraint eliminated over 90% of generated ecosystems, leaving 1,315 ecosystems for the ESA and 1,514 ecosystems for the WSA, which were deemed sufficient numbers for later steps.

3. Each of the resulting models was run for 30 years (time step of one year) with no perturbations to give a "baseline" value and confidence limits for year-30 biomass of each functional group. These runs (and those below) were automated with ECOSIM algorithms in a routine called EcoSense, implemented in Visual Basic by K. Aydin (code available upon request). To ensure accuracy, the EcoSense results were compared to EwE results, and EcoSense code was compared to relevant sections of EwE code provided by Villy Christensen.

4. Each perturbation was run for 30 years in the exploratory mode for the two base models (in EwE and EcoSense) to determine baseline (ECOSIM predicted) change. The final year-30 biomass of each functional group is reported.

5. Each perturbation was run for 30 years in each generated, non-discarded ecosystem. The results reported are the difference, for each

generated ecosystem, between the non-perturbed ecosystem year-30 biomass and the perturbed ecosystem year-30 biomass. The median and confidence levels for these differences are reported.

Four parameter types – vulnerability (Walters *et al.* 1997), foraging time adjust rate (Christensen *et al.* 2000), handling time (Christensen *et al.* 2000), and passive respiration percentage (Aydin and Friday 2001) – additionally govern each predator/prey functional response. For these parameter types, no methodology exists for setting perceived or reasonable error ranges. For all of these parameters except handling time, step (5) above was re-run using combinations of "high" and "low" global defaults based on ranges used or published in other ECOSIM models. This is meant as a measure of global bias resulting from changing the EwE defaults for these parameters. Handling time was removed as a factor as the parameter requires an iterative summing of prey which dramatically increases computer time: the default ECOSIM assumption is that handling time is unimportant in comparison with vulnerability.

It is important to note that, while this procedure escapes the equilibrium assumptions of the EwE approach, the method still assumes that the ECOPATH equilibrium state is the center of each distribution. The only way to move away from equilibrium as a null-hypothesis is to obtain historical (time trend) data for species biomass levels. For determining "unmeasurable" parameters such as vulnerability, these data are critical (Christensen *et al.* 2000; Aydin and Friday 2001). Fitting to time trend data is the approach favored by EwE and EcoSense fitting routines, and the single greatest lack in the ESA and WSA data lies in the lack of time trend data for tuning bias in species projections.

Finally, these results take into account error in parameterization of food web effects only. Recruitment process error, perhaps the most studied and greatest in magnitude type of error in fisheries biology, is not considered and may outweigh the multi-species considerations covered here.

Perturbation results

<u>Uncertainty in the ECOPATH base equilibrium</u>

Figure 7 shows the median and 95% distribution limits for the percentage difference, for each functional group between the ECOPATH equilibrium biomass and year-30 biomass for the generated ecosystems (with no external perturbations). The 95% distribution is shown, in this and all subsequent simulations, for the case in which vulnerability equals 0.30 for all functional groups, passive respiration (as a percentage of total respiration) equals 0%, and foraging time adjustment is turned off (adjust rate equals 0).

Examination of all high and low combinations for these three parameters (applied to all functional groups simultaneously) indicated that foraging time adjustment was important for the transient behavior of the model but less so for the long-term (year-30) "equilibrium" level for biomass. Other combinations showed that pairwise, interactions between passive respiration and vulnerability were more or less additive. Therefore four distinct cases are illustrated in Figure 7 and subsequent figures: the base case (dashes and error bars); the base case with high global vulnerability equals 0.5 (triangles); the base case with low global vulnerability equals 0.1 (circles); and the base case with passive respiration equals 20% total respiration (open diamonds).

The results in Figure 7 show that trophic uncertainty is generally largest in the middle of the food web. Thermodynamics constrains the highly aggregated lower trophic levels of both food webs (phytoplankton through copepods) due to aggregation of those groups and the requirements that the groups provide sufficient forage. As predation mortality is the greatest source of uncertainty in these models, uncertainty in top trophic levels is also limited. Salmon and squid tend to have the highest uncertainty with the 95% confidence intervals in both models ranging between –90% and +800%.

The increased top-down control indicated by high vulnerability scenarios increases projected

Box A

1. Each of the ECOPATH input parameters for each functional group (B, P/B, Q/B, and DC) was given an index of error between +/-10% (low uncertainty) and +/-90% (high uncertainty). This data grading procedure was the result of workshop discussions (Appendix A).
2. 20,000 modeled dynamic ecosystems for each of the ESA and the WSA were created using the master ECOSIM equations as re-written in the "Methods" section and drawing from distributions to select the following parameters for the equations. For each predator:

   a. PB(start) was selected from a Uniform distribution in the P/B error range;
   b. GE was selected from a Uniform distribution in the Q/B error range;
   c. Each element of the predator's diet composition was selected from a Uniform distribution in the DC error range and re-normalized (giving each diet component a normal distribution);
   d. Since the above three parameters are multiplied to determine the starting M2 for the predator's prey, the M2 component had a resulting log-normal distribution deemed appropriate for variable consumption/feeding data;
   e. M0 was chosen from a uniform distribution around its original ECOPATH value using the P/B error range. Since ECOPATH sets M0 from EE to "balance" the dynamic equations, at the mean value for all input parameters, the system is in the original ECOPATH equilibrium; however by selecting M0 independently the system begins away from equilibrium;
   f. The initial biomass of each functional group was chosen from a Uniform distribution with the B error range. Initial fishing rate F was not changed for any species;
   g. Parameters for the predator/prey functional response for which no methodology existed (vulnerability, passive respiration rate, foraging time) were set to vul=0.30; foraging adjust rate =0 (no foraging adjust); passive respiration rate=0; handling time=1000 (handling time unimportant.

3. Each model was run for 30 years and the distribution of year-30 biomass values was examined relative to starting ECOPATH values. The models began out of equilibrium and 30 years was generally sufficient for models to approach within 10% of each model's unique equilibrium state. Investigation of these distributions indicated that most functional groups had a bi-modal distribution of year-30 biomass, with one mode centered around the original (ECOPATH) equilibrium biomass levels and a second, larger mode at zero. In other words, in most generated ecosystems a subset of functional groups "died out" of the ecosystem over 30 years.

Closer examination revealed that most of these extinctions resulted from the dying out of complete trophic levels. In other words, the lack, in most models, of an equilibrium state in which all functional groups had a positive biomass was not due to competitive exclusion. Rather, it was due to drawing sets of parameters that were thermodynamically inconsistent, in that they represented evolutionarily unrealistic over-consumption of entire sections of the food web.

Therefore, all generated models were rejected if, after running the base case for 30 years, at least one functional had decreased to 1/1000 of its ECOPATH biomass, or increased to 1000 times its ECOPATH biomass. These criteria rejected over 90% of generated ecosystems from consideration and eliminated the lower (zero) peak from all output distributions. Rejecting such inconsistent models was seen to represent the adding of thermodynamic information into output distributions and allowed the exploration of non-equilibrium initial states while guaranteeing that the model allowed the broad functional groups that existed in the ECOPATH model to persist over time.

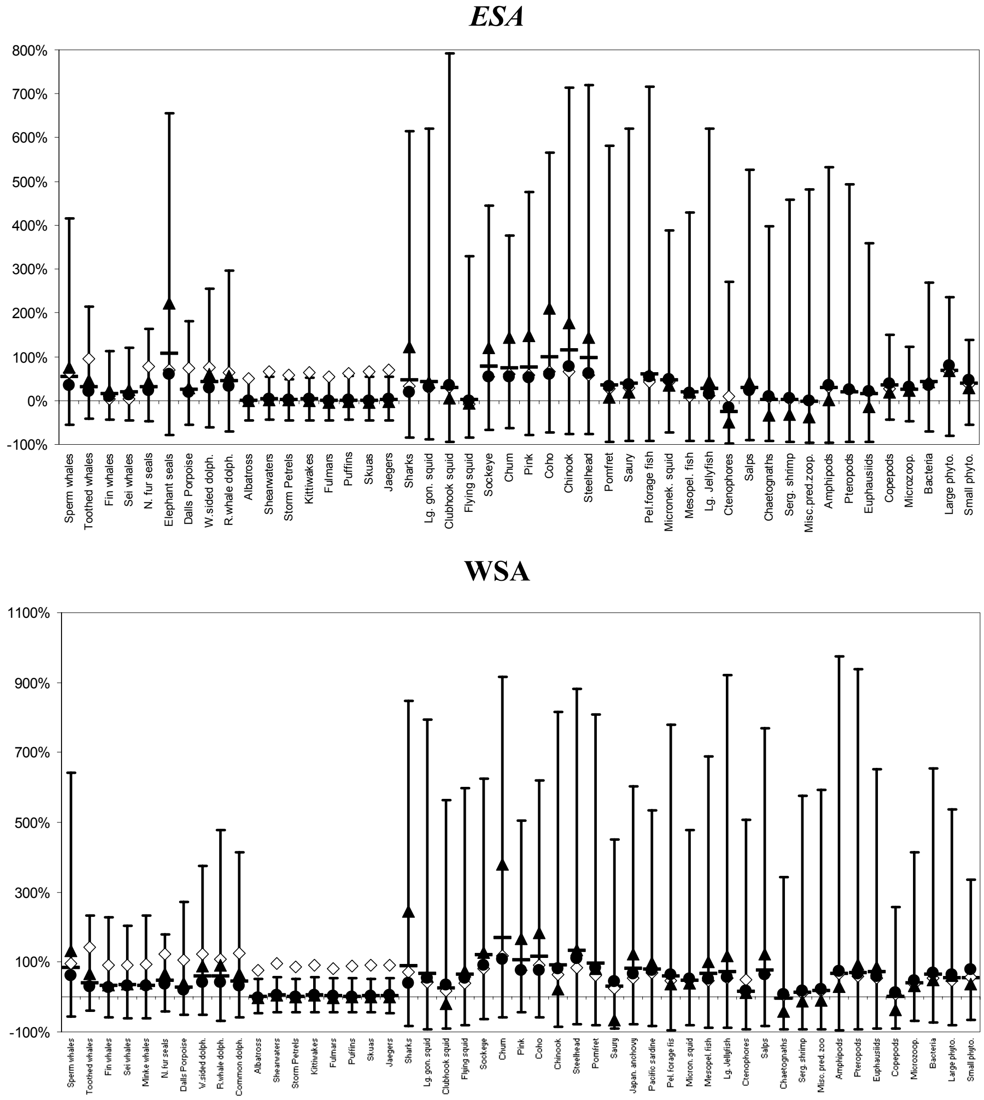


Fig. 7 Percentage difference between ECOPATH year-30 equilibrium biomass (zero-line) and year-30 biomass levels for thermodynamically acceptable Monte-Carlo ECOSIM runs (1,315 accepted ecosystems for the ESA, 1,514 accepted ecosystems for the WSA). Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, passive respiration=0%, foraging time adjust rate=0. Triangle shows median result for vulnerability=0.5 (high vulnerability); circle shows median result for vulnerability=0.1 (low vulnerability); open diamond shows median result for passive respiration=20%.

biomass levels for sharks and salmon in both models, while decreasing projected levels for large zooplankton species. The effect of passive respiration is to provide a bioenergetics "damper" on biomass growth, and this is seen as a positive effect in homeothermic birds and mammals for which respiration rates are much greater.

For the remainder of the simulations, the change reported is the difference between each base case (summarized in Figure 7 distributions) and each manipulated case, summarized as a distribution of change direction and magnitude. In other words, if (in a particular generated ecosystem run generated for Figure 7) a year-30 biomass goes up to 200% of the ECOPATH equilibrium, but in the manipulated case the year-30 biomass only goes up to 150% of year-30 biomass, the reported change is negative (150-200)/200x100% = negative 25%). The results reported are thus the distributions of direction and magnitude of manipulated change given the trajectory of each "unmanipulated" ecosystem. This must be placed against the background of uncertainty in Figure 7 to determine the overall uncertainty of year-30 biomass levels due to trophic interactions.

Manipulation I: Bottom-up pulse

To simulate the effects of a global increase in primary production, the primary production rate constant (in the PP half-saturation curve) was increased by 20% for both small and large phytoplankton. This increase was applied in three ways for each ecosystem: to small phytoplankton only, to large phytoplankton only, and to both small and large phytoplankton. As the results differed in magnitude but not direction, only the results for raising both groups simultaneously are reported. As discussed in Appendix A, the biomass and production levels in the ECOPATH models represent the annual averages, and thus this increase should be taken as an "overall increase" or interannual anomaly applied throughout the year without regard to seasonal timing or differential occupancy rates.

In both the ESA model (Fig. 8) and the WSA model (Fig. 9), the ECOSIM base case (gray bars in both figures) shows a general 20% increase in year-30 biomass as a result of the 20% increase in long-term primary production. The exception is the birds for which the respirative cost of increasing biomass is relatively high. However, if that respiration is made partly passive (20% passive, open diamonds in both figures), all birds and mammals then show a consistent 20% increase along with the fish. The passive metabolic cost acts as a stabilizer to allow biomass to accumulate. Since the "background" metabolic costs of homeothermy are high, it is likely that birds and mammals have a higher passive metabolism than fish.

Clubhook squid show an extremely large amount of variation around the base increase; it is not certain what drives this difference. In general, the fish and lower trophic levels are more variable than birds or mammals, and the 95% confidence limits for fish are greater than the relatively limited systematic change effected by changing vulnerability levels. This larger variability is consistent through most scenarios and is possibly due to the larger number of trophic links giving room for larger ranges in variability.

It should be noted that these confidence intervals as drawn do not display the covariance that exists between output biomass levels. Especially in bottom-up scenarios, covariance between species of the same trophic levels would generally prevent all of those species from increasing simultaneously. Disaggregation may be another source of the variability in the mid-trophic levels: more functional groups within a trophic level gives rise to more variation in pathways between generated ecosystems, so that it is more likely that only select subsets of species will benefit in each given ecosystem.

Manipulation II: Removal of squid

Neon flying squid. There is considerable confidence in the salmon diet composition for both gyres and discernible differences in relative proportion of micronektonic squid, forage fish and mesopelagic fish between the two gyre models. Since neon flying squid and clubhook are probable competitors for micronektonic squid and forage fishes their removal may have implications for prey availability for salmonids. Two experiments were run for each gyre: the removal of neon flying squid and the removal of clubhook squid.

Neon flying squid were completely removed from each gyre model by application of a fishing rate of 5.0 (instantaneous mortality) over the 30-year simulation (Fig. 10). In the ESA there were substantial increases in many functional groups, including several salmon species, saury, pomfret and competing squid species. Sharks were as likely to decrease as increase (increase in the ECOSIM base case), reflecting whether the randomly drawn shark diets favored flying squid or flying squid competitors. The WSA model

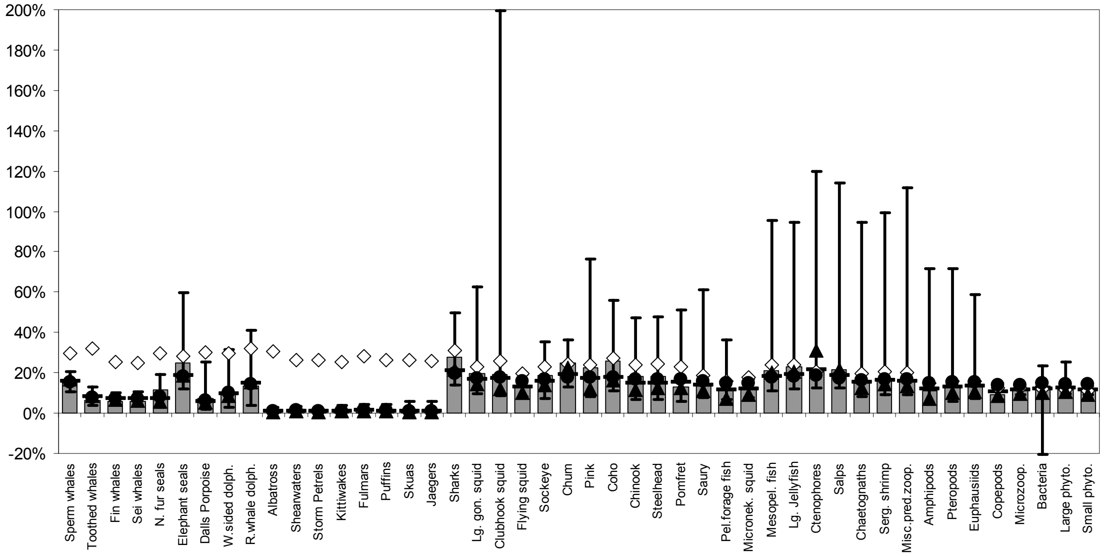


Fig. 8 Percentage difference between year-30 biomasses with no fishing and year-30 biomasses with a 20% increase in primary production, summarized over the acceptable models for the ESA. Bars indicate ECOSIM predicted difference. Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, and passive respiration=0%. Triangle shows median result for vulnerability=0.5; circle shows median result for vulnerability=0.1; open diamond shows median result for passive respiration=20%. Only species for which the ECOSIM base change was at least +/-1% are shown.

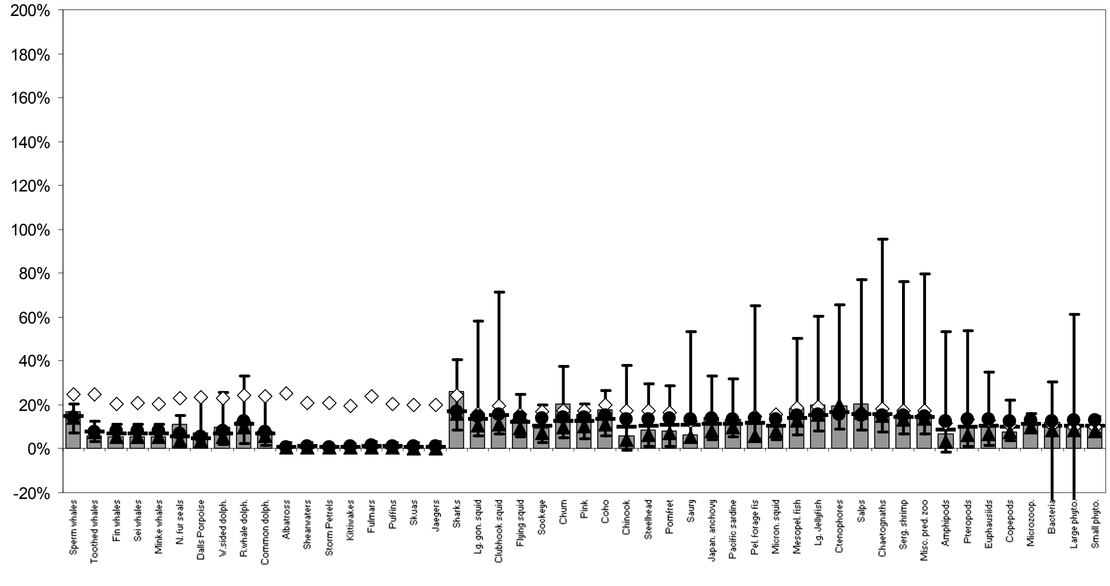


Fig. 9 Percentage difference between year-30 biomasses with no fishing and year-30 biomasses with a 20% increase in primary production, summarized over the acceptable models for the WSA. Bars indicate ECOSIM predicted difference. Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, and passive respiration=0%. Triangle shows median result for vulnerability=0.5; circle shows median result for vulnerability=0.1; open diamond shows median result for passive respiration=20%. Only species for which the ECOSIM base change was at least +/-1% are shown.

showed a minor increase in saury, Japanese anchovy and pomfret. There was a small, decrease in some salmon species, which could not be immediately explained by direct effects.

This scenario suggests that the removal of neon flying squid releases predation pressure on forage fish. In the ESA, forage fish are a large component of boreal clubhook squid, coho, chinook and steelhead salmon diet. The baseline biomass estimate of neon flying squid was an order of magnitude higher in the ESA than in the WSA model, so it is not surprising that their removal had more of an impact on the ESA model. The effects of changing vulnerability are generally consistent with this view. Competing species such as salmon increase more with increasing vulnerability (triangles in Fig. 10), as increasing vulnerability leads to increasing top-down effects, this result indicates that salmon are positively influenced by increasing their top-down ability to get food when flying squid are removed.

Boreal clubhook squid. Since the removal of neon flying squid did not have a dramatic effect on the WSA model, boreal clubhook squid were removed separately from each gyre model by the same fishing method as above (Fig. 11). In this case the response was negligible in the ESA. In the WSA, there was a dramatic increase in the biomass of pomfret, sockeye, coho and chinook salmon. Fulmars and storm petrels also increased in biomass as did large gonate squid. The likely link for these increases is through released predation pressure on micronektonic squid by boreal clubhook squid. Micronektonic squid is a large component of pomfret, coho and chinook salmon diet.

The fact that increasing vulnerability to 0.5 did not have a positive effect on competitors as in the flying squid scenario (Fig. 11) suggests a different positioning of clubhook squid in the WSA versus flying squid in the ESA. This is also seen by the fact that several forage species, such as pelagic forage fish, saury, Pacific sardine and Japanese anchovy decreased in the WSA with the removal of clubhook squid, while all forage species increased with the decrease of flying squid in the ESA.

As seen in Figures 5-6, flying squid feed on a range of forage species while clubhook squid specialize on one type of forage, micronektonic squid. As a result, the removal of flying squid allows a general increase for all of its competitors that feed on forage species, and this increase is magnified with greater top-down control. On the other hand, the removal of clubhook squid releases micronektonic squid which then outcompete other forage species, so the effects on species such as salmon is more mixed and increasing top-down control does not necessarily have a positive effect.

Manipulation III: Removal of salmon

Assuming that salmon abundance is determined outside the gyre system (*e.g*. Beamish and Mahnken 2001), changes in abundance will greatly affect other trophic levels if salmon are a driving force within the gyre system. The results of removing salmon are shown in Figure 12. Removing all salmon from the ESA model has a limited impact on the biomass of other species groups; forage species and salmon competitors such as squid and squid-eaters increase, while sharks decrease.

In the WSA model, when salmon were removed, large changes in the biomass of other species groups occurred. Since pink salmon are the most abundant fish group in the WSA model, the forcing is likely driven by their removal. When only pink salmon were removed the large changes in biomass were almost identical. The largest effect was for the forage fish, with their abundance increasing. As a result, other species, such as clubhook and neon flying squid and other salmon that feed on forage fish, increased in biomass. Increasing vulnerability had a large positive effect on the direction of this response.

The results in the ESA suggest that salmon are not an important group within that gyre for overall dynamics. It is likely that salmon biomass relative to the rest of the species is too small to be an influence to the gyre system. The WSA results suggest that pink salmon are an important competitor controlling the system in the gyre. One way of verifying these dynamics is to look for pomfret and neon flying squid abundance time

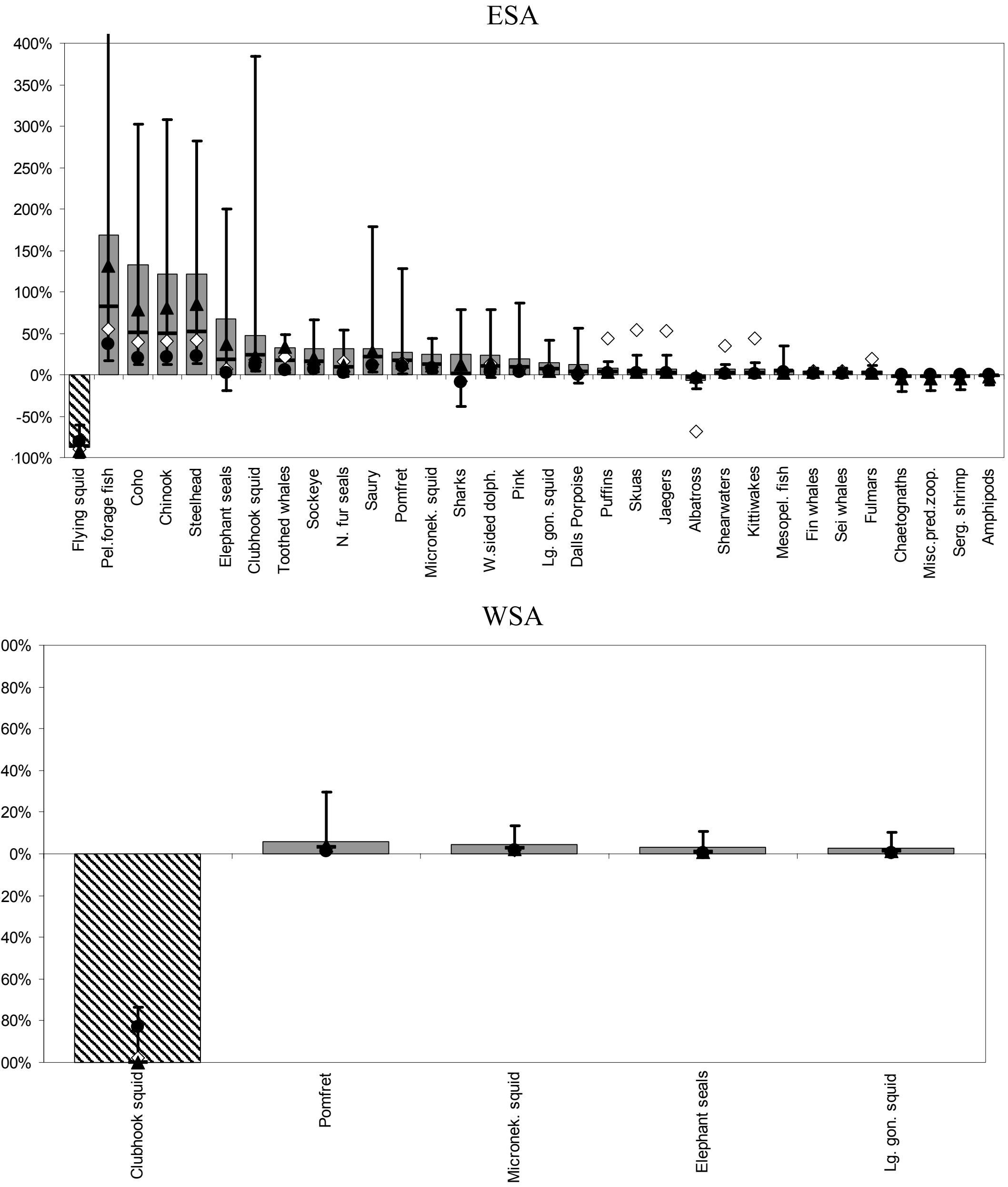


Fig. 10 Percentage difference between year-30 biomasses with no fishing and year-30 biomasses with removal of neon flying squid, summarized over the acceptable models. Bars indicate ECOSIM predicted difference. Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, and passive respiration=0%. Triangle shows median result for vulnerability=0.5; circle shows median result for vulnerability=0.1; open diamond shows median result for passive respiration=20%. Only species for which the ECOSIM base change was at least +/-1% are shown.

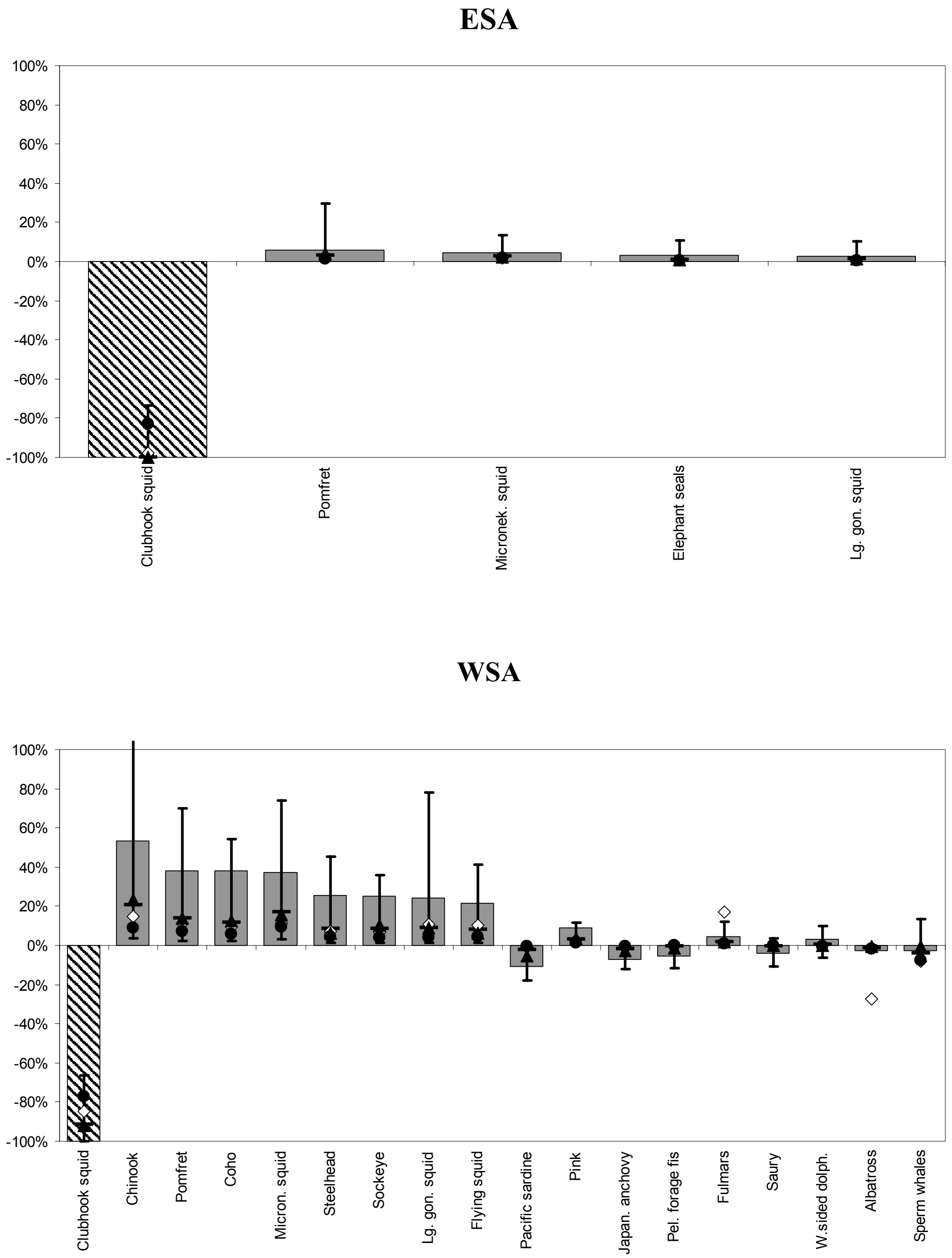


Fig. 11 Percentage difference between year-30 biomasses with no fishing and year-30 biomasses with removal of clubhook squid, summarized over the acceptable models. Bars indicate ECOSIM predicted difference. Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, and passive respiration=0%. Triangle shows median result for vulnerability=0.5; circle shows median result for vulnerability=0.1; open diamond shows median result for passive respiration=20%. Only species for which the ECOSIM base change was at least +/-1% are shown.

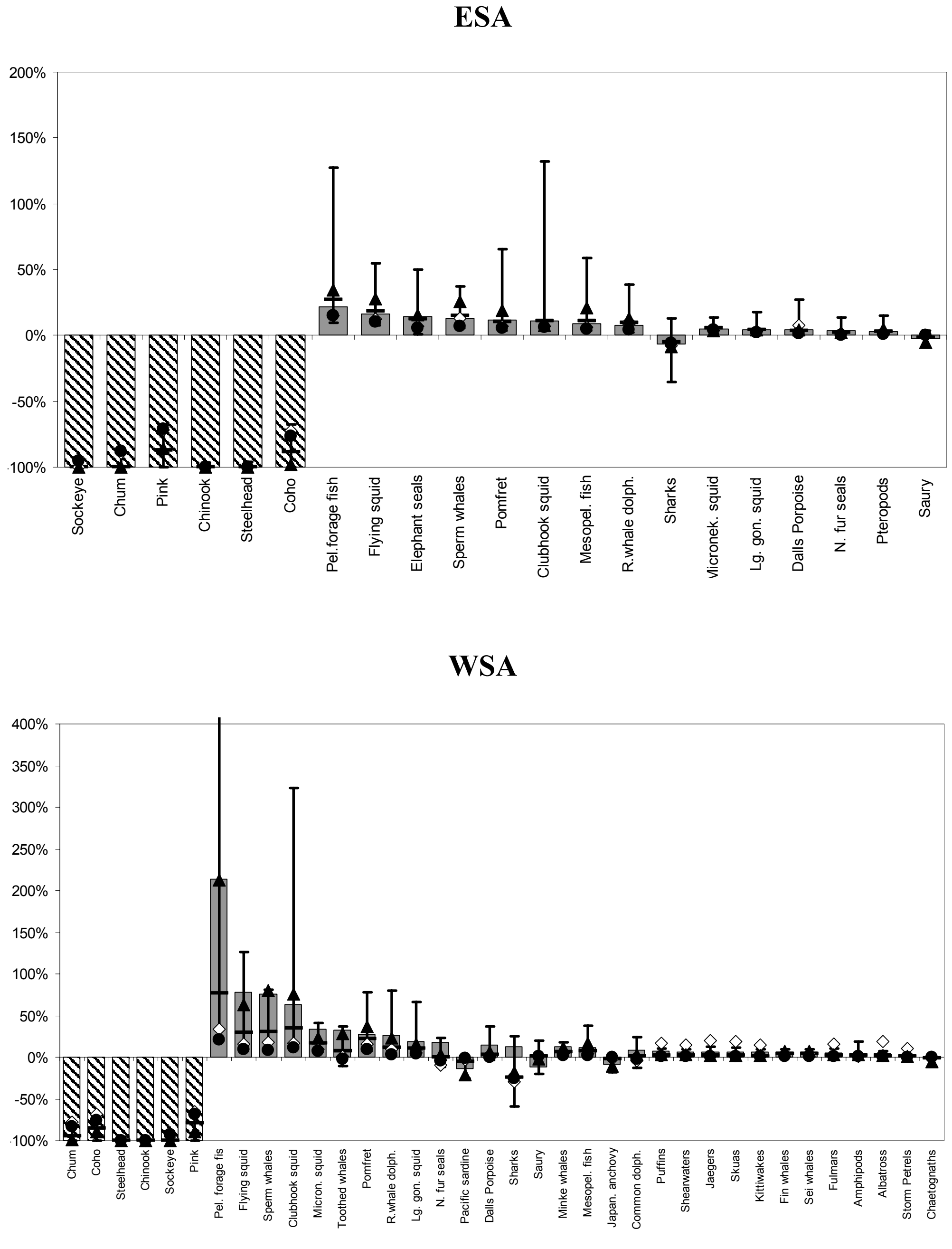
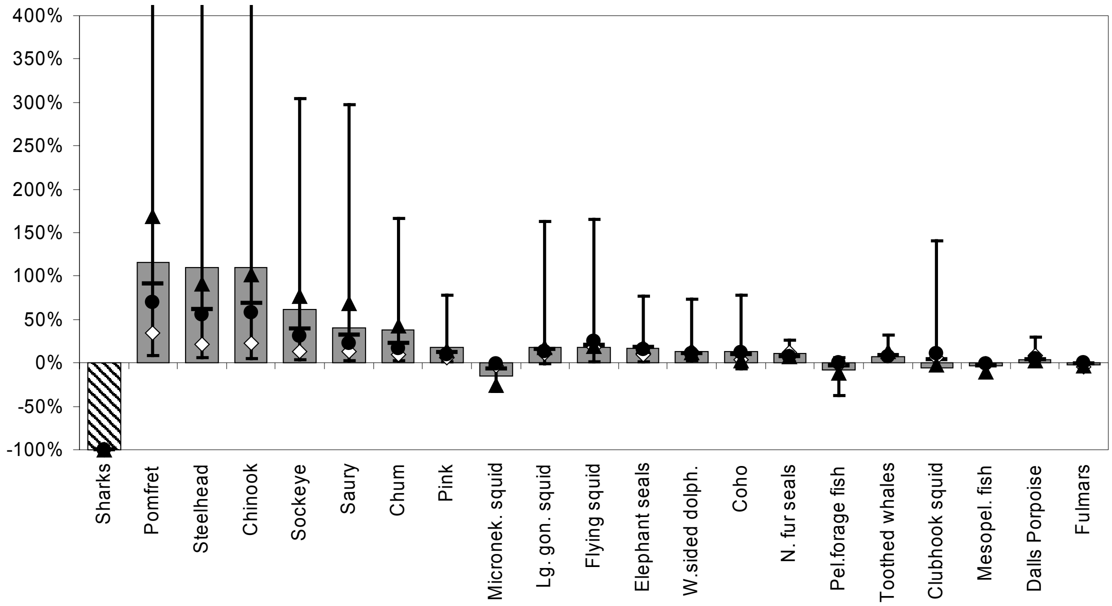


Fig. 12 Percentage difference between year-30 biomasses with no fishing and year-30 biomasses with removal of Pacific salmon, summarized over the acceptable models. Bars indicate ECOSIM predicted difference. Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, and passive respiration=0%. Triangle shows median result for vulnerability=0.5; circle shows median result for vulnerability=0.1; open diamond shows median result for passive respiration=20%. Only species for which the ECOSIM base change was at least +/-1% are shown.

ESA



WSA

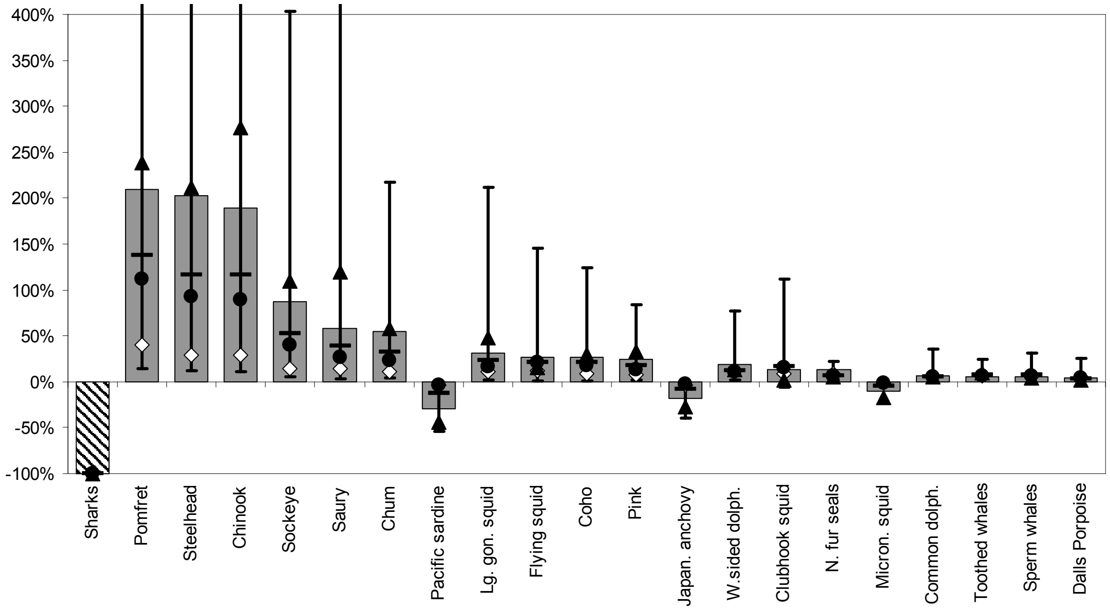


Fig. 13 Percentage difference between year-30 biomasses with no fishing and year-30 biomasses with removal of sharks, summarized over the acceptable models. Bars indicate ECOSIM predicted difference. Horizontal lines and error bars indicate median and 95% distribution limits for year-30 biomass with vulnerability=0.3, and passive respiration=0%. Triangle shows median result for vulnerability=0.5; circle shows median result for vulnerability=0.1; open diamond shows median result for passive respiration=20%. Only species for which the ECOSIM base change was at least +/-1% are shown.

series for the WSA. If these responses are realistic, pomfret and neon flying squid should have increased in abundance during the 1960s when pink salmon abundance was low. In addition, these results suggest that the WSA is sensitive to salmon biomass fluctuations. This has implications for the influence of coastal mechanisms (including hatchery salmon production) on gyre dynamics filtered through salmon biomass.

As noted above, the difference of salmon impact between the east and the west could be attributable to a north/south difference in the location of the gyres or to areas within each gyre where data were available.

Manipulation IV: Removal of sharks

As shown in Figure 4, sharks are the dominant species in the highest trophic levels and thus were selected for an apex predator removal experiment (Fig. 13).

A note of caution is required for the results of shark removal with respect to Pacific salmon. The above scenarios involved changing salmon forage opportunities through competitive effects. Since Pacific salmon growth rates are highest during the gyre phase of their life cycle (Ishida *et al.* 1993), it is reasonable to suggest that the changes in their biomass due to changes in their available forage are reflective of what might occur. Changes due to mortality reduction, however, are more difficult to interpret. It is believed that the majority of salmon mortality occurs in boundary and shelf regions (Beamish and Mahnken 2001) and thus in regions uncaptured in this model. Increases in salmon due to reduction in mortality, therefore, should be tempered with the knowledge that a far greater proportion of salmon mortality remains unaccounted for in this model.

With this in mind, it is clear that the effect of removing sharks from the gyres is a classic trophic cascade. All species preyed upon by sharks (salmon and squid) increase, while their own prey decrease. This change is amplified with increasing vulnerability level (Fig. 13).

Fitting to NEMURO

ECOSIM allows the input of production anomalies by month for time periods up to 100 years. The input of primary production anomalies was used to tune by eye the response of lower trophic levels to match as best as possible the patterns shown by initial outputs of the NEMURO model (see Appendix A for NEMURO references). At the time of the exercise, only ESA NEMURO results were available so the WSA model was not so tuned. The ECOSIM numerical timestep is generally rough on such short time-intervals (fitted to daily data) so the best results provided a rough pattern only (Fig. 14; the NEMURO results have since been superceded by new versions of that model).

While this exercise was used later to provide an initial seeding of a seasonal cycle for the ECOSIM fitting routines, it also served to examine a few lower trophic level assumptions within the two models. First of all, it was not possible to fit output from NEMURO (a model without a microbial loop) to the ECOSIM model with bacterial cycling. In order to match the two models, the ECOSIM bacterial group had to be removed and detritus exported from the system. This indicated that, in either model, the assumption of a microbial loop dramatically changed the results.

Secondly, the only group that was not possible to match reasonably between ECOSIM and NEMURO was the predatory zooplankton, which had a cycle with a consistently larger amplitude in NEMURO than in ECOSIM (Fig. 14). Predatory zooplankton are the top trophic level in NEMURO and thus subject to constant mortality; this result indicates that upper trophic level food web effects may indeed feed back into the lower trophic levels, a fact which most NPZ-type models do not consider.

Regime-fitting style projections

Pacific salmon are one of the first ocean species for which long-term climate regimes have been linked to abundance and biomass (Beamish 1993, Mantua *et al.* 1997). In the Eastern and Western

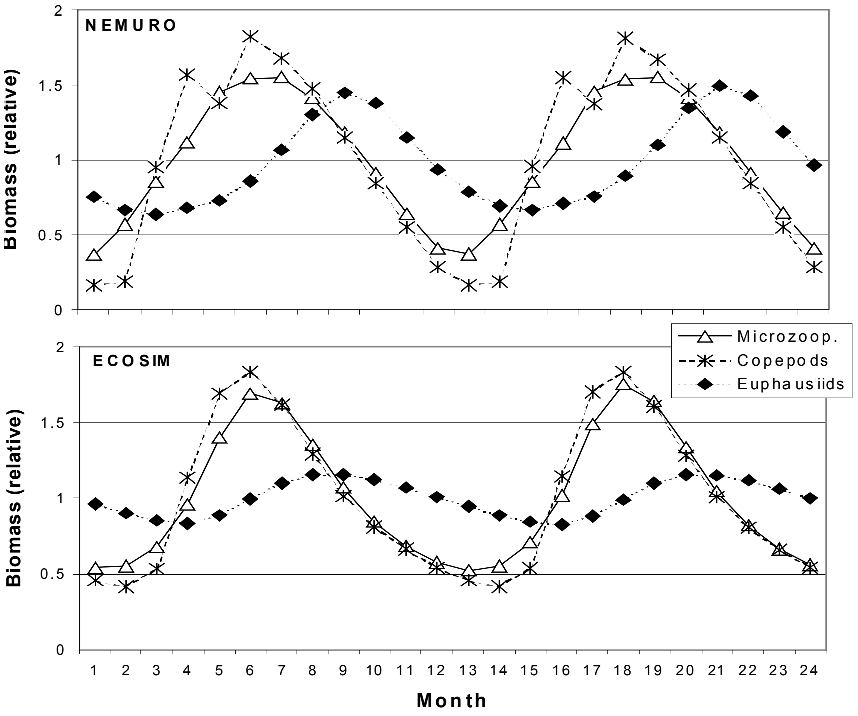


Fig. 14 Best fitting of ECOSIM by eye to the NEMURO seasonal cycle of the ESA, with a monthly resolution. NEMURO results have since been updated, specifically removing the large spring bloom of large phytoplankton which is known not to occur in the Eastern Subarctic Gyres.

Gyres, these are the only species for which long-term time series exist. It has been suggested that the changes in the gyres were across multiple trophic levels and thus may be the result of food web effects, especially from the bottom-up (Brodeur and Ware 1995).

Unfortunately, the only five functional groups for which time series existed for the gyre food web models were Pacific salmon. Correlations between climate indices such as the Aleutian Low Pressure Index or Pacific Decadal Oscillation Index (Beamish 1993, Mantua *et al.* 1997) have been demonstrated. Adding this relationship to the model would add no new information. Moreover, the life cycle of the Pacific salmon, with out-of-the-gyre fishing effects, escapement-based management, and hatchery supplementation is not particularly suited to explaining the trends of salmon biomass through gyre processes alone.

Still, the BASS Task Team considered it worthwhile to examine various hypotheses for historical salmon biomass levels using the exploratory modes of ECOSIM. Several hypotheses were developed: for example, that top-down control (shark biomass) was directly linked to climate and caused changes in salmon abundance, or that flying squid was the “source” of the anomaly which affected salmon through the food web. Using the basic ECOSIM fitting tools, many of these hypotheses were quickly discarded as not being able to simultaneously fit trends of the five salmon species taken as a whole.

Since salmon abundance is considered to be set outside the ecosystem, one other experiment made was to drive the model over time with set salmon abundance: this exercise was performed in both systems and is shown for the WSA in Fig. 15 and the front cover. Here, flat, stairstep lines represent the forced species of salmon, while jagged lines represent the responding species, especially responding to the pink salmon two-year life cycle (Fig. 15). However, in terms of regimes this pattern was thought to be non-explanatory.

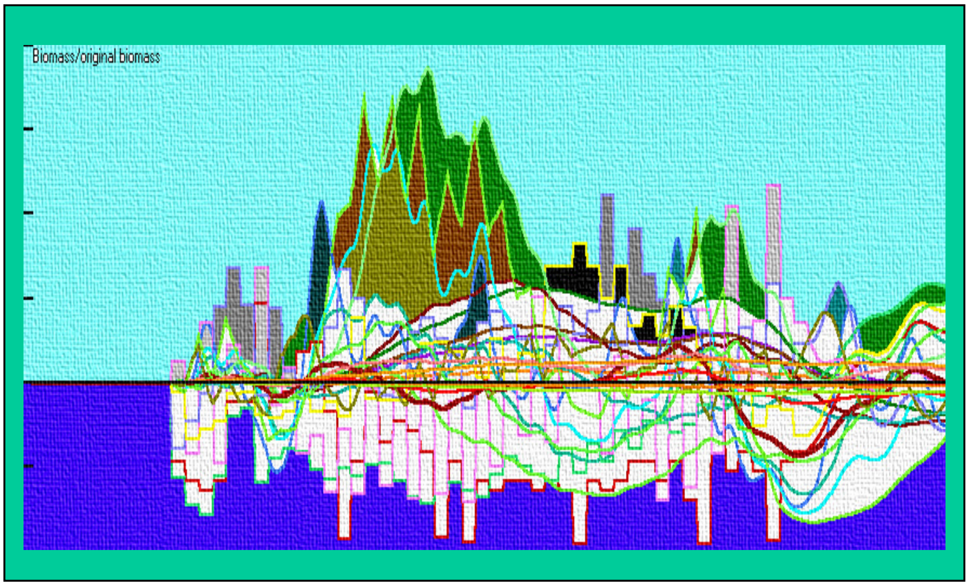


Fig. 15 Biomass trajectories as output from ECOSIM: the effects of input historical juvenile coastal abundances of Pacific salmon (float-topped lines) on the remainder of the Western Subarctic Gyre system (wavy lines), 1950-1998. The coloring is somewhat conjectural.

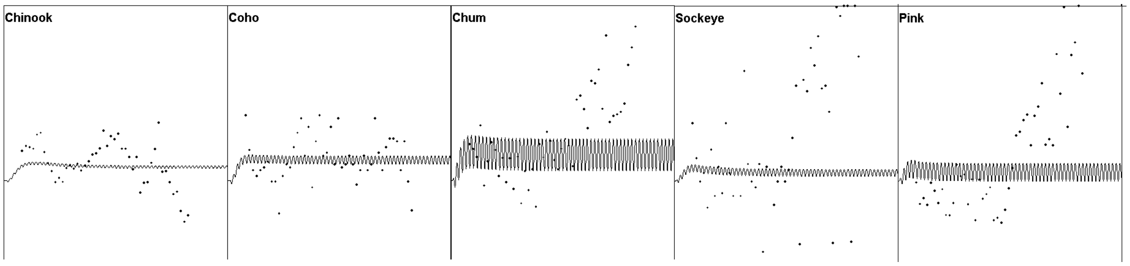


Fig. 16 Historical Pacific salmon biomass levels in the ESA from 1950-1998 (points) and ECOSIM-predicted initial biomass trends (50 years of NEMURO-tuned biomass predictions, solid lines).

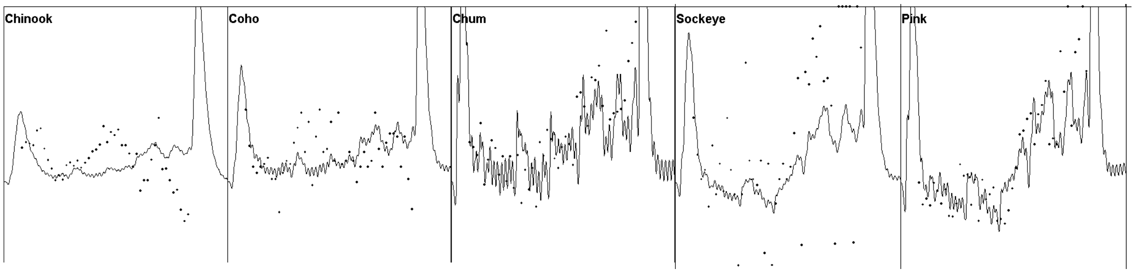


Fig. 17 Historical Pacific salmon biomass levels in the ESA from 1950-1998 (points) and ECOSIM-final biomass trends after primary production anomaly fitting (solid lines).

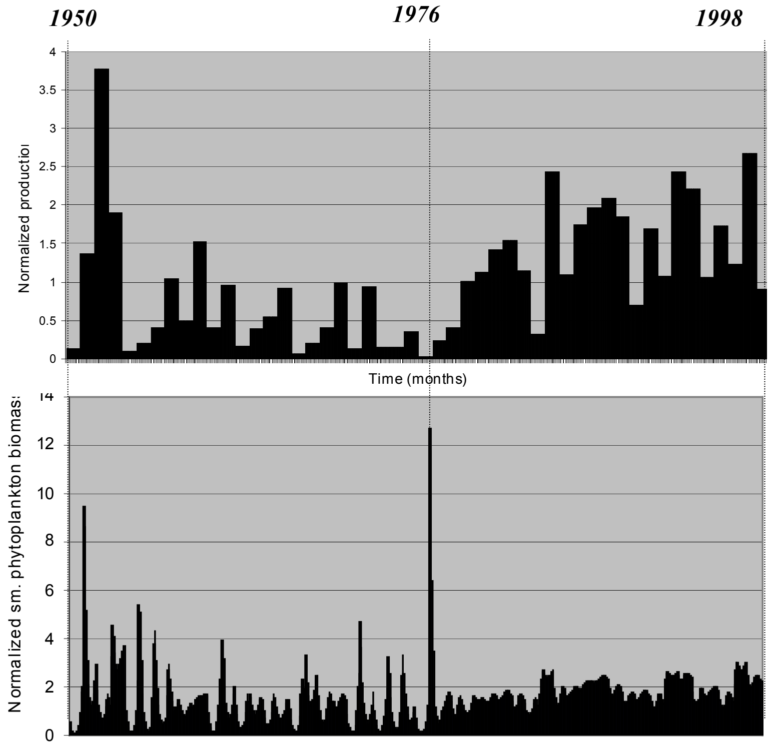


Fig. 18 Upper and lower fits vary in the densities of the splines used for fitting (low on the upper panel, high on the lower panel). Upper panel shows yearly production anomaly plots with best "explanation" (lowest simple sum of squares error) for zooplanktivorous salmon trends while lower panel shows seasonal small phytoplankton standing stock anomalies with best "explanation".

Sufficient evidence existed for positive correlation between salmon and other species such as zooplankton (Brodeur and Ware 1995), so that salmon increasing and applying middle-out control was considered to be only a partial explanation: a change in prey supply would also be required in the gyres to explain historical changes. To this end, the ESA ECOSIM model was seeded with 50 years of the default seasonal cycle (Fig. 14) as propagated through the food web. This was compared to time series of salmon biomasses from 1950-1998 (see Appendix A for references). The initial comparison is shown in Figure 16.

The ECOSIM uses a non-linear search routine with varying degrees of freedom to find a "lower trophic level" anomaly (in this case tied to small phytoplankton) that minimized the simple sum of squares error fit to the provided data. This routine was run several times and the resulting fits are shown in Figure 17. In general, the trends in the zooplanktivorous salmon are well-captured by the fitting routines.

It is possible to fit any trend by eliminating sufficient degrees of freedom, and this routine is meant as an exploratory rather than complete statistical analysis. However, in this case it is interesting to note the production anomalies that gave rise to these better fits (Fig. 18).

Two types of fits were found depending on the order of the splines used for fitting. The upper panel shows an interannual anomaly plot; this provides limited information as it is equivalent to a correlation between salmon and a generic "climate" anomaly that is forced to fit a common pattern. However, the pattern on the lower panel is distinct. Rather than showing an interannual increase in production over time, it indicates a change in seasonal dynamics across the 1976 regime shift (point found by fitting). Specifically, while the peak (summer) biomass levels do not increase and even may decrease during the periods of high salmon abundance, it is the lessening of the "winter troughs" which provide the explanation for the change.

It is important to note that, since these patterns are fit to a single trophic level (salmon), they do not represent "primary" production anomalies, but rather anomalies in the level of food supply reaching salmon. As such, the changes shown, if indications of a real process, may result from the shifting of winter pathways between plankton and salmon rather than the shifting in plankton themselves. Winter, while a slow growth period for salmon, may be a critical time for salmon density dependence (Aydin 2000). It is intriguing, even given the exploratory nature of this analysis, that changes in this time of lower seasonal production may affect the overall growth opportunities for these species.

As described in both the "Methods" section and Appendix A, these fitting results are based on gyres-only processes and approximations of gyre usage by Pacific rim salmon stocks over time: more detailed models of process linkages should be pursued.

CONCLUSIONS

Overall, the results presented here of two quantitative food webs, one for each of the Eastern and Western Subarctic Pacific Gyres, should be seen as exploratory analyses given the available data. The results, while intriguing, suggest several specific avenues for future work. From a data perspective, for this multi-species modeling to be useful, it is critical that time series data on biomass or relative biomass trends be collected for as many species as possible, especially competitors and predators of salmon such as flying squid, pomfret and sharks. While limited fisheries exist in the gyre regions, the interest in climate change and the known relationship between Pacific salmon and climate makes examining multi-species interactions an area in which research should be promoted.

Despite the limitations outlined above, the results of the regime-fitting style projections provide some interpretation on the processes linking climate variation to population dynamics of Pacific salmon. Using the gyre models, it appears that Pacific salmon abundance is primarily driven by processes occurring outside of the gyre system *i.e.* in coastal ecosystems. A next step should be to integrate coastal, marginal seas and gyre system models to examine linkages (energy transfer) between these systems. An integrative study connecting gyres to such boundary regions could also explore the dynamics of other migratory species (*e.g.* squid, pomfret, marine mammals and birds) along with the influence of shifting fronts and currents. In order to examine the influence of these processes, seasonal data (especially during transition times) are required. It is important that the gyre models developed here are based on summer data.

Improvements to the gyre models require improved biomass estimates for a number of key species (Table B4), especially species common to both gyres (*e.g.* marine mammals and birds). For a number of species, diet data for the gyre regions were not available, and therefore, diet data from other regions were used. Researchers should be encouraged to collect diet data from the gyre regions. At a minimum, the data collected should include prey identified to the lowest taxonomic group possible, along with number and volume of each prey item.

This study has provided a snapshot of the two sub-arctic gyre systems and increased our understanding of their dynamics and how each system may respond to climate forcing. This work should form the basis for future research in understanding the role of the gyre system in marine productivity of the North Pacific.

APPENDIX A: DATA GATHERING REVIEW, RESULTS AND BALANCING

Outline of provided data and methods

The accumulation of data sources led to several successive iterations of the Eastern and Western Subarctic (ESA and WSA) ECOPATH models. Initial data gathering led to the creation of "unbalanced" models which were adjusted for balance prior to and during the 2001 BASS/MODEL Workshop in Honolulu (Appendix D). During and after the meeting, additional data sources were made available. Changes made to the model solely for the purpose of thermodynamic balance are described under "Balancing the models", below.

Further changes were made to the models due to the provision of new data by workshop participants, the discussion of studies containing differing range of values, or if work with ECOSIM projections revealed "pathological" results. Even at late stages of the simulation process during and after the 2002 BASS/MODEL Workshop in La Paz (Appendix F), new data sources continued to be provided. Some of these data sources became available after a significant number of the ECOSIM simulations and scenarios had been projected and discussed, and some of these data were provided in response to the results themselves.

The approach taken for the purposes of this publication, was to "freeze" the models in the state that they existed at the beginning of the La Paz Workshop, as the bulk of the results in the main section of this report stemmed from that meeting. To aid in duplication and expansion of results, the complete list of model parameters Tables in the Appendix B represent these La Paz models. However, in this Appendix, sources of data that might supercede the parameters in the La Paz models are indicated. Future researchers are encouraged to explore differences in modeled outcomes arising from using these differing values.

Tables B1-B3 contain the primary literature values and references used for the primary parameters of biomass (B), production/biomass (P/B) and consumption/biomass (Q/B) for all functional groups in the WSA and ESA models. In cases where a value could be taken directly from the literature with no changes excepting a unit, time, or area conversion, the original references are listed in these tables and not noted in the text. The conversion of yearly instantaneous mortality estimates (Z) to P/B values are considered a unit conversion.

Cases where additional calculations, assumptions or conversions were required to transform literature values into model parameters are indicated with a (*) on Tables B1-B3. Descriptions of the methods used for these parameters can be found under "Model data review", below, under the section for the appropriate species group. Text descriptions of parameters by species groups are also included if the majority of the data used was unpublished. Diet data and references are described generally in the text and complete diets are shown in Tables B7-B8.

Data were graded for quality and uncertainty by workshop discussions of the literature search results. The quality ranking of each parameter depended on the data source and included consideration of collection methodology, coverage, and appropriate time period. The criteria for ranking were based on a "pedigree" methodology described for ECOPATH by Christensen and Pauly (1992). Table A1 shows the criteria used to assign a rank to each parameter, and the uniform range about each point parameter estimate associated with each quality rank (as a proportion of the point estimate). The overall "uncertainty" of the model is illustrated in Table B4 where the assessed uncertainty ranges of all parameters are shown.

Tables B5-B8 contain parameters as they were entered into the WSA and ESA models, including diet information and detrital flow assumptions, formatted as ECOPATH input tables.

Table A1 Criteria for ranking data quality for each parameter from good (rank 1) to poor (rank 8). Number in parenthesis is assumed range for each rank, as a proportion of the input parameter.

Rank	Biomass	P/B	Q/B	Diet
1.	Assessment with thorough data (0.1)	Same group, same system (0.1)	Same group, same system (0.1)	Quantitative, detailed, same time (0.1)
2.	Sampling with high precision (0.1)	Same group, similar system (0.2)	Same group, similar system (0.2)	Quantitative but limited (0.3)
3.	Sampling with low precision (0.5)	Similar group, same system (0.3)	Similar group, same system (0.3)	Quantitative, different time (0.5)
4.	Higly variable population (0.5)	Similar group, similar system (0.4)	Similar group, similar system (0.4)	Qualitative for specific prey (0.6)
5.	Approximate or indirect method (0.5)	Empirical relationship (0.5)	Empirical relationship (0.8)	Qualitative for broad prey (0.7)
6.	Guesstimate (0.8)	From other ECOPATH model (0.6)	From other ECOPATH model (0.6)	General knowledge of same group (0.8)
7.	From other ECOPATH model (0.8)	Guesstimate (0.7)	Guesstimate (0.7)	From other ECOPATH model (0.8)
8.	Estimated by ECOPATH (0.8)	Estimated by ECOPATH (0.8)	Estimated by ECOPATH (0.8)	General knowledge of related group (0.8)

The data in these tables should be sufficient to reproduce the models described in the text. Estimated ecotrophic efficiency (EE) and growth efficiency (GE) values are included in these tables for confirmation purposes. These models are also available from the primary author (Kerim Aydin, Kerim.Aydin@noaa.gov) as ECOPATH input (.eii) files.

Balancing the models

Migration

While the oceanography of the subarctic Pacific provides some biological basis for bounding the Eastern and Western Subarctic Gyres, both ecosystems are characterized by having top trophic level species that are extraordinarily migratory. Marine mammals and birds are only present part of the year in the ecosystems (Springer *et al.* 1999), while Pacific salmon possess a complex life cycle for which the gyres are an important but not isolated habitat.

ECOPATH is generally designed to model a closed system; however, several methods are provided for the inclusion of migration data. Migration rates may be added explicitly, feeding may be assigned to diet “import”, or biomass, production and consumption rates may be scaled for the portion of the year that each species spends in the gyres.

All of these methods give similar results for the ECOPATH “balance” model; however, all of these methods are known to lead to unrealistic projections in dynamic ECOSIM (Aydin unpublished). The method selected to minimize errors was the last method mentioned above, that of scaling biomass for residence time (for marine mammals and birds) or biomass, production, and consumption (for Pacific salmon), as described below.

Diet scaling

Diet data for higher trophic levels, especially birds and mammals, tended to be highly aggregated and contained insufficient resolution to cover all potential prey items in the models. For example, it was common for prey to be apportioned in literature between "fish" and "squids" without further taxonomic resolution. In these cases, the diet of each predator that the literature apportioned to a major taxon, for example to "fish", was split among all fish groups in the model with a "neutral" preference, *i.e.*, split in proportion to the biomass of each fish type in the model.

However, this "neutral preference" approach could not be used directly due to data gaps in the forage species biomass, specifically for "other" forage fish and micronektonic squid. For these species, biomass estimates were unavailable and thus biomass was to be estimated from consumption requirements. However the preference method noted above used biomass estimates to estimate consumption, thus introducing a circular estimation problem.

This circular data gap was resolved iteratively as follows: micronektonic squid and fish were considered to be a small proportion (~10%) of squid and fish in diets of top predators for which the preference model was used. In most cases this led to "unbalanced" (EE>1) predation rates on specific (non-forage) fish and squid groups. When this occurred, the diets of predators were gradually shifted from specific fish and squid to the more general categories, and the biomass of these general categories increased in estimation accordingly.

Thus, the estimated consumption of specific fish and squid groups in the model is close to the maximum possible under constraints balance, *i.e.*, under constraints of production being equal to or greater than consumption for each individual group. On the other hand, the biomass of the general forage species are estimated to be the minimum required for providing the remainder of dietary requirements to upper trophic levels. The low grading of the diet data reflects the uncertainty inherent in this method.

Additional adjustments

The stepwise shifting of top predator diets from specific fish to general "forage" fish, in conjunction with allowing micronektonic squid and forage fish to be estimated based on demand, generally ensured that most of the species were thermodynamically "in balance" in the models (with EEs<1.0) without further drastic adjustments. As mentioned in "Diet scaling" above, overly high EEs of fish species such as salmon and large squid led to shifting diets of top predators towards forage fish. This repeated shifting was necessary mainly for sharks and Pacific whitesided dolphin.

In addition to the general balancing, six other changes were made in the biomass levels of groups due to the specific needs of balancing the model. Five of these changes were due to perceived mismatches in coverage; either because existent data was dominated by mismatching border region data rather than central gyre data, or due to lack of seasonal data. Balance was achieved in these cases by scaling biomass estimates as appropriate for the gyre as a whole over the whole year. The sixth change was due to the difficulty of capturing cannibalism in a highly productive species. The changes were as follows:

1. Predation by toothed whales (Orca) included predation on mammals and birds, which caused EEs of some mammals and birds to be too high (between 2 and 3). Feeding on birds and mammals is a characteristic of "transient" types of Orcas which are thought to be low in numbers and shore-based. Toothed whale biomass was reduced by 80% from the initial (shore-based) estimate.

2. The EE of Pacific sardines in the WSA model was initially too high (EE greater than 5). This was primarily due to predation by Pacific pomfret. Both pomfret and sardines are predominantly southern species with biomass levels that are much higher in the Kuroshio Current. In this case, the diet information

came from southern sampling where the pomfret/sardine connection would be strong, but the biomass of sardines in the model came from Kamchatka Current studies and reflected their low presence in the northern gyre regions. The biomass of Pacific sardines was increased from 0.017 to 0.05 t/km^2 to account for the influence of the "southern" regions of the model. To aid in selecting appropriate adjustments for sardines, several ECOSIM scenarios were explored which allowed for "invasions" of sardines in response to possible regime-scale shifts in abundance.

3. Chaetognaths in the WSA were the source of a great deal of predation and led to an imbalance in several zooplankton groups, including amphipods, pteropods and euphausiids. The initial chaetognath biomass estimate came from studies in the Kamchatka Current and was calculated to be 53 t/km^2, higher then copepods or microzooplankton. This biomass was cut approximately in half to 25 t/km^2 which was the maximum that allowed balance. This puts chaetognath biomass in a similar range as other large predatory zooplankton in the central gyre.

4. WSA microzooplankton biomass as estimated from Kamchatka Current data was half copepod biomass and possessed an EE>1. Microzooplankton biomass was set equal to copepod biomass as a first approximation.

5. Overall in the WSA, the EEs of amphipods, pteropods, and euphausiids were higher than 1.0 even after cheatognath reduction, while the EE of copepods was extremely low (less than 0.2). This was considered to be partially due to seasonal sampling: very little dietary sampling captured spring periods when copepods might dominate the diets of large zooplankton such as shrimp and chateognaths. For these highest trophic levels of zooplankton, predation on amphipods, euphausiids and pteropods was decreased, and predation on copepods increased. Finally, 10% of copepod consumption on micro-zooplankton was shifted to phytoplankton. As WSA phytoplankton was "top-down" balanced, the resulting phytoplankton biomass levels were set as sufficient to fuel the system.

6. Flying squid in the ESA initially had an EE greater than 4, but almost all of this was due to cannibalism. Cannibalism, when it occurs, would be best modeled by creating two biomass pools and having adult flying squid feed on juveniles, as juveniles would have a higher production rate and therefore be able to balance the demand. Due to lack of data on squid recruitment dynamics, this method was not pursued. Instead, 50% of the "cannibalism" in flying squid diets was shifted to micronektonic squid, which might include juvenile flying squid.

In the initial versions of the model, two species, Spiny dogfish and daggertooth, were included as separate groups but were dropped from the models during the balancing process. Spiny dogfish do occur in the gyres and have been caught in central gyre research gillnets with catch rates similar to those for some large squid species (Pearcy *et al.* 1999). Also, examination of dogfish stomachs near ocean Station P has revealed evidence of recent zooplankton consumption in these regions (Pearcy, unpublished data; Aydin, unpublished). However, it was felt that these animals might be migratory with little residence time or feeding effort expended in the central gyres (McFarlane and King, in press). The combination of low production rates and assumptions of predation by larger animals made the species difficult to balance reasonably, and they were removed. Daggertooth (sp), even at maximum reasonable assumptions of density, were less than 1% of the biomass of any trophic level and less than 0.5% of any species' predation mortality and were thus dropped from the model due to lack of data and importance of the species as a whole.

Initial versions of the model had substantial nutrient groups as detrital pools to simulate nitrogen cycling in conjunction with NEMURO. However, the ECOSIM formulations are generally unsuited for fast turnover rates required for nutrient pool dynamics (Walters, pers. comm). Therefore, detrital pools were simplified into dissolved organic matter (NH_3) and particulate organic matter (POM) which were fed on by bacteria, and represent the only accounting detrital recyclers in the final model. A considerable proportion of lower trophic-level regulation in the gyres may be due to nutrient recycling (Harrison *et al.* 1999). The current ECOPATH models should not be used to explore hypotheses based on specific mechanistic lower-trophic level links, for which a model such as NEMURO would be more appropriate.

Model data review

Physical variations

Two gyres dominate Subarctic Pacific: the Eastern gyre and the Western gyre. In the Eastern Gyre, the centre of the gyre is at approximately 52ºN, 155ºW, and the gyre extends westward nearly to the dateline. Much of the research on lower trophic levels for the Eastern gyre was carried out in its southeast corner at Ocean Station P (50ºN, 145ºW). The Western Gyre is northeast of Japan, southeast of Kamchatka Peninsula, at 155–165º E, 45–50º N. The gyres are bounded to the south by the slow, eastward flowing Subarctic Current at approximately 45-50ºN, formed in the west by the convergence of the Oyashio and Kuroshio Currents. The Subarctic Current splits at approximately 48ºN, 130ºW, and becomes the northward flowing Alaska Current, and the southward flowing California Current.

The Aleutian Low atmospheric system dominates the region in winter. Winds peak in winter at 12 m/s, and decrease to 7 m/s in July. High precipitation, low evaporation and freshwater land runoff result in an upper layer with a strong shallow halocline and winter mixed layer depths in the center of the Eastern Gyre to 75-100 m. Surface cooling and winter wind mixing cause mean surface temperature to be <6ºC in February. Also in February, salinity peaks at 32.7 psu, the mixed layer deepens to ~120 m, and nitrate and silicate levels increase.

Severe winter storms and the dominant Aleutian Low result in upwelling in the gyres, which maintains high nutrient concentrations in surface waters. Harrison *et al.* (1999) noted that the Subarctic North Pacific is one of 3 major high-nitrate-low-chlorophyll regions.

Sea surface temperatures in the Western Gyre (3–9.5ºC) are colder than in the Eastern Gyre (6–12ºC). Nitrate, Nitrite, Silicate and Phosphate concentrations are higher in the Western than in the Eastern Gyre. The Western Gyre has higher nutrient concentrations, higher chlorophyll concentrations than the Eastern Gyre, but similar summer primary productivity. In summer the mixed layer depth and photic zone are shallower in the Western than in the Eastern Gyre. Mean chlorophyll concentrations are twice as high in the Western than the Eastern Gyre, but depth-integrated chlorophyll concentrations are nearly equal, as the photic zone is deeper in the Eastern than it is in the Western Gyre (Harrison *et al.* 1999). An area about 500 km in radius around Station P has been sampled for spatial nutrient and temperature variations. Water temperatures increase to the east and south of Station P. Nutrients increase to the west and north (toward the centre of the Eastern Gyre). Salinity increases to the north, south and west.

Interannual and interdecadal changes in nutrients have been observed in the Eastern Gyre. During the 1989 La Niña, Station P was cold, less saline and had nitrate-rich surface water in the winter. During the transition to El Niño from 1991 to 1994, the surface waters at Station P warmed by 2ºC, became 0.3 psu more saline, and 30% lower in nitrate. A seaward extension of the nitrate-depleted surface layer occurred in 1994, due to a reduction in winter nitrate concentrations. This reduction was caused by an intrusion of warmer, lower nitrate water from the south during El Niño. Lower winter nitrate levels are estimated to have reduced new production by 40% and possibly shifted phytoplankton community structure. From the 1970s to the 1990s, winter silicate and nitrate uptake has declined by 3.6 μm and 2.5 μm respectively, which may indicate an iron supply reduction in the last twenty years.

Species groups

Species inhabiting each gyre system were identified using existing reviews on the ecosystem dynamics of both areas (Taniguchi 1999; Mackas and Tsuda 1999; Brodeur *et al.* 1999; Beamish *et al.* 1999; Springer *et al.* 1999; Hunt *et al.* 2000). The species groups selected were equivalent for the Eastern and Western Gyre systems with five exceptions: Minke whales, common dolphins, Japanese anchovy and Pacific sardine were in the Western Gyre model only, and northern elephant seals were in the Eastern Gyre model only. Highly aggregated groups such as "micronektonic squid", "other forage fish", or "copepods" would likely differ in species composition between the gyres but are treated as functionally equivalent between the two models.

Biomass, diet composition and production estimates were compiled using published estimates, and when possible, using data collected from 1990-1993, or as close to this time period as possible. Estimates are annual values and are made from data collected in offshore areas only. While biomass estimates differed between gyres, the P/B and Q/B ratios for each species group were assumed to be equivalent for both gyre models. This latter assumption was made due to data limitations, but within the Subarctic climate regime, P/B and Q/B values for species would be expected to be more similar than different. Diet composition data are expressed as percentage of biomass.

Marine mammals

Cetaceans were divided into nine functional groups, each one containing a single species. Seven of these groups are present in both the Eastern and Western Gyres: sperm whale (*Physeter catodon*); orca (*Orcinus orca*); fin whale (*Balaenoptera physalus*); sei whale (*Balaenoptera borealis*); Dall's porpoise (*Phocoenoides dalli*); Pacific white sided dolphin (*Lagenorhynchus obliquidens*) and northern right whale dolphin (*Lissodelphis borealis*). The additional two groups, minke whale (*Balaenoptera acutorostrata*) and common dolphin (*Delphinus delphis*) were present in the Western Gyre only.

Two pinniped groups were used in the Eastern Gyre model: northern fur seal (*Callorhinus ursinus*) and northern elephant seal (*Mirounga angustirostris*). Only one pinniped group (northern fur seal) was used in the Western Gyre model. Although actual routes of migration are not well understood, Springer *et al.* (1999) noted that in general, pinnipeds remain close to shore throughout the year, and are not considered to be part of the fauna of the subarctic gyres. Some other species of whales and pinnipeds have also been reported in the Western Gyre (Springer *et al.* 1999), but have not been included in the models due to low numbers.

Most species of cetaceans are highly migratory, particularly the Mysticetes which reside in higher latitudes in the summer for feeding, and move to lower latitudes in winter for breeding. They are widespread and appear to be equally abundant in both the gyres. Most biomass estimates reported were available for the North Pacific as a whole, or in the case of pinnipeds, based on counts at breeding sites, throughout the Pacific rim. Migration patterns have been suggested as one indication of differences in marine mammalian behaviour between regions of the Pacific. For example, in the western Pacific region, Dall's porpoise have a larger migration, from the Sea of Okhotsk in summer, to the Japan/East Sea, and northwestern North Pacific regions in winter. On the east side of the North Pacific they have been observed migrating smaller distances, onshore/offshore only (Springer *et al.* 1999).

The migration of species was taken into account by performing a broad North Pacific synthesis to scale North Pacific abundance and body weight estimates by residence time in both gyres, and spread across the gyres (Table A2). P/B values for marine mammals were all taken from estimates of yearly mortality (Z) as cited in Table B1. Q/B values came from daily allometric energy requirements listed in Hunt *et al.* (2000, Appendix 9) and caloric energy densities of typical prey types (Table A3).

Diet estimates for marine mammals were highly aggregated. A review by Hunt *et al.* (2000) indicated no source of data for marine mammals that was specific to the ESA or WSA. For these regions, the only source of data was Pauly *et al.* (1998), who reviewed general marine mammal diets around the world. They divided marine mammal prey into 8 categories: benthic invertebrates, pelagic zooplankton, small squid, large squid, small epipelagic fish, mesopelagic fish, misc. fish, and birds and mammals. Prey proportions by predator are found in Hunt *et al.* (2000, Table 10.6-10.7). As described above, diets in the ESA and WSA models were split to species within each broad category in proportion to the biomass of the species (Tables B7-B8).

Table A2 Synthesis of North Pacific abundance estimates and area residence times for marine mammals, used to provide biomass estimates for ESA and WSA models.

Species	**Values used for estimate and literature sources**
Sperm whale	Kato *et al.* (1997) give 2,300 individuals in WSA only; Pauly and Christensen (1996) give 2,000 in North Pacific. Since feeding occurs in the Bering Sea also (Aydin *et al.* 2002) we assumed population was N. Pacific overall. Used 2,000 individuals * 18,518 kg/individual (Kato *et al.* 1997) * ½ year / 20 million km^2 (total N. Pacific area); this is most likely a minimal estimate.
Toothed whales	The only available estimates of ESA orca biomass were from Pauly and Christensen (1996) and covered the “transient” type of orca (mammal-consumer) only. These species were left in the model and reduced for balance, although it is not known if this life-history type feeds in the subarctic gyres.
Fin whale	20,000 individuals * 55,590 kg/individual (Evans 1987; Gambell 1985a) * ½ year / 20 million km^2 (total N. Pacific area).
Sei whale	14,000 individuals * 16,811 kg/individual (Gambell 1985b) * ½ year / 20 million km^2 (total N. Pacific area).
Minke whale	In the initial model a minimal estimate of 0.001 t/km^2 was assumed. Buckland *et al.* (1992) estimate of 5,841 individuals over 2.1 million km^2 (WSA area) for half the year (0.009 t/km^2).
Northern fur seal	Springer *et al.* (1999) estimate 175,000 over 20 million km^2 (total N. Pacific area) south of the Aleutian Islands for half the year. (Compare to 190,000 from Buckland *et al.* 1993). An average body weight of 28 kg is given by Hunt *et al.* (2000). Small and DeMaster (1995) give a population of 1 million individuals in the Pribilof Islands while Bigg (1990) notes that 10-15% of these travel into the gyres for half the year or less.
Elephant seal	Stewart *et al.* 1994 give a eastern North Pacific estimate of 127,000; however only adult males forage in the Eastern Gyre. Scaling gives 8,400 animals at 371 kg body weight over, 3,600,000 km (eastern Pacific), for ½ year.
Dall’s porpoise	1,925,000 (Hunt *et al.* 2000 Table 9.11); compare to 1,200,000 from Buckland *et al.* 1993 * 61 kg each/ 20 million km^2 (subarctic and transition zones).
Pacific whitesided dolphin	1 million at 79 kg each/20 million km^2 (Buckland *et al.* 1993). Estimate may be high due to vessel attraction during surveys (Angliss *et al.* 2001).
Northern right whale dolphin	740,000 (Hunt *et al.* 2000, Table 9.7) at 105 kg each over 20 million km^2 (subarctic and transition zones), compare to 68,000 for ESA (Buckland *et al.* 1993).
Common dolphin	Minimal estimate of 0.001 t/km^2 was used.

Table A3 Values used to compute yearly consumption/biomass (Q/B) rates for marine mammals. Calculated values are italicized. Energy required and body weight are taken from Hunt *et al.* (2000). Prey energy density is assumed for two feeding modes, zooplanktivorous and piscivorous, with ESA fish and zooplanton energy densities from Davis *et al.* (1998).

Species	Energy required (kcal/day)	Prey density (kcal/g)	Prey consumed (kg/day)	Body weight (kg)	Q/B (daily)	Q/B (yearly)
Sperm whales	502,867	1.5	*335.24*	18518	*0.01810*	*6.61*
Toothed whales (orca)	104,539	1.5	*69.69*	2280	*0.03057*	*11.16*
Fin	694,768	1.0	*694.77*	55590	*0.01250*	*4.56*
Sei	283,325	1.0	*283.33*	16811	*0.01685*	*6.15*
Minke	139,990	1.0	*139.99*	6566	*0.02132*	*7.78*
Northern fur seals	4,491	1.5	*2.99*	28	*0.10693*	*39.03*
Elephant seals	16,890	1.5	*11.26*	371	*0.03035*	*11.08*
Dall's porpoise	7,000	1.5	*4.67*	62	*0.07526*	*27.47*
Pacific white sided dolphin	8,385	1.5	*5.59*	79	*0.07076*	*25.83*
Northern right whale dolphin	10,416	1.5	*6.94*	105	*0.06613*	*24.14*
Common dolphin	(values unknown, averaged Q/B from other dolphins)					

Table A4 Bird residency days in the WSA and ESA, and body weights, used to weight total bird biomass by percentage of each species. Data is from Hunt *et al.* (2000).

Species	Body weight (kg)	WSA residency days	WSA percent		Species	ESA residency days	ESA percent
Laysan Albatross	3.04	1,100,000	40.8%		Sooty Shearwater	1,600,000	45.7%
Sooty Shearwater	0.79	3,100,000	29.7%		Northern Fulmar	470,000	9.3%
Tufted Puffin	0.79	892,000	8.5%		Tufted Puffin	255,000	7.2%
Northern Fulmar	0.54	600,000	4.0%		South-Polar Skua	160,000	6.7%
Black-legged kittiwake	0.41	610,000	3.0%		Black-legged kittiwake	440,000	6.5%
Short-tailed Shearwater	0.53	430,000	2.8%		Long-Tailed Jaiger	440,000	4.7%
Fork-tailed Storm Petrel	0.06	3,600,000	2.4%		Short-tailed Shearwater	220,000	4.3%
South-Polar Skua	1.15	150,000	2.1%		Fork-tailed Storm Petrel	1,900,000	3.8%
Leach's Storm Petrel	0.04	3,500,000	1.7%		Leach's Storm Petrel	2,200,000	3.2%
Pormarine Jaeger	0.69	190,000	1.6%		Black-footed Albatross	23,000	2.6%
					Laysan Albatross	21,000	2.3%

Birds

Total bird biomass density in the gyres is reported to be 0.0008 in the ESA and 0.0038 in the WSA (Hunt *et al.* 2000). To weight this total by different bird groups, species were weighted by residency days in the gyres and body weight to find the percentage of the total bird biomass consisting of each species. Species representing the cumulative 95% of the bird biomass were included in the model, groups as albatrosses, shearwaters, storm petrels, kittiwakes, fulmars, puffins, skuas and jaegers (Table A4).

Mortality rates were not obtained and taken to be similar to eastern Bering Sea estimates of 0.05 to 0.075 for large predatory birds, and 0.1 for smaller birds (Aydin *et al.* 2002). Consumption rates and diets were taken from Hunt *et al.* (2000) (which reported allometric energy requirements and prey by general categories) and weighted by biomass of prey species within each category.

Cephalopods

Neon flying squid (*Ommastrephes bartrami*), boreal clubhook squid (*Onychoteuthis borealijaponica*), large gonatid squid (Family Gonatidae), and micronektonic squid were used in each gyre model. Biomass for clubhook and large gonatid species in the ESA was calculated from measurements of catch-per-unit-effort in Hokkaido University research gillnet studies from the 1994-1999, published yearly (for example, Faculty of Fisheries Hokkaido 2000). The CPUE values were reported for Pacific salmon and other fish of similar size, including pomfret and large squid (as individuals per unit of research net). It was assumed that the ratio of CPUE (non-salmon species) / CPUE (total salmon) was equal to the ratio of biomass (non-salmon species) / biomass (total salmon). To solve for the biomass of non-salmon species, the biomass of salmon species used was that from the run reconstruction method detailed below. Neon flying squid biomass was reported by Shimizaki (1986). In the WSA, squid biomass was taken from Russian sources cited in Table B2. P/B ratios for all of the large squid was taken to be the same as reported for neon flying squid, of 0.07 per 10 days or 2.555 per year (Murata and Shimazu 1982). Q/B ratios from Brodeur *et al.* (1999) are reported as 0.02 per day for clubhook and large gonatid squid (7.3/year) and 0.017 for neon flying squid (6.2/year). Squid diets were from research gillnet studies (Ishida unpublished data).

Micronektonic squid, primarily gonatids such as *Berryteuthis anonychus* and *Gonatus onyx* are an extremely important food source for species across the subarctic gyres, especially in the Subarctic Current (Pearcy *et al.* 1988; Aydin *et al.* 1998). No estimate for their biomass was available so it was estimated by setting their EE to 0.90 in both models. References for P/B and Q/B ratios are given in Table B2.

Fish

Pacific salmon. Six species of Pacific salmon were included in the models as separate groups: steelhead (*Onchorhynchus mykiss*); chinook salmon (*O. tshawytscha*); coho salmon (*O. kisutch*); sockeye salmon (*O. nerka*); chum salmon (*O. keta*); and pink salmon (*O. gorbuscha*). Due to their commercial importance salmon were the species with the most data available, however much of this data is concentrated around the early or late stages of their life cycle outside of the gyres.

For biomass, two basic methods were available. The first was to use run (returning salmon) reconstruction records (catch + escapement) for Pacific Rim stocks in conjunction with mortality and migration studies, to determine the percentage of each salmon stock's life-history cycle in the gyres. The second was to use direct survey estimates. The first method has the advantage of taking into account all seasons and life stages of the salmon, as well as allowing for reconstruction historical biomass levels. Its disadvantage is that it relies on indirect measures of migration such as non-quantitative tagging studies. The second method provides a direct point estimate of a catch-per-unit-effort, but this may be difficult to calibrate to biomass and in addition may cover only brief periods of the year.

Initially, the first method was used for both gyres combining Pacific-wide stock-specific run reconstructions from 1950-1998 (Rogers 1999) with salmon body weight by month (Ishida *et al.* 1993), mortality estimates (Pauly and Christensen 1996) and tagging studies (Myers *et al.* 1996). The values are averaged for the period 1990-98 and shown in Table A5. For the ESA, the run reconstruction values show a pattern similar to results from Pauly and Christensen (1996).

In the WSA, two additional sources of data were provided from surveys. The first, a combination of values from Shuntov *et al.* (1993 a,b) and Shuntov *et al.* (1995) was used in the final model. These data were collected from the northwest sections of the WSA near Kamchatka. However, original data from research cruises (TINRO 1998 a,b) provided finer spatial resolution; when "Kamchatka Current" stations were removed the results were a synthesis of TINRO data sources that were oriented towards the central gyres. The biomass levels from this TINRO synthesis are more similar to run reconstruction values than Shuntov *et al.* (1993 a,b; 1995), especially in showing a lower level of pink salmon biomass.

Overall, the run reconstruction methods showed a considerably higher proportion of sockeye and chum salmon in gyres, and a lower proportion of pink salmon, when compared with survey methods. This is because the surveys are geared towards catching adult (maturing) salmon while the reconstructions take into account the juvenile biomass present in the multi-year life history of chum and sockeye salmon.

For historical fitting found in the main text, the run reconstructions for both the ESA and WSA were used to estimate gyre salmon biomass between 1951-1996 (Fig. A1).

Table A5 Estimated 1990s biomass of Pacific salmon in the WSA and ESA according to different estimation methods. Values used in the final model are shown in bold.

	WSA			**ESA**	
	Shuntov *et al* 1993 a,b; 1995.	TINRO synthesis	Run reconstruction	Run reconstruction	Pauly and Christensen 1996
Sockeye	**0.00310**	0.0223	0.0283	**0.0897**	0.109
Chum	**0.0152**	0.112	0.303	**0.0541**	0.051
Pink	**0.197**	0.0981	0.020	**0.0233**	0.083
Coho	**0.0058**	0.0209	0.00304	**0.00445**	1.830
Chinook	**0.0039**	0.00628	0.00438	**0.00930**	0.335
Steelhead	**0.0039(*)**			**0.00930(*)**	0.100

(*) Steelhead values not available so assumed equal to chinook.

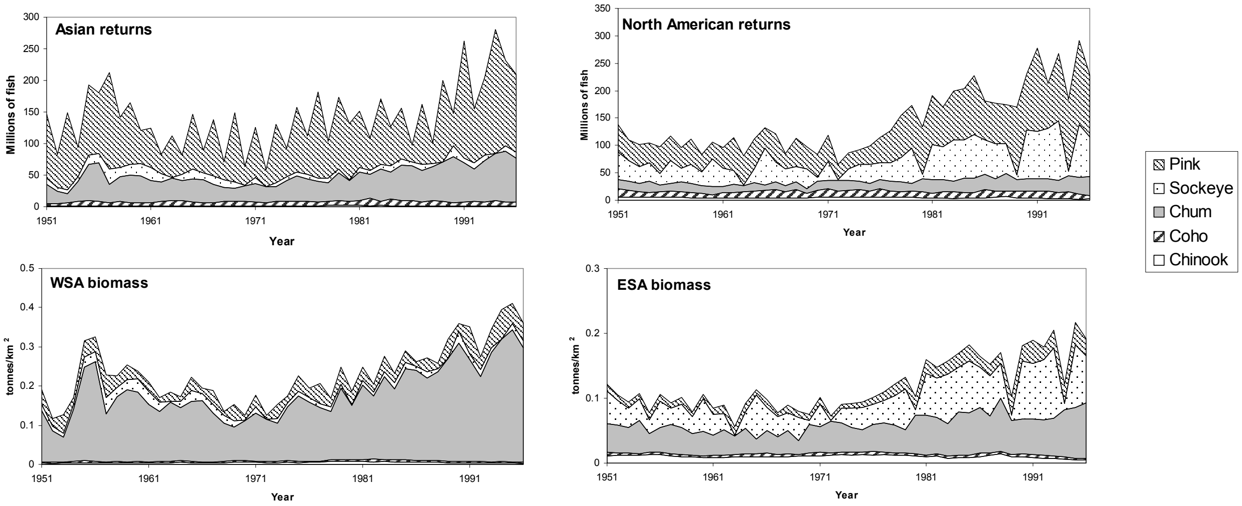


Fig. A1 Top Panels: Run sizes (returns) of North American and Asian Pacific salmon (catch+escapment); from Rogers (1999); and reconstructed biomass densities (averaged throughout year for all age-classes) for the WSA and ESA. Bottom panels: Notice difference in scales between two bottom panels.

P/B and Q/B values for Pacific salmon were constructed from detailed bioenergetics models (Aydin 2000) based on growth rates reported by Ishida *et al.* (1998). The freshwater and early ocean, and late (fishery) stages are not included, so this model does not capture the dynamics of the salmon fisheries implied by management of escapement and hatcheries, and no fishing of salmon is modeled.

Diet habits of Pacific salmon for the 1990s can be found for the ESA in detail in Aydin (2000), and in summary in Kaeriyama *et al.* (2000); the original data from these studies were pooled to construct the ESA diet tables. WSA salmon diet data from similar studies were provided by Y. Ishida.

Other fish. The other piscivorous fish in the ESA and WSA models were sharks, primarily salmon sharks (sp) and pacific pomfret (*Brama japonica*). As mentioned under "Balancing the model" above, Pacific dogfish (*Squalus acanthias*) and daggertooth (*Anotopterus pharao*) were included in initial model drafts but later dropped.

Several forage fish groups were modeled in the two systems. Mesopelagic fish (mainly myctophidae, particularly *Stenobrachius leucopsarus*, see Beamish *et al.* 1999c for species lists); miscellaneous forage fish (mainly sticklebacks *Gasterosteus aculeatus*); and saury (*Cololabis saira*) were modeled in both systems. There were two additional teleost groups in WSA gyre model: Pacific sardine (*Sardinops sagax*) and Japanese anchovy (*Engraulis japonica*).

The data sources for biomass, P/B, and Q/B for these species are listed in Table B2; the exception is for ESA pomfret biomass which was estimated by computing its CPUE ratio to total salmon biomass as described in the section on squids, above.

Plankton

For the ECOPATH model, zooplankton were divided into eleven groups: microzooplankton (zooplankton <200 μm, typically meroplanktonic larvae and copepod nauplii); copepods; euphausiids; pteropods; amphipods (mainly hyperiids); sergestidae; chaetognaths; salps; ctenophores; large jellyfish; and an other group (mainly Larvaceans and Polychaetes). A bacterial component was included in the initial balancing stages and in the model for Appendix B; however this group was not used for ECOSIM simulations that included seasonal dynamics.

ECOPATH model estimates for lower trophic levels were taken from outputs from the NEMURO model (Tables A6-A10). NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) is a lower trophic level model (LTL) of a marine ecosystem that was developed by the PICES CCCC MODEL Task Team during a modeling workshop held in Nemuro, Japan, in 2000 (Eslinger *et al*. 2000, Megrey *et al.* 2000). NEMURO simulates the annual dynamics of phytoplankton, zooplankton and nutrient concentrations for two locations in the North Pacific, Ocean Station P (50ºN 145ºW) and station A7 (41.30ºN 145.30ºE) off the "A-line", an oceanographic sampling line off Hokkaido Island, Japan. For the ECOPATH models, only Ocean Station P results were used. The diet composition for zooplankton groups were very similar in both gyre models. Copepods, microzooplankton and phytoplankton are generally the major component of zooplankton diet. Large jellyfish, chaetognaths, sergestid shrimp and amphipods feed mainly on copepods (60-80%). The remaining zooplankton groups feed on copepods (25-40%), microzooplankton (20-40%) and phytoplankton (25-70%). Microzooplankton diet is composed of small phytoplankton (75%) and bacteria (25%).

The annual, gyre-scale averages used for zooplankton in the ECOPATH models cover a wide range of spatial, seasonal, and interannual variability which was not explicitly modeled. Mackas and Tsuda (1999) found that timing of spawning and age at first maturation for zooplankton have been later, slower and more narrowly seasonal in the northern parts of both gyres, particularly in the cold waters of the high latitude western marginal seas. They further suggested that in all regions the annual biomass peak of mesozooplankton coincides with the time

Table A6 Results of NEMURO/MATLAB Box model simulations.

Variable	NEMURO Group (ECOPATH Groups)	Model Value
P/B daily P/B annual B mean	PS (Small phytoplankton)	0.108-0.636 /d mean = 0.355/d ~ 0.12
P/B daily P/B annual B mean	PL (Large phytoplankton)	0.032-0.212/d mean = 0.116/d ~0.11
P/B daily P/B annual B mean	ZS (Microzooplankton)	0.081-0.222/d mean = 0.134/d ~0.055
P/B daily P/B annual B mean	ZL (Copepods)	0.026-0.127/d mean = 0.065/d ~0.055
P/B daily P/B annual B mean	ZP (Euphausiids, amphipods, pteropods)	0.001-0.015/d mean = 0.007/d ~0.08
Q/B	ZS (Microzooplankton)	0.387-1.06/d mean = 0.639/d
Q/B	ZL (Copepods)	0.124-0.604/d mean = 0.308/d
Q/B	ZP (Euphausiids, amphipods, pteropods)	0.004-0.070/d mean = 0.033/d

Table A7 Estimates of Station P primary production.

Method	Average Daily PP ($gC/m^2/d$)	Annual PP ($gC/m^2/yr$)	Source
C14		140	Wong *et al.* 1995
Nitrate depletion		133	Wong *et al.* 1995
Particle flux		120	Wong *et al.* 1995
Chl a	0.55	199	Longhurst *et al.* 1995
Secchi disc data		167	Falkowski & Wilson 1992

Table A8 Average annual biomass (B1-B4), P/B, and annual primary production (PP) for PS and PL.

Group	B1 µmolN/l	B2 µmolC/l	B3 gC/m^3	B4 gC/m^2	P/B d^{-1}	PP gC/m^2/yr
PS	0.12	0.792	0.0095	0.760	0.355	98.5
PL	0.11	0.726	0.0087	0.697	0.116	29.5
PS + PL	0.23	1.518	0.0182	1.457		128

Calculations:

1. B2 = 6.6 (Redfield ratio) x B1.
2. B3 = 0.012 x B2 (Table 6).
3. B4 = 80 m x B3 (Table 7).
4. PP = P/B x B4 x 365 d.

Table A9 Conversion factors.

Variable	Value	Source
C/N (Redfield)	6.6	Wong *et al.* 1995
C/N	7.8	Kawamiya *et al.* 1997
N/Chl a	7.5	Kawamiya *et al.* 1997
C/Chl a	50	Kawamiya *et al.* 1997

Table A10 Station P characteristics.

Variable	Value	Source
Euphotic zone	80 m	Wong *et al.* 1995
Average Chl a (annual)	0.4 mg/m^3 (µg/L)	Wong *et al.* 1995
f-ratio	0.25	Wong *et al.* 1995
f-ratio (summer)	0.25-0.52	Wong *et al.* 1998

period when late copepodites of *Neocalanus* spp. are the most abundant above the pycnocline (sometime between May and July).

Taniguchi (1999) noted that the Eastern Gyre area generally has the lowest chlorophyll levels (0.3 µg/L) in the North Pacific, while Western Gyre levels are slightly higher (0.5 µg/L). Station P exhibits a consistently low biomass with little seasonality. Chlorophyll concentrations are very low but annual primary productivity is quite high, primarily from small phytoplankton <5 µm (prasinophytes, prymnesiophytes, cryptophytes and cyanobacteria). The productivity is derived mainly from regenerated production, and about 21% from new production. Taniguchi (1999) reported nitrate levels of 16 µg/L in winter, and 8 µg/L in summer.

Nitrogen uptake rates are influenced by light, temperature, available nitrogen sources, iron concentration, and competition from bacteria. Harrison *et al.* (1999) suggest that nitrogen uptake by larger (>5 µm) diatom cells may be influenced by iron concentration, which can be introduced to the gyre system by various sources, one of the most important being atmospheric transport of dust from land sources.

Harrison *et al.* (1999) found that small cells in the Eastern Gyre can grow at near maximum growth rates, and are grazer controlled. Small phytoplankton are controlled by grazing microzooplankton, which can grow rapidly to respond to changes in growth rate of the small phytoplankton, and may exert a greater control than mesozooplankton grazing.

Harrison *et al.* (1999) reported greater seasonality in phytoplankton in the Western Gyre compared to the Eastern Gyre. Diatom cells have been reported in higher numbers in the Western than in the Eastern Gyre in spring and summer. Picoplankton (<2 µm) are predominant in the summer, but when chlorophyll concentrations are over 1 µg/L, phytoplankton >10 µm make up 60% of the total chlorophyll concentration. There is a late autumn increase in chlorophyll concentration in the Western Gyre, but summer productivity values are similar between the Western Gyre and values obtained at Station P.

One iron enrichment study in the Western Gyre indicated that iron may limit primary productivity of large cells in this gyre as well. Larger cells are dominated by *Thalassiosira*, unlike the Eastern Gyre where pennate diatoms were observed with iron enrichment. The 10 µM ambient nitrate was depleted in 5 days, and ambient chlorophyll increased from 1.3 to 5 µg/L with the introduction of iron. Surface iron concentrations in the Western Gyre are low during the low dust season (summer and fall), at which time the iron levels are similar to those found in the Eastern Gyre. Deposition of dust has been suggested to result in an increase in primary productivity during the dusty season.

Taniguchi (1999) suggested the Western Gyre contains a similar percent contribution from micro-sized dinoflagellates to total flagellate biomass as is found in the Eastern Gyre. He also noted that the Western Gyre has more standing stock of microzooplankton than the Oyashio Region, but less than the Eastern Gyre. Microzooplankton grazing may control phytoplankton in most regions of the subarctic Pacific, except in the Oyashio region.

Harrison *et al.* (1999) reported inshore stations in the Eastern Gyre have diatom dominated spring and summer blooms, when growth rate is likely limited by nitrogen, and sedimentation occurs as diatoms sink out. Oceanic stations show little seasonality in biomass; however, they have a pronounced seasonal cycle in primary production. The biomass is dominated by small cells. Sedimentation is low compared to inshore stations. Higher diatom abundance is recorded occasionally, maybe indicating variation in the iron supply.

Mackas and Tsuda (1999) found higher population biomass and individual growth rates of zooplankton near land and on the Asian side of the basin, consistent with the hypothesis that the rate of supply of iron from land limits some primary productivity.

Brodeur and Ware (1992) found an increase in the biomass of mesozooplankton in the Gulf of Alaska (ESA) from 113 mg wet weight/m^3 in 1956-1962, to 194 mg wet weight/m^3 in 1980-1989. Findings by Mackas and Tsuda (1999) are in agreement, indicating that the summer season biomass of mesozooplankton in the Eastern Gyre was a factor or two higher in the 1980s than in the 1950s and 1960s, and these changes correlated with large scale atmospheric and oceanographic changes, as well as interdecadal changes in pelagic fish production.

Brodeur and Ware (1995) reported that biomass for the Eastern Gyre was 213 mg wet fish weight/m^3 before 1980, and 168 mg wet weight/m^3 after 1980. Mackas and Tsuda (1999) found a similar decrease in zooplankton from the mid-1960s – early 1970s through to the late 1970s and 1980s in the Kuroshio-Oyashio transition area of the Western North Pacific.

APPENDIX B: DATA TABLES

Table B1 Literature references and values for biomass (t/km^2), production/biomass ($year^{-1}$), and consumption/biomass ($year^{-1}$) for marine mammals and birds in the WSA and ESA ECOPATH models.

	WSA Biomass		**ESA Biomass**		**Production/Biomass**		**Consumption/Biomass**	
Sperm whale	0.000929	See Table A2 (*)	0.000929	See Table A2 (*)	0.059	Chapman 1980	6.61	From daily ration and caloric requirement estimates in Hunt *et al.* 2000; see Table A3 (*)
Toothed whale	0.00028	Reduced 80% from Pauly and Christensen 1996 for balance	0.000028	Reduced 80% from Pauly and Christensen 1996 for balance	0.025	Olesiuk *et al.* 1990	11.16	
Fin whale	0.027883	See Table A2 (*)	0.027883	See Table A2 (*)	0.02	Midrange from Doi *et al.* 1967, Ohsumi 1979, Horwood 1990	4.56	
Sei whale	0.005902		0.005902		0.02		6.15	
Minke whale	0.001		-	Not present	0.02		7.78	
Northern fur seal	0.000246		0.000246	See Table A2 (*)	0.235	Chapman 1973	39.03	
Elephant seal	-	Not present	0.00043		0.368	Clinton and LeBoeuf 1993	11.08	
Dall's porpoise	0.005986	See Table A2 (*)	0.005986		0.1	Kuzin *et al.* 2000	27.47	
P. whitesided dolphin	0.003962		0.003962		0.14	Tanaka 1993	25.83	
N. right whale dolphin	0.003897		0.003897		0.16	Tanaka 1993	24.14	
Common dolphin	0.001		-	Not present	0.1	Hobbs and Jones 1993	24.98	
Albatross	0.00155	Synthesis from Hunt *et al.* 2000 (*)	0.00004	Synthesis from Hunt *et al.* 2000 (*)	0.05	Ogi *et al.* 1993 (Midway Atoll)	81.59	Synthesis from Hunt *et al.* 2000 (*)
Shearwaters	0.001237		0.0004		0.1	Average eastern Bering Sea estimates pooled for "birds" group in Aydin *et al.* 2002	100.1	
Storm petrels	0.000157		0.000056		0.1		152.1	
Kittiwakes	0.000115		0.000052		0.1		123	
Fulmars	0.000151		0.000074		0.1		100.3	
Puffins	0.000322		0.000058		0.1		104.3	
Skuas	0.00008		0.000054		0.075		96.6	
Jaegers	0.000061		0.000038		0.075		96.6	

(*) See Appendix A text under indicated species or tables for details.

Table B2 Literature references and values for biomass (t/km^2), production/biomass (year^{-1}), and consumption/biomass (year^{-1}) for fish and squids in the WSA and ESA ECOPATH models.

	WSA Biomass		ESA Biomass		Production/Biomass		Consumption/Biomass	
Sharks	0.0247	Shuntov *et al.* 1993 a,b, 1995	0.05	Bonfil 1994	0.2	Approx. from Atlantic porbeagle (Aasen 1963)	10.95	Pauly and Christensen 1996
Large gonatid squids	0.0472	Shuntov *et al.* 1993 a,b, 1995	0.03	(*)CPUE ratio to flying squid in research gillnet	2.555	Murata and Shimazu 1982 (Z=0.07/10 days)	7.3	Brodeur *et al.* 1999
Clubhook squid	0.074	Savinikh and Chuchukalo 1996	0.01	(*)CPUE ratio to flying squid in research gillnet	2.555	Murata and Shimazu 1982 (Z=0.07/10 days)	7.3	Brodeur *et al.* 1999
Neon flying squid	0.022	Belayev and Ivanov, 1999	0.45	Shimizaki 1986	2.555	Murata and Shimazu 1982 (Z=0.07/10 days)	6.205	Brodeur *et al.* 1999
Sockeye salmon	0.0031	Shuntov *et al.* 1993 a,b, 1995	0.0897	Run reconstruction (*)	1.27	Growth reconstruction (*)	10.13	Bioenergetics reconstruction (*)
Chum salmon	0.0152		0.0541		1.93		14.51	
Pink salmon	0.1973		0.0233		3.37		18.49	
Coho salmon	0.0058		0.0045		2.47		16.55	
Chinook salmon	0.0039		0.0093		0.8		5.333	
Steelhead	0.0039		0.0093		0.8		5.333	
Pacific pomfret	0.0531	Belayev and Ivanov 1999	0.21	(*)CPUE ratio to flying squid in research gillnet	0.75	Watanabe *et al.* 1997	3.75	From P/B assuming growth efficiency=0.2
Pacific saury	0.0473	Belayev and Ivanov 1999	0.45	Shimizaki 1986	1.6	Z from Hughes 1964; FAJ gives Z= 1 to 1.5	7.9	Empirical method of Pauly and Christensen 1996
Japanese anchovy	0.1758	TINRO data synthesis (*)	-	Not present	1.5	N. Calif. anchovy (Field 2001)	5	N. Calif. anchovy (Field 2001)
Pacific sardine	0.05	Raised from 0.0171 in TINRO data synthesis (*), to balance model	-	Not present	0.4	N. Calif. sardine (Field 2001)	3	N. Calif. sardine (Field 2001)
Misc. forage fish	-	ECOPATH estimate using EE = 0.90	-	ECOPATH estimate using EE = 0.90	1.5	Considered similar to anchovy	5	Considered similar to anchovy
Micronektonic squid	-	ECOPATH estimate using EE = 0.90	-	ECOPATH estimate using EE = 0.90	3.0	Pauly and Christensen 1996	15	Lapashina 1988 reports B. anonychus =14.6
Mesopelagic fish	6.5	Beamish *et al.* 1999c	4.5	Beamish *et al.* 1999	0.9	Trites *et al.* 1999	3	Trites *et al.* 1999

(*) See Appendix A text under indicated species for details.

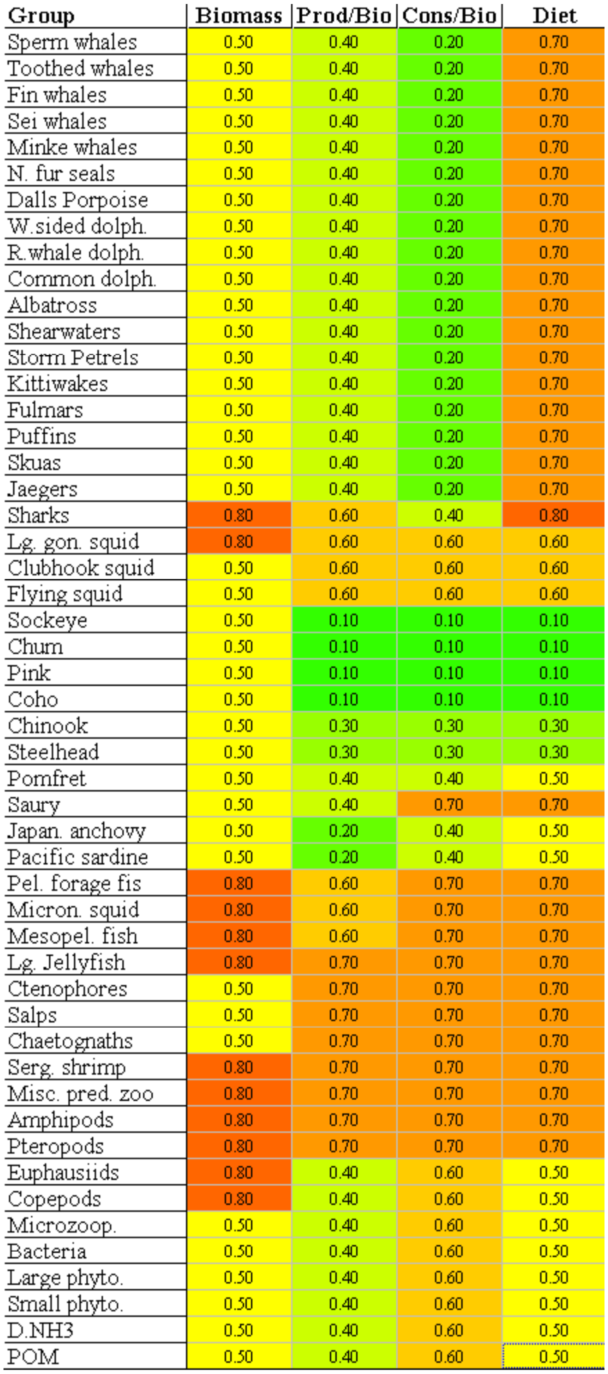
Table B3 Literature references and values for biomass (t/km^2), production/biomass (year^{-1}), and consumption/biomass (year^{-1}) for plankton in the WSA and ESA ECOPATH models.

	WSA Biomass		**ESA Biomass**		**Production/Biomass**		**Consumption/Biomass**	
Large jellyfish	0.469	TINRO synthesis (*)	4	Set to approximately half of Ctenophores	3	Pauly and Christensen 1996	10	Pauly and Christensen 1996
Ctenophores	10	Rounded up from ESA biomass	9.1	Aglantha from Pauly and Christensen 1996	4	Pauly and Christensen 1996	110	“High” est. from Pauly and Christensen 1996
Salps	10	Rounded up from ESA biomass	8	Purcell 1996	9	Pauly and Christensen 1996	30	Pauly and Christensen 1996
Chaetognaths	25	Down from 53.0 in TINRO synthesis (*)	6.6	Pauly and Christensen 1996	2.555	NEMURO predatory. zoop P/B (*)	12.05	NEMURO pred. zoop Q/B (*)
Sergestid shrimp	8.134	Assumed similar to “other pred. zoop”	5	Assumed similar to “other pred. zoop”	2.555		12.05	
Other pred. zoop.	8.134	10% of euphausiid biomass	5.0688	10% of NEMURO predatory zoop. (*)	2.555		12.05	
Amphipods	8.51	Belayev and Ivanov 1999	10.138	20% of NEMURO predatory zoop. (*)	2.555		12.05	
Pteropods	16.268	20% of euphausiid biomass	10.138	20% of NEMURO predatory zoop. (*)	2.555		12.05	
Euphausiids	40.67	Belayev and Ivanov 1999	25.344	50% of NEMURO predatory zoop. (*)	2.555		12.05	
Copepods	46.71	Belayev and Ivanov 1999	34.848	NEMURO lg. zoop (*)	23.73	NEMURO lg. zoop. (*)	112.4	NEMURO lg, zoop (*)
Microzooplankton	46.71	Up from 22.7 in TINRO data synthesis	35	NEMURO sm. zoop. (*)	48.91	NEMURO sm. zoop. (*)	233.2	NEMURO sm. zoop. (*)
Bacteria	-	ECOPATH estimate using EE = 0.90	-	ECOPATH estimate using EE = 0.90	18.45	Pauly and Christensen 1996	25	Pauly and Christensen 1996
L. phytoplankton		ECOPATH estimate using EE = 0.90	69.7	NEMURO lg. phyto (*)	42.34	NEMURO lg. phyto (*)	-	No consumption
Sm. phytoplankton		ECOPATH estimate using EE = 0.90	76	NEMURO sm. phyto (*)	129.6	NEMURO sm. phyto (*)	-	-No consumption
DNH3	-	50% of living outflow	-	50% of living outflow	-	No new production	-	No consumption
POM	-	50% of living outflow	-	50% of living outflow	-	No new production	-	No consumption

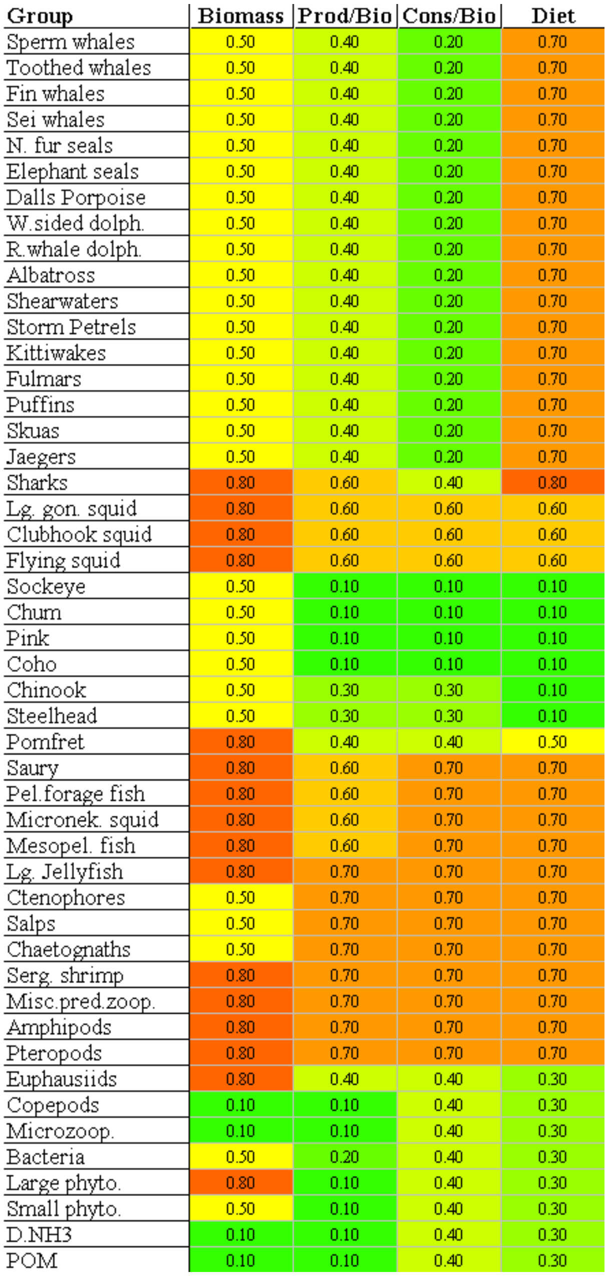
(*) See Appendix A text under indicated species for details.

Table B4 Data quality as determined by data pedigree method (Table A1).

Values indicate range as +/- proportion of point estimate used in ECOPATH model. Colours highlight range from poor (red, range ~ 0.8) to acceptable (yellow, range ~ 0.5) and excellent (green, range ~ 0.1).



Group	Biomass	Prod/Bio	Cons/Bio	Diet
Sperm whales	0.50	0.40	0.20	0.70
Toothed whales	0.50	0.40	0.20	0.70
Fin whales	0.50	0.40	0.20	0.70
Sei whales	0.50	0.40	0.20	0.70
Minke whales	0.50	0.40	0.20	0.70
N. fur seals	0.50	0.40	0.20	0.70
Dalls Porpoise	0.50	0.40	0.20	0.70
W.sided dolph.	0.50	0.40	0.20	0.70
R.whale dolph.	0.50	0.40	0.20	0.70
Common dolph.	0.50	0.40	0.20	0.70
Albatross	0.50	0.40	0.20	0.70
Shearwaters	0.50	0.40	0.20	0.70
Storm Petrels	0.50	0.40	0.20	0.70
Kittiwakes	0.50	0.40	0.20	0.70
Fulmars	0.50	0.40	0.20	0.70
Puffins	0.50	0.40	0.20	0.70
Skuas	0.50	0.40	0.20	0.70
Jaegers	0.50	0.40	0.20	0.70
Sharks	0.80	0.60	0.40	0.80
Lg. gon. squid	0.80	0.60	0.60	0.60
Clubhook squid	0.50	0.60	0.60	0.60
Flying squid	0.50	0.60	0.60	0.60
Sockeye	0.50	0.10	0.10	0.10
Chum	0.50	0.10	0.10	0.10
Pink	0.50	0.10	0.10	0.10
Coho	0.50	0.10	0.10	0.10
Chinook	0.50	0.30	0.30	0.30
Steelhead	0.50	0.30	0.30	0.30
Pomfret	0.50	0.40	0.40	0.50
Saury	0.50	0.40	0.70	0.70
Japan. anchovy	0.50	0.20	0.40	0.50
Pacific sardine	0.50	0.20	0.40	0.50
Pel. forage fis	0.80	0.60	0.70	0.70
Micron. squid	0.80	0.60	0.70	0.70
Mesopel. fish	0.80	0.60	0.70	0.70
Lg. Jellyfish	0.80	0.70	0.70	0.70
Ctenophores	0.50	0.70	0.70	0.70
Salps	0.50	0.70	0.70	0.70
Chaetognaths	0.50	0.70	0.70	0.70
Serg. shrimp	0.80	0.70	0.70	0.70
Misc. pred. zoo	0.80	0.70	0.70	0.70
Amphipods	0.80	0.70	0.70	0.70
Pteropods	0.80	0.70	0.70	0.70
Euphausiids	0.80	0.40	0.60	0.50
Copepods	0.80	0.40	0.60	0.50
Microzoop.	0.50	0.40	0.60	0.50
Bacteria	0.50	0.40	0.60	0.50
Large phyto.	0.50	0.40	0.60	0.50
Small phyto.	0.50	0.40	0.60	0.50
D.NH3	0.50	0.40	0.60	0.50
POM	0.50	0.40	0.60	0.50



Group	Biomass	Prod/Bio	Cons/Bio	Diet
Sperm whales	0.50	0.40	0.20	0.70
Toothed whales	0.50	0.40	0.20	0.70
Fin whales	0.50	0.40	0.20	0.70
Sei whales	0.50	0.40	0.20	0.70
N. fur seals	0.50	0.40	0.20	0.70
Elephant seals	0.50	0.40	0.20	0.70
Dalls Porpoise	0.50	0.40	0.20	0.70
W.sided dolph.	0.50	0.40	0.20	0.70
R.whale dolph.	0.50	0.40	0.20	0.70
Albatross	0.50	0.40	0.20	0.70
Shearwaters	0.50	0.40	0.20	0.70
Storm Petrels	0.50	0.40	0.20	0.70
Kittiwakes	0.50	0.40	0.20	0.70
Fulmars	0.50	0.40	0.20	0.70
Puffins	0.50	0.40	0.20	0.70
Skuas	0.50	0.40	0.20	0.70
Jaegers	0.50	0.40	0.20	0.70
Sharks	0.80	0.60	0.40	0.80
Lg. gon. squid	0.80	0.60	0.60	0.60
Clubhook squid	0.80	0.60	0.60	0.60
Flying squid	0.80	0.60	0.60	0.60
Sockeye	0.50	0.10	0.10	0.10
Chum	0.50	0.10	0.10	0.10
Pink	0.50	0.10	0.10	0.10
Coho	0.50	0.10	0.10	0.10
Chinook	0.50	0.30	0.30	0.10
Steelhead	0.50	0.30	0.30	0.10
Pomfret	0.80	0.40	0.40	0.50
Saury	0.80	0.60	0.70	0.70
Pel.forage fish	0.80	0.60	0.70	0.70
Micronek. squid	0.80	0.60	0.70	0.70
Mesopel. fish	0.80	0.60	0.70	0.70
Lg. Jellyfish	0.80	0.70	0.70	0.70
Ctenophores	0.50	0.70	0.70	0.70
Salps	0.50	0.70	0.70	0.70
Chaetognaths	0.50	0.70	0.70	0.70
Serg. shrimp	0.80	0.70	0.70	0.70
Misc.pred.zoop.	0.80	0.70	0.70	0.70
Amphipods	0.80	0.70	0.70	0.70
Pteropods	0.80	0.70	0.70	0.70
Euphausiids	0.80	0.40	0.40	0.30
Copepods	0.10	0.10	0.40	0.30
Microzoop.	0.10	0.10	0.40	0.30
Bacteria	0.50	0.20	0.40	0.30
Large phyto.	0.80	0.10	0.40	0.30
Small phyto.	0.50	0.10	0.40	0.30
D.NH3	0.10	0.10	0.40	0.30
POM	0.10	0.10	0.40	0.30

Table B5 Parameters for the WSA ECOPATH model.

Shaded values were estimated by the model. Shown are: trophic level (TL), biomass (B, t/km^2), production/biomass (P/B, 1/year), consumption/biomass (Q/B, 1/year), ecotrophic efficiency (EE, proportion), growth efficiency (PC, proportion) biomass accumulation (BA t/km^2/year), unassimilated respiration (UnAss, proportion) and the proportion of detritus flowing to NH_3 and POM, respectively (proportions).

Group	TL	B	P/B	Q/B	EE	PC	BA	UnAss	DNH3	POM
Sperm whales	5.4	0.00093	0.0596	6.61	0	0.00902	0	0.2	0.5	0.5
Toothed whales	5.3	0.0002	0.0252	11.16	0	0.00226	0	0.2	0.5	0.5
Fin whales	4.3	0.02788	0.02	4.56	0.83384	0.00439	0	0.2	0.5	0.5
Sei whales	4.3	0.0059	0.02	6.15	0.83391	0.00325	0	0.2	0.5	0.5
Minke whales	4.4	0.001	0.02	7.78	0.83385	0.00257	0	0.2	0.5	0.5
N. fur seals	5.2	0.00025	0.235	39.03	0.0709	0.00602	0	0.2	0.5	0.5
Dalls porpoise	5.2	0.00599	0.1	27.47	0.16678	0.00364	0	0.2	0.5	0.5
W. sided dolph.	5.2	0.00396	0.14	25.83	0.11914	0.00542	0	0.2	0.5	0.5
R. whale dolph.	5.2	0.0039	0.16	24.14	0.10424	0.00663	0	0.2	0.5	0.5
Common dolph.	5.1	0.001	0.1	24.98	0.16677	0.004	0	0.2	0.5	0.5
Albatross	5.5	0.00155	0.05	81.59	0.33357	0.00061	0	0.2	0.5	0.5
Shearwaters	4.8	0.00124	0.1	100.13	0.16671	0.001	0	0.2	0.5	0.5
Storm petrels	4.7	0.00016	0.1	152.08	0.16651	0.00066	0	0.2	0.5	0.5
Kittiwakes	4.7	0.00012	0.1	123	0.16679	0.00081	0	0.2	0.5	0.5
Fulmars	5.1	0.00015	0.1	100.26	0.167	0.001	0	0.2	0.5	0.5
Puffins	4.8	0.00032	0.1	104.33	0.16672	0.00096	0	0.2	0.5	0.5
Skuas	4.9	0.00008	0.075	96.6	0.22327	0.00078	0	0.2	0.5	0.5
Jaegers	4.9	0.00006	0.075	96.6	0.22267	0.00078	0	0.2	0.5	0.5
Sharks	5.3	0.0247	0.2	10.95	0	0.01826	0	0.2	0.5	0.5
Lg. gon. squid	4.4	0.0472	2.555	7.3	0.60967	0.35	0	0.2	0.5	0.5
Clubhook squid	5.1	0.074	2.555	7.3	0.62916	0.35	0	0.2	0.5	0.5
Flying squid	5.1	0.022	2.555	6.205	0.91361	0.41176	0	0.2	0.5	0.5
Sockeye	4.4	0.0031	1.27	10.13	0.53851	0.12537	0	0.2	0.5	0.5
Chum	3.9	0.0152	1.93	14.51	0.35435	0.13301	0	0.2	0.5	0.5
Pink	4.1	0.1973	3.37	18.49	0.20294	0.18226	0	0.2	0.5	0.5
Coho	4.8	0.0058	2.47	16.55	0.27688	0.14924	0	0.2	0.5	0.5
Chinook	4.9	0.0039	0.8	5.33333	0.85488	0.15	0	0.2	0.5	0.5
Steelhead	4.8	0.0039	0.8	5.33333	0.85488	0.15	0	0.2	0.5	0.5
Pomfret	5	0.0531	0.75	3.75	0.91187	0.2	0	0.2	0.5	0.5
Saury	3.5	0.0473	1.6	7.9	0.77662	0.20253	0	0.2	0.5	0.5
Japan. anchovy	3.8	0.17585	1.5	5	0.5585	0.3	0	0.2	0.5	0.5
Pacific sardine	3.2	0.05	0.4	3	0.79211	0.13333	0	0.2	0.5	0.5
Pel. forage fish	4.1	0.35754	1.5	5	0.9	0.3	0	0.2	0.5	0.5
Micronek. squid	4.1	0.83651	3	15	0.9	0.2	0	0.2	0.5	0.5
Mesopel. fish	3.9	6.5	0.9	3	0.07373	0.3	0	0.2	0.5	0.5
Lg. jellyfish	3.7	0.469	3	10	0	0.3	0	0.2	0.5	0.5
Ctenophores	2.7	10	4	110	0.00392	0.03636	0	0.2	0.5	0.5
Salps	2.7	10	9	30	0.00174	0.3	0	0.2	0.5	0.5
Chaetognaths	3.5	25	2.555	12.045	0.12036	0.21212	0	0.2	0.5	0.5
Serg. shrimp	3.5	8.134	2.555	12.045	0.06295	0.21212	0	0.2	0.5	0.5
Misc. pred. zoop.	3.5	8.134	2.555	12.045	0.06768	0.21212	0	0.2	0.5	0.5
Amphipods	3.1	8.51	2.555	12.045	0.88585	0.21212	0	0.2	0.5	0.5
Pteropods	3.1	16.268	2.555	12.045	0.64871	0.21212	0	0.2	0.5	0.5
Euphausiids	3.1	40.67	2.555	12.045	0.67193	0.21212	0	0.2	0.5	0.5
Copepods	2.4	46.71	23.725	112.42	0.97288	0.21104	0	0.2	0.5	0.5
Microzoop.	2.3	46.71	48.91	233.235	0.98078	0.2097	0	0.2	0.5	0.5
Bacteria	2	164.023	18.45	25	0.9	0.738	0	0.2	0.5	0.5
Large phyto.	1	68.44435	42.34		0.9		0		0.5	0.5
Small phyto.	1	86.57507	129.575		0.9		0		0.5	0.5
DNH3	1				0.61500		0		0	0
POM	1				0.61500		0		0	0

Table B6 Parameters for the ESA ECOPATH model.

Shaded values were estimated by the model. Shown are: trophic level (TL), biomass (B, t/km^2), production/biomass (P/B, 1/year), consumption/biomass (Q/B, 1/year), ecotrophic efficiency (EE, proportion), growth efficiency (PC, proportion) biomass accumulation (BA t/km^2/year), unassimilated respiration (UnAss, proportion) and the proportion of detritus flowing to NH_3 and POM, respectively (proportions).

Group	TL	B	P/B	Q/B	EE	PC	BA	UnAss	DNH3	POM
Sperm whales	5.4	0.000929	0.0596	6.61	0	0.00902	0	0.2	0.5	0.5
Toothed whales	5.2	0.000028	0.0252	11.16	0	0.00226	0	0.2	0.5	0.5
Fin whales	4.1	0.027883	0.02	4.56	0.12912	0.00439	0	0.2	0.5	0.5
Sei whales	4.1	0.005902	0.02	6.15	0.1358	0.00325	0	0.2	0.5	0.5
N. fur seals	5.2	0.000246	0.235	39.03	0.01083	0.00602	0	0.2	0.5	0.5
Elephant seals	5.2	0.00043	0.368	11.08	0.00692	0.03321	0	0.2	0.5	0.5
Dalls porpoise	5.2	0.00598636	0.1	27.47	0.02546	0.00364	0	0.2	0.5	0.5
W. sided dolph.	5.2	0.00396248	0.14	25.83	0.01819	0.00542	0	0.2	0.5	0.5
R. whale dolph.	5.3	0.00389728	0.16	24.14	0.01592	0.00663	0	0.2	0.5	0.5
Albatross	5.9	0.00004	0.05	81.59	0.05043	0.00061	0	0.2	0.5	0.5
Shearwaters	4.7	0.0004	0.1	100.13	0.02547	0.001	0	0.2	0.5	0.5
Storm Petrels	4.6	0.000056	0.1	152.08	0.02546	0.00066	0	0.2	0.5	0.5
Kittiwakes	4.6	0.000052	0.1	123	0.02549	0.00081	0	0.2	0.5	0.5
Fulmars	4.9	0.000074	0.1	100.26	0.02557	0.001	0	0.2	0.5	0.5
Puffins	4.7	0.000058	0.1	104.33	0.02535	0.00096	0	0.2	0.5	0.5
Skuas	4.8	0.000054	0.075	96.6	0.0338	0.00078	0	0.2	0.5	0.5
Jaegers	4.8	0.000038	0.075	96.6	0.03388	0.00078	0	0.2	0.5	0.5
Sharks	5.4	0.05	0.2	10.95	0	0.01826	0	0.2	0.5	0.5
Lg. gon. squid	4.2	0.03	2.555	7.3	0.19453	0.35	0	0.2	0.5	0.5
Clubhook squid	4.9	0.012	2.555	7.3	0.19453	0.35	0	0.2	0.5	0.5
Flying squid	5.3	0.45	2.555	6.205	0.91095	0.41176	0	0.2	0.5	0.5
Sockeye	4.3	0.08965573	1.27	10.13	0.32249	0.12537	0	0.2	0.5	0.5
Chum	3.7	0.05413587	1.93	14.51	0.21221	0.13301	0	0.2	0.5	0.5
Pink	4.2	0.02326662	3.37	18.49	0.12153	0.18226	0	0.2	0.5	0.5
Coho	4.9	0.00445349	2.47	16.55	0.16581	0.14924	0	0.2	0.5	0.5
Chinook	4.9	0.00930315	0.8	5.33333	0.51195	0.15	0	0.2	0.5	0.5
Steelhead	4.9	0.0093	0.8	5.33333	0.51212	0.15	0	0.2	0.5	0.5
Pomfret	4.8	0.21	0.75	3.75000	0.54697	0.2	0	0.2	0.5	0.5
Saury	3.8	0.45	1.6	7.9	0.5545	0.20253	0	0.2	0.5	0.5
Pel.forage fish	3.9	0.92156	1.5	5	0.9	0.3	0	0.2	0.5	0.5
Micronek. squid	3.9	0.87135	3	15	0.9	0.2	0	0.2	0.5	0.5
Mesopel. fish	3.9	4.5	0.9	3	0.16002	0.3	0	0.2	0.5	0.5
Lg. jellyfish	3.6	4	3	10	0	0.3	0	0.2	0.5	0.5
Ctenophores	2.7	9.1	4	110	0.05269	0.03636	0	0.2	0.5	0.5
Salps	2.7	8	9	30	0.02371	0.3	0	0.2	0.5	0.5
Chaetognaths	3.5	6.6	2.555	12.045	0.27638	0.21212	0	0.2	0.5	0.5
Serg. shrimp	3.5	5	2.555	12.045	0.18813	0.21212	0	0.2	0.5	0.5
Misc.pred.zoop.	3.5	5.0688	2.555	12.045	0.18871	0.21212	0	0.2	0.5	0.5
Amphipods	3.1	10.1376	2.555	12.045	0.64429	0.21212	0	0.2	0.5	0.5
Pteropods	3.1	10.1376	2.555	12.045	0.53491	0.21212	0	0.2	0.5	0.5
Euphausiids	3.1	25.344	2.555	12.045	0.53934	0.21212	0	0.2	0.5	0.5
Copepods	2.4	34.848	23.725	112.42	0.88106	0.21104	0	0.2	0.5	0.5
Microzoop.	2.3	35	48.91	233.235	0.99619	0.2097	0	0.2	0.5	0.5
Bacteria	2	122.90310	18.45	25	0.9	0.738	0	0.2	0.5	0.5
Large phyto.	1	69.7	42.34		0.67337		0		0.5	0.5
Small phyto.	1	76	129.575		0.77256		0		0.5	0.5
DNH3	1				0.42757		0		0	0
POM	1				0.42757		0		0	0

Table B7 (1 of 5) Proportion by biomass of prey (rows) in the diets of predators (columns) for the WSA ECOPATH model.

Shaded cells show matrix diagonal

Group	**Sperm whales**	**Toothed whales**	**Fin whales**	**Sei whales**	**Minke whales**	**N. fur seals**	**Dalls Porpoise**	**W. sided dolph.**	**R. whale dolph.**	**Common dolph.**
Sperm whales										
Toothed whales										
Fin whales		0.20827								
Sei whales		0.04409								
Minke whales		0.00747								
N. fur seals		0.00184								
Dalls porpoise		0.04472								
W. sided dolph.		0.0296								
R. whale dolph.		0.02911								
Common dolph.		0.00747								
Albatross		0.01158								
Shearwaters		0.00924								
Storm petrels		0.00117								
Kittiwakes		0.00086								
Fulmars		0.00113								
Puffins		0.0024								
Skuas		0.0006								
Jaegers		0.00046								
Sharks										
Lg. gon. squid	0.1236	0.01648	0.00824	0.00824		0.04944	0.07416	0.0412	0.0824	0.04944
Clubhook squid	0.19378	0.02584	0.01292	0.01292		0.07751	0.11627	0.06459	0.12919	0.07751
Flying squid	0.05761	0.00768	0.00384	0.00384		0.02304	0.03457	0.0192	0.03841	0.02304
Sockeye	5.5E-05	0.00142	3.3E-05	3.3E-05		0.00262	0.00131	0.00437	0.00028	0.00175
Chum	0.00027	0.00694	0.00016	0.00016		0.01287	0.00644	0.02145	0.00139	0.00858
Pink	0.0035	0.09012	0.0021	0.0021		0.16706	0.08353	0.2784	0.01802	0.11137
Coho	0.0001	0.00265	6.2E-05	6.2E-05		0.00491	0.00246	0.00818	0.00053	0.00327
Chinook	6.9E-05	0.00178	4.2E-05	4.2E-05		0.0033	0.00165	0.0055	0.00036	0.0022
Steelhead	6.9E-05	0.00178	4.2E-05	4.2E-05		0.0033	0.00165	0.0055	0.00036	0.0022
Pomfret	0.00094	0.02425	0.00057	0.00057		0.04496	0.02248	0.07493	0.00485	0.02997
Saury	0.00084	0.02161	0.0005	0.0005		0.04005	0.02003	0.06674	0.00432	0.0267
Japan. anchovy	0.00312	0.08033	0.00187	0.00187	0.13666	0.11389	0.09111	0.06832	0.01607	0.04555
Pacific sardine	0.0003	0.00784	0.00018	0.00018	0.01334	0.01111	0.00889	0.00667	0.00157	0.00445
Pel. forage fish	0.125	0.261	0.075	0.075	0.15	0.146	0.11	0.11	0.052	0.064
Micron. squid	0.375	0.05	0.025	0.025		0.15	0.225	0.12498	0.25	0.15
Mesopel. fish	0.11529		0.06918	0.06918	0.05	0.15	0.2	0.09999	0.4	0.4
Lg. jellyfish										
Ctenophores										
Salps										
Chaetognaths			0.2349	0.2349	0.19086					
Serg. shrimp			0.03579	0.03579	0.02908					
Misc. pred. zoop			0.03579	0.03579	0.02908					
Amphipods			0.03745	0.03745	0.03042					
Pteropods			0.07158	0.07158	0.05816					
Euphausiids			0.17896	0.17896	0.1454					
Copepods			0.20553	0.20553	0.167					
Microzoop.										
Bacteria										
Large phyto.										
Small phyto.										
DNH3										
POM										

Table B7 (2 of 5) WSA diet matrix (continued).

Group	Albatross	Shearwaters	Storm Petrels	Kittiwakes	Fulmars	Puffins	Skuas	Jaegers	Sharks
Sperm whales									
Toothed whales									
Fin whales									
Sei whales									
Minke whales									
N. fur seals									
Dalls porpoise									
W. sided dolph.									
R. whale dolph.									
Common dolph.									
Albatross									
Shearwaters									
Storm petrels									
Kittiwakes									
Fulmars									
Puffins									
Skuas									
Jaegers									
Sharks									
Lg. gon. squid	0.197								0.07611
Clubhook squid	0.338								0.11933
Flying squid	0.065								0.03548
Sockeye									0.005
Chum									0.02451
Pink									0.31816
Coho									0.00935
Chinook									0.00629
Steelhead									0.00629
Pomfret									0.08563
Saury	0.01968	0.05413	0.00984	0.07873		0.07873	0.09841	0.09841	0.07627
Japan. anchovy	0.07318	0.20123	0.03659	0.2927		0.2927	0.36588	0.36588	
Pacific sardine	0.00714	0.01964	0.00357	0.02857		0.02857	0.03571	0.03571	
Pel. forage fish	0.1	0.275	0.05	0.4	0.04	0.4	0.5	0.5	0.122
Micron. squid	0.2	0.3	0.6		0.96	0.1			0.11554
Mesopel. fish									
Lg. jellyfish									
Ctenophores									
Salps									
Chaetognaths									
Serg. shrimp									
Misc. pred. zoop.									
Amphipods		0.01138	0.02276	0.01518		0.00759			
Pteropods		0.02176	0.04351	0.02901		0.0145			
Euphausiids		0.05439	0.10878	0.07252		0.03626			
Copepods		0.06247	0.12494	0.08329		0.04165			
Microzoop.									
Bacteria									
Large phyto.									
Small phyto.									
DNH3									
POM									

Table B7 (3 of 5) WSA diet matrix (continued).

Group	Lg. gon. squid	Clubhook squid	Flying squid	Sockeye	Chum	Pink	Coho	Chinook	Steelhead	Pomfret
Sperm whales										
Toothed whales										
Fin whales										
Sei whales										
Minke whales										
N. fur seals										
Dalls porpoise										
W. sided dolph.										
R. whale dolph.										
Common dolph.										
Albatross										
Shearwaters										
Storm petrels										
Kittiwakes										
Fulmars										
Puffins										
Skuas										
Jaegers										
Sharks										
Lg. gon. squid										
Clubhook squid										
Flying squid			0.15							
Sockeye										
Chum										
Pink										
Coho										
Chinook										
Steelhead										
Pomfret										
Saury			0.058							0.02
Japan. anchovy			0.14532							0.232
Pacific sardine			0.01418							0.03
Pel. forage fish	0.01	0.01	0.1595	0.025	0.01	0.075	0.121	0.011	0.201	
Micron. squid	0.33	0.99	0.368	0.36	0.02	0.14	0.539	0.749	0.4	0.6
Mesopel. fish			0.105	0.025	0.01	0.075	0.12	0.01	0.2	0.1
Lg. jellyfish										
Ctenophores					0.19					
Salps					0.19					
Chaetognaths	0.19379									0.0014
Serg. shrimp	0.02953									0.0009
Misc. pred. zoop.	0.02953			0.04	0.03	0.02				0.001
Amphipods	0.03089			0.18	0.09	0.19	0.02			0.005
Pteropods	0.05906			0.01	0.3	0.02	0.01			0.005
Euphausiids	0.14764			0.19	0.11	0.17	0.18	0.23	0.199	0.005
Copepods	0.16956			0.17	0.05	0.31	0.01			
Microzoop.										
Bacteria										
Large phyto.										
Small phyto.										
DNH3										
POM										

Table B7 (4 of 5) WSA diet matrix (continued).

Group	Saury	Japan. anchovy	Pacific sardine	Pel. forage fish	Micron. squid	Mesopel. fish	Lg. jellyfish	Ctenophores	Salps
Sperm whales									
Toothed whales									
Fin whales									
Sei whales									
Minke whales									
N. fur seals									
Dalls porpoise									
W. sided dolph.									
R. whale dolph.									
Common dolph.									
Albatross									
Shearwaters									
Storm petrels									
Kittiwakes									
Fulmars									
Puffins									
Skuas									
Jaegers									
Sharks									
Lg. gon. squid									
Clubhook squid									
Flying squid									
Sockeye									
Chum									
Pink									
Coho									
Chinook									
Steelhead									
Pomfret									
Saury									
Japan. anchovy									
Pacific sardine									
Pel. forage fish									
Micron. squid					0.05				
Mesopel. fish									
Lg. jellyfish									
Ctenophores							0.0245		
Salps							0.0245		
Chaetognaths		0.02		0.29363	0.27895	0.15	0.13079		
Serg. shrimp				0.04474	0.0425	0.03	0.01993		
Misc. pred. zoop.		0.02		0.04474	0.0425	0.03	0.01993		
Amphipods	0.05	0.17	0.03901	0.04681	0.04447	0.24	0.02085		
Pteropods	0.05	0.03	0.07457	0.08948	0.085	0.031	0.03986		
Euphausiids	0.07	0.4	0.18642	0.22369	0.21251	0.171	0.09964		
Copepods	0.83	0.36	0.4	0.25692	0.24407	0.348	0.62	0.25	0.25
Microzoop.			0.02					0.25	0.25
Bacteria									
Large phyto.			0.14					0.25	0.25
Small phyto.			0.14					0.25	0.25
DNH3									
POM									

Table B7 (5 of 5) WSA diet matrix (continued).

Group	Chaetognaths	Serg. shrimp	Misc. pred. zoop.	Amphipods	Pteropods	Euphausiids	Copepods	Microzoop.	Bacteria
Sperm whales									
Toothed whales									
Fin whales									
Sei whales									
Minke whales									
N. fur seals									
Dalls porpoise									
W. sided dolph.									
R. whale dolph.									
Common dolph.									
Albatross									
Shearwaters									
Storm petrels									
Kittiwakes									
Fulmars									
Puffins									
Skuas									
Jaegers									
Sharks									
Lg. gon. squid									
Clubhook squid									
Flying squid									
Sockeye									
Chum									
Pink									
Coho									
Chinook									
Steelhead									
Pomfret									
Saury									
Japan. anchovy									
Pacific sardine									
Pel. forage fish									
Micron. squid									
Mesopel. fish									
Lg. jellyfish									
Ctenophores									
Salps									
Chaetognaths									
Serg. shrimp									
Misc. pred. zoop.									
Amphipods	0.02601	0.02601	0.02601						
Pteropods	0.04971	0.04971	0.04971						
Euphausiids	0.12428	0.12428	0.12428						
Copepods	0.8	0.8	0.8	0.4	0.4	0.4			
Microzoop.				0.4	0.4	0.4	0.3		
Bacteria								0.25	
Large phyto.				0.2	0.2	0.2	0.4		
Small phyto.							0.3	0.75	
DNH3									0.5
POM									0.5

Table B8 (1 of 5) Proportion by biomass of prey (rows) in the diets of predators (columns) for the ESA ECOPATH model.

Shaded cells show matrix diagonal.

Diets	**Sperm whales**	**Toothed whales**	**Fin whales**	**Sei whales**	**N. fur seals**	**Elephant seals**	**Dalls Porpoise**	**W. sided dolph.**	**R. whale dolph.**
Sperm whales									
Toothed whales									
Fin whales		0.22725							
Sei whales		0.04811							
N. fur seals		0.002							
Elephant seals		0.00351							
Dalls porpoise		0.04879							
W. sided dolph.		0.03229							
R. whale dolph.		0.03176							
Albatross		0.00032							
Shearwaters		0.00326							
Storm petrels		0.00046							
Kittiwakes		0.00042							
Fulmars		0.00061							
Puffins		0.00047							
Skuas		0.00044							
Jaegers		0.00031							
Sharks									
Lg. gon. squid	0.02287	0.00305	0.001524	0.001524	0.00915	0.0122	0.01372	0.00762	0.01524
Clubhook squid	0.00915	0.00122	0.000609	0.000609	0.00366	0.00488	0.00549	0.00305	0.0061
Flying squid	0.34299	0.04573	0.022866	0.022866	0.1372	0.18293	0.20579	0.11433	0.22866
Sockeye	0.00208	0.0249	0.001245	0.001245	0.02988	0.01132	0.01494	0.03984	0.00498
Chum	0.00125	0.01504	0.000752	0.000752	0.01804	0.00683	0.00902	0.02406	0.00301
Pink	0.00054	0.00646	0.000323	0.000323	0.00775	0.00294	0.00388	0.01034	0.00129
Coho	0.0001	0.00124	6.185E-5	6.185E-5	0.00148	0.00056	0.00074	0.00198	0.00025
Chinook	0.00022	0.00258	0.000129	0.000129	0.0031	0.00117	0.00155	0.00413	0.00052
Steelhead	0.00022	0.00258	0.000129	0.000129	0.0031	0.00117	0.00155	0.00413	0.00052
Pomfret	0.00486	0.05833	0.002917	0.002917	0.06999	0.056	0.035	0.09332	0.01167
Saury	0.01042	0.12498	0.006250	0.006250	0.14998	0.12	0.07499	0.19997	0.025
Pel.forage fish	0.126	0.264	0.076	0.076	0.267	0.2	0.208	0.172	0.053
Micronek. squid	0.375	0.05	0.025	0.025	0.15	0.4	0.225	0.225	0.25
Mesopel. fish	0.10416		0.062499	0.062499	0.15		0.2	0.1	0.4
Lg. jellyfish									
Ctenophores									
Salps									
Chaetognaths			0.054357	0.054357					
Serg. shrimp			0.041179	0.041179					
Misc.pred.zoop.			0.041746	0.041746					
Amphipods			0.083492	0.083492					
Pteropods			0.083492	0.083492					
Euphausiids			0.20873	0.20873					
Copepods			0.287004	0.287004					
Microzoop.									
Bacteria									
Large phyto.									
Small phyto.									
DNH3									
POM									

Table B8 (2 of 5) ESA diet matrix (continued).

Diets	Albatross	Shearwaters	Storm petrels	Kittiwakes	Fulmars	Puffins	Skuas	Jaegers	Sharks
Sperm whales									
Toothed whales									
Fin whales									
Sei whales									
N. fur seals									
Elephant seals									
Dalls porpoise									
W. sided dolph.									
R. whale dolph.									
Albatross									
Shearwaters									
Storm petrels									
Kittiwakes									
Fulmars									
Puffins									
Skuas									
Jaegers									
Sharks									
Lg. gon. squid	0.04573								0.01782
Clubhook squid	0.01829								0.00713
Flying squid	0.68598								0.26724
Sockeye									0.05324
Chum									0.03215
Pink									0.01382
Coho									0.00264
Chinook									0.00552
Steelhead									0.00552
Pomfret									0.12471
Saury	0.1	0.275	0.05	0.4		0.4	0.5	0.5	0.26724
Pel.forage fish	0.1	0.275	0.05	0.4	0.04	0.4	0.5	0.5	0.103
Micronek. squid	0.05	0.3	0.6		0.96	0.1			0.1
Mesopel. fish									
Lg. jellyfish									
Ctenophores									
Salps									
Chaetognaths									
Serg. shrimp									
Misc.pred.zoop.									
Amphipods		0.0189	0.0378	0.0252		0.0126			
Pteropods		0.0189	0.0378	0.0252		0.0126			
Euphausiids		0.04724	0.09449	0.06299		0.0315			
Copepods		0.06496	0.12992	0.08661		0.04331			
Microzoop.									
Bacteria									
Large phyto.									
Small phyto.									
DNH3									
POM									

Table B8 (3 of 5) ESA diet matrix (continued).

Diets	Lg. gon. squid	Clubhook squid	Flying squid	Sockeye	Chum	Pink	Coho	Chinook	Steelhead	Pomfret
Sperm whales										
Toothed whales										
Fin whales										
Sei whales										
N. fur seals										
Elephant seals										
Dalls porpoise										
W. sided dolph.										
R. whale dolph.										
Albatross										
Shearwaters										
Storm Petrels										
Kittiwakes										
Fulmars										
Puffins										
Skuas										
Jaegers										
Sharks										
Lg. gon. squid										
Clubhook squid										
Flying squid			0.295							
Sockeye										
Chum										
Pink										
Coho										
Chinook										
Steelhead										
Pomfret										
Saury			0.058							0.04
Pel.forage fish	0.01	0.01	0.319	0.10982	0.00802	0.068096	0.367206	0.367206	0.367206	
Micronek. squid	0.33	0.99	0.223	0.07968	0.03929	0.034823	0.205691	0.205691	0.205691	0.75
Mesopel. fish			0.105	0.10982	0.00802	0.068096	0.367206	0.367206	0.367206	0.08
Lg. jellyfish										
Ctenophores				0.01609	0.20285	0.003826	7.305E-5	7.305E-5	7.305E-5	
Salps				0.01609	0.20285	0.003826	7.305E-5	7.305E-5	7.305E-5	
Chaetognaths	0.04484				0.00043					0.01
Serg. shrimp	0.03397									0.01
Misc.pred.zoop.	0.03444			0.00171	0.01474	8.64E-06				0.01
Amphipods	0.06888			0.29328	0.07363	0.321620	0.008047	0.008047	0.008047	0.03
Pteropods	0.06888			0.23976	0.06719	0.440933	0.046230	0.046230	0.046230	0.01
Euphausiids	0.1722			0.10058	0.08491	0.038951	0.002736	0.002736	0.002736	0.05
Copepods	0.23678			0.03318	0.29806	0.019816	0.002736	0.002736	0.002736	0.01
Microzoop.										
Bacteria										
Large phyto.										
Small phyto.										
DNH3										
POM										

Table B8 (4 of 5) ESA diet matrix (continued).

Diets	Saury	Pel. forage fish	Micronek. squid	Mesopel. fish	Lg. Jellyfish	Ctenophores	Salps
Sperm whales							
Toothed whales							
Fin whales							
Sei whales							
N. fur seals							
Elephant seals							
Dalls porpoise							
W. sided dolph.							
R. whale dolph.							
Albatross							
Shearwaters							
Storm petrels							
Kittiwakes							
Fulmars							
Puffins							
Skuas							
Jaegers							
Sharks							
Lg. gon. squid							
Clubhook squid							
Flying squid							
Sockeye							
Chum							
Pink							
Coho							
Chinook							
Steelhead							
Pomfret							
Saury							
Pel.forage fish							
Micronek. squid			0.05				
Mesopel. fish							
Lg. jellyfish							
Ctenophores					0.04356		
Salps					0.03829		
Chaetognaths	0.05298	0.06795	0.06455	0.15	0.03159		
Serg. shrimp	0.04014	0.05147	0.0489	0.03	0.02393		
Misc.pred.zoop.	0.04069	0.05218	0.04957	0.03	0.02426		
Amphipods	0.08138	0.10437	0.09915	0.24	0.04852		
Pteropods	0.08138	0.10437	0.09915	0.031	0.04852		
Euphausiids	0.20344	0.26091	0.24787	0.171	0.12131		
Copepods	0.5	0.35875	0.34082	0.348	0.62	0.25	0.25
Microzoop.						0.25	0.25
Bacteria							
Large phyto.						0.25	0.25
Small phyto.						0.25	0.25
DNH3							
POM							

Table B8 (5 of 5) ESA diet matrix (continued).

Diets	Chaetognaths	Serg. shrimp	Misc.pred.zoop.	Amphipods	Pteropods	Euphausiids	Copepods	Microzoop.	Bacteria
Sperm whales									
Toothed whales									
Fin whales									
Sei whales									
N. fur seals									
Elephant seals									
Dalls porpoise									
W. sided dolph.									
R. whale dolph.									
Albatross									
Shearwaters									
Storm petrels									
Kittiwakes									
Fulmars									
Puffins									
Skuas									
Jaegers									
Sharks									
Lg. gon. squid									
Clubhook squid									
Flying squid									
Sockeye									
Chum									
Pink									
Coho									
Chinook									
Steelhead									
Pomfret									
Saury									
Pel.forage fish									
Micronek. squid									
Mesopel. fish									
Lg. jellyfish									
Ctenophores									
Salps									
Chaetognaths									
Serg. shrimp									
Misc.pred.zoop.									
Amphipods	0.04444	0.04444	0.04444						
Pteropods	0.04444	0.04444	0.04444						
Euphausiids	0.11111	0.11111	0.11111						
Copepods	0.8	0.8	0.8	0.4	0.4	0.4			
Microzoop.				0.4	0.4	0.4	0.3		
Bacteria								0.25	
Large phyto.				0.2	0.2	0.2	0.4		
Small phyto.							0.3	0.75	
DNH3									0.5
POM									0.5

APPENDIX C: BASS WORKSHOP ON *THE DEVELOPMENT OF A CONCEPTUAL MODEL OF THE SUBARCTIC PACIFIC BASIN ECOSYSTEMS*

At the PICES Sixth Annual Meeting, the BASS Task Team sponsored a symposium on the ecosystem dynamics of the Eastern and Western Subarctic Gyres. The purpose was to bring together available information on the two gyres in a comparative framework. Topics included: 1) ocean responses to climate forcing, 2) nutrients and primary production, 3) structure of the lower trophic levels, the mesozooplankton communities, and the epipelagic nekton, 4) the role of midwater fishes, and 5) the importance of these areas to marine birds and mammals. Papers presented at the meeting were published in 1999, in a special issue of *Progress in Oceanography* (Vol. 43, No. 2-4) entitled *Ecosystem Dynamics in the Eastern and Western Gyres of the Subarctic Pacific* (Guest Editors: R.J. Beamish, S. Kim, M. Terazaki and W.S. Wooster). The following "key" research problems were pointed out during discussion at the symposium: 1) the need for information on short-term or seasonal changes in the mixed layer, 2) how climate-variation may be changing the stability of the water column, 3) the role of iron: understanding transport mechanisms, 4) community dynamics and the need for small scale diet studies, and 5) biomass estimates of some "key" species.

Members of the BASS Task Team felt that the next step should be to develop a conceptual model of the subarctic Pacific basin ecosystems and begin to examine appropriate models. A 2-day BASS Workshop on this topic was convened prior to the PICES Ninth Annual Meeting in Hakodate, Japan (October 20-21, 2000). The objective of this workshop was to identify appropriate approaches, not only modelling approaches but also how to develop studies which will answer some of the questions.

At the workshop, a number of presentations were made on ecosystem models that participants had used (see Endnote C1 for attendance). These models were reviewed and discussed with respect to their utility for gyre systems. Trophodynamic linkages that were likely to be common, as well as those that were model-specific, were identified, and shortfalls were highlighted. Discussions included identifying data groups and potential data sources, incorporating climate and oceanographic changes in models, and linking gyre models to coastal area models. Extended abstracts of papers given at the workshop are published in PICES Scientific Report No. 17, 2001.

As the PICES CCCC Program enters its synthesis phase, modelling will play a more prominent role in CCCC activity. Participants recommended the BASS and MODEL Task Teams to convene a joint workshop to examine the feasibility of using the ECOPATH/ECOSYSTEM modelling approach as a means to organize our understanding of the marine ecosystems of the subarctic gyres. Specific objectives are to:

- synthesize all trophic level data in a common format;
- examine trophic relations in both gyres using ECOPATH/ECOSIM/ECOSPAC; and
- examine methods of incorporating the PICES NEMURO lower trophic level model into the analysis.

Participants recommended that collaboration and synthesis of the data into a common format take place prior to the workshop. Gordon McFarlane would co-ordinate this issue for North America and Andrei Krovnin and Akihiko Yatsu for Asia. Kerim Aydin will synthesize the data into the ECOPATH format. If possible, the workshop should be held in conjunction with the PICES Census of Marine Life Workshop to be convened March 7-9, 2001, in Honolulu. Locating the venue in Hawaii at this time is seen as a cost-effective way to involve workshop participants from both sides of the Pacific and would lead to a more balanced scientific representation from the nations of the North Pacific.

Endnote C1

Participation List

Canada
- Gordon A. McFarlane (convenor)
- Richard J. Beamish (convenor)
- Jacquelynne R. King
- James Irvine
- Steven J.D. Martell

China
- Ling Tong

Japan
- Akihiko Yatsu (convenor)
- Masahide Kaeriyama
- Yukimasa Ishida
- Takashige Sugimoto

Russia
- Andrei S. Krovnin (convenor)
- Victor Tsiger

U.S.A.
- Jeffrey J. Polovina
- Kerim Y. Aydin
- Albert J. Hermann
- Dale B. Haidvogel

APPENDIX D: BASS/MODEL WORKSHOP ON *HIGHER TROPHIC LEVEL MODELING*

The PICES BASS/MODEL Workshop to examine the feasibility of using ECOPATH/ECOSIM as a tool to model higher trophic level components of the Subarctic gyre systems, was held March 5-6, 2001, in Honolulu, U.S.A. The participants are listed in Endnote D1. Objectives of the workshop were to:

- synthesize all trophic level data in a common format;
- examine trophic relationships in both the Eastern Subarctic Gyre (ESA) and Western Subarctic Gyre (WSA) using ECOPATH/ECOSIM; and
- examine methods of incorporating the PICES NEMURO lower trophic level model into the analysis.

Overview of ECOPATH/ECOSIM

Kerim Aydin gave a brief overview of ECOPATH/ECOSIM. An ECOPATH model creates a quantitative food web using the principle of mass-balance. Each "box" in an ECOPATH model may represent a single species or a species guild. The units may vary from model to model. The following quantities were used as input for the initial ESA and WSA models:

- Biomass (t/km^2)
- Production per unit biomass (year^{-1})
- Consumption per unit biomass (year^{-1})
- Fisheries catch (t/km^2/year)
- Diet matrix for each predator (% of diet by weight, shown here as trophic level)

From this information, ECOPATH calculates an "Ecotrophic Efficiency" for each box, which represents the ratio between the production of each box and the amount of biomass "demanded" by the predators and fisheries on a box. An Ecotrophic Efficiency greater than 1 indicates that, according to the model, more is being demanded of a box than is being produced. This quantity is a useful diagnostic tool for examining the quality of data between boxes.

The inputs used for each box in the ESA and WSA models are shown in Tables D1 and D2. No fishing was included in the model as befits the subarctic North Pacific in the early 1990s. These values represent the model as it existed at the end of the workshop and incorporate adjustments made over the course of the workshop. This model was "mass-balanced" in that all Ecotrophic Efficiency values were less than 1.

Data quality was categorized as follows (Tables D1 and D2):

- Acceptable: generally considered to be "reasonable" estimates for model use;
- General: consistent with known patterns for the species in question, but may be improved through re-examination of existing data, or further consultation with other researchers;
- Poor: little information for these species, or the information available to the workshop was known to be potentially inaccurate (collected outside the model domain);
- N/A: no data available; estimates were derived from ECOPATH model.

There is considerable room for improving the estimates, and every attempt should be made to upgrade most of the estimates from "General" to "Acceptable" before the model is considered "functional". It was felt that much improvement in data quality could be accomplished by re-reviewing existing data using this preliminary model as a framework. Final data quality is a combination of two properties: the quality of each datum, and the sensitivity of the model to that input.

Table D1 Biomass estimates used in the ESA/WSA ECOPATH models.

Group	Eastern Gyre t	t/km^2	Western Gyre t	t/km^2	Data Quality
Sperm whales	3,364	0.000929	2,014	0.000929	Acceptable
Toothed whales (orca)	100	0.000028	2,168	0.001000	General
Fin	100,992	0.027883	60,450	0.027883	Poor
Sei	21,379	0.005902	12,796	0.005902	Not. Avail.
Minke	-	-	2,168	0.001000	
Northern fur seals	890	0.000246	533	0.000246	
Elephant seals	1,558	0.000430	-	-	
Dall's porpoise	21,683	0.005986	12,978	0.005986	
Pacific white sided dolphin	14,352	0.003962	8,591	0.003962	
Northern right whale dolphin	14,116	0.003897	8,449	0.003897	
Common dolphin	-	-	2,168	0.001000	
Albatross	143	0.000040	3,361	0.001550	
Shearwaters	1,449	0.000400	2,681	0.001237	
Storm petrels	203	0.000056	340	0.000157	
Kittiwakes	189	0.000052	249	0.000115	
Fulmars	269	0.000074	328	0.000151	
Puffins	209	0.000058	698	0.000322	
Skuas	195	0.000054	174	0.000080	
Jaegers	137	0.000038	132	0.000061	
Sharks (Blue & Salmon)	181,100	0.050000	53,550	0.024700	
Dogfish	181,100	0.050000	53,550	0.024700	
Daggertooth	18,110	0.005000	2,003	0.000924	
Large gonatid squid	108,660	0.030000	102,330	0.047200	
Clubhook squid	43,464	0.012000	160,432	0.074000	
Flying squid	1,629,900	0.450000	47,696	0.022000	
Sockeye	324,733	0.089656	6,721	0.003100	
Chum	196,080	0.054136	32,954	0.015200	
Pink	84,272	0.023267	427,746	0.197300	
Coho	16,131	0.004453	12,574	0.005800	
Chinook	33,696	0.009303	8,455	0.003900	
Steelhead	33,696	0.009303	8,455	0.003900	
Pomfret	760,620	0.210000	115,121	0.053100	
Saury	1,629,900	0.450000	102,546	0.047300	
Japanese anchovy	-	-	381,250	0.175853	
Pacific sardine	-	-	37,207	0.017162	
Misc. forage (Stickleback)	3,763,258	1.039000	897,552	0.414000	
Micronektonic squid	3,462,632	0.956000	1,903,504	0.878000	
Mesopelagic fish	16,299,000	4.500000	14,092,000	6.500000	
Lg. jellyfish	14,488,000	4.000000	1,017,264	0.469217	
Ctenophores	32,960,200	9.100000	21,680,000	10.000000	
Salps	28,976,000	8.000000	21,680,000	10.000000	
Chaetognaths	23,905,200	6.600000	115,737,135	53.384287	
Sergestid shrimp	18,110,000	5.000000	17,634,512	8.134000	
Oth. Lg. Zoop. (Larv., Poly)	18,359,194	5.068800	17,634,512	8.134000	
Amphipods (most. Hyp)	36,718,387	10.137600	18,449,680	8.510000	
Pteropods	36,718,387	10.137600	35,269,024	16.268000	
Euphausiids	91,795,968	25.344000	88,172,560	40.670000	
Copepods	126,219,456	34.848000	101,267,280	46.710000	
Microzooplankton	126,219,456	34.848000	49,232,701	22.708810	
Bacteria	75,880,000	35.000000	355,601,864	164.023000	
Large phytoplankton	252,453,400	69.700000	148,386,592	68.444000	
Small phytoplankton	275,272,000	76.000000	187,694,600	86.575000	
DNH3	-	-	-	-	
DNO3	-	-	-	-	
PON	-	-	-	-	

Table D2 Life history and diet parameters of the ESA and WSA ECOPATH models.

Group	Prod./Bio. (year^{-1})	Cons./Bio. (year^{-1})	Trophic Level East	Trophic Level West	Data Quality
Sperm whales	0.060	6.608	5.4	5.4	Acceptable
Toothed whales (orca)	0.025	11.157	5.3	5.3	General
Fin	0.020	4.562	4.1	4.3	Poor
Sei	0.020	6.152	4.1	4.3	Not. Avail.
Minke	0.020	7.782	-	4.4	
Northern fur seals	0.235	39.030	5.2	5.2	
Elephant seals	0.368	11.078	5.2	-	
Dall's porpoise	0.100	27.471	5.3	5.2	
Pacific white sided dolphin	0.140	25.828	5.2	5.2	
Northern right whale dolphin	0.160	24.138	5.3	5.2	
Common dolphin	0.100	24.983	-	5.2	
Albatross	0.050	81.586	5.9	5.5	
Shearwaters	0.100	100.127	4.7	4.8	
Storm petrels	0.100	152.083	4.6	4.7	
Kittiwakes	0.100	123.000	4.6	4.7	
Fulmars	0.100	100.256	4.9	5.1	
Puffins	0.100	104.333	4.7	4.8	
Skuas	0.075	96.600	4.8	4.9	
Jaegers	0.075	96.600	4.8	4.9	
Sharks (Blue & Salmon)	0.200	10.950	5.4	5.3	
Dogfish	0.200	10.950	4.9	5.0	
Daggertooth	1.000	10.000	5.0	5.0	
Large gonatid squid	2.555	7.300	4.2	4.4	
Clubhook squid	2.555	7.300	4.9	5.1	
Flying squid	2.555	6.205	5.3	5.1	
Sockeye	1.265	10.132	4.3	4.4	
Chum	1.932	14.507	3.7	3.9	
Pink	3.373	18.494	4.2	4.1	
Coho	2.472	16.548	4.9	4.8	
Chinook	0.800	5.333	4.9	4.9	
Steelhead	0.800	5.333	4.9	4.8	
Pomfret	0.750	3.750	4.8	5.0	
Saury	1.600	7.900	3.8	3.5	
Japanese anchovy	1.500	5.000	-	3.8	
Pacific sardine	0.400	3.000	-	3.2	
Misc. forage (Stickleback)	1.500	5.000	3.9	4.1	
Micronektonic squid	3.000	15.000	3.9	4.1	
Mesopelagic fish	0.900	3.000	3.9	3.9	
Lg. Jellyfish	3.000	10.000	3.6	3.7	
Ctenophores	4.000	110.000	2.7	2.7	
Salps	9.000	30.000	2.7	2.7	
Chaetognaths	2.555	12.045	3.5	3.5	
Sergestid shrimp	2.555	12.045	3.5	3.5	
Oth. Lg. Zoop. (Larv., Poly)	2.555	12.045	3.5	3.5	
Amphipods (most. Hyp)	2.555	12.045	3.1	3.1	
Pteropods	2.555	12.045	3.1	3.1	
Euphausiids	2.555	12.045	3.1	3.1	
Copepods	23.725	112.420	2.4	2.4	
Microzooplankton	48.910	233.235	2.3	2.3	
Bacteria	18.450	25.000	2.0	2.0	
Large phytoplankton	42.340	-	1.0	1.0	
Small phytoplankton	129.575	-	1.0	1.0	
DNH3	-	-	1.0	1.0	
DNO3	-	-	1.0	1.0	
PON	-	-	1.0	1.0	

The boundary areas selected for the two ECOPATH models coincide with PICES' definitions of the Western Subarctic and the Eastern Subarctic, namely the regions above 45°N, bounded by the shelf breaks and divided by 165°W. The total areas for the WSA and the ESA are 2,168,000 km^2 and 3,622,000 km^2 respectively.

Overview of NEMURO

Bernard Megrey gave a brief review of the NEMURO lower trophic level model focusing on recent improvement to NEMURO. Topics included the addition of diagnostic calculations, validation to Station P data, addition of zooplankton vertical migration, examining the effects of including a microbial loop approximation, and performing a sensitivity analysis and data assimilation.

Diagnostic calculations

In order to perform regional comparisons of model performance, several diagnostic calculations were added to NEMURO. These included production/ biomass (P/B) ratios for phytoplankton and zooplankton, food consumption/biomass (C/B) ratios for small, large and predatory zooplankton, and ecotrophic efficiency (a measure of how much primary production transfers up the food web to the zooplankton species and ultimately to higher trophic level species) calculations.

Comparison of model output and measurements

NEMURO was parameterized for Ocean Station P and output was compared to data collected from that site. Results were favourable. The C/B and P/C ratios are both reasonable. Annual primary production from the model (149 gC/m^2/yr) is only 6% higher than the best current estimate (140 gC/m^2/yr). An f-ratio (assuming that the production of the large phytoplankton is primarily fuelled by "new" nitrogen was 0.23.

Vertical migration

At Station P, during spring, the large zooplankton component (ZP) should be dominated by *Calanus/Neocalanus* spp. which undergo a strong ontogenetic vertical migration. Thus, the model population should increase in biomass in the early spring independently of food availability/grazing. Later in the year, the population should decrease by some amount to simulate the descent of the large zooplankton to deeper depths. NEMURO was modified to reflect this situation.

Results without migration of predatory zooplankton (ZP) show a large diatom bloom around day 73. The prevailing view is that there is no spring bloom at Station P. Thus the bloom is an artifact of the "box" nature of the model. With ZP migration, values of PL drop by a factor of 2 and generate more reasonable diagnostics. The estimates of Ecotropic Efficiency are not significantly affected.

Microbial loop approximation

Climate change patterns that produce warmer water and greater rainfall enhance stratification of the water column. This lowers primary production by reducing or eliminating the mixing that is needed to propel nutrients into the surface photic zone. Data from Station P show decreased nitrogen and reduced primary production with warmer temperatures over a period of about 25 years. These conditions change the quantity of phytoplankton as well as the phytoplankton assemblage. With high nutrient concentrations, large phytoplankton that are eaten by copepods dominate the phytoplankton assemblage (*i.e.* the pelagic food chain). This energy is transferred to larval and adult planktivorous fishes. With low nutrient concentrations, the phytoplankton assemblage is altered, with the microbial loop food chain being favoured over the pelagic food chain. Small nanoplankton are favoured, which are eaten by protozoans like rotifers, with secondary production generally becoming unavailable to fish.

A pragmatic approach to including the microbial food web is through the variable BetaZS (growth efficiency of Small Zooplankton, ZS)

$$\text{BetaZS} = 0.3\ (1+ \text{PhySn}/(\text{PhySn}+\text{PhyLn}))$$

This means that the gross growth efficiency of the small zooplankton can vary between 0.09 and 0.3, and will probably average about 0.16 over the year at Station P. For the base model run, a constant BetaZS=0.3 was used.

Including a microbial loop had only a small impact on the standing stocks of small and large zooplankton. Predatory zooplankton decreased by about one half reducing potentially available biomass for fish production. These differences are due to the decreased net trophic efficiency of the system, which results when a large portion of the primary production passes through a microbial community before entering the zooplankton community.

Sensitivity analysis

A Monte Carlo analysis of the WSA with 600 replications randomly varied the input parameters and initial values by ±10% using a uniform error distribution. Principal component analysis (PCA) reduced the 600 sets of output of biological parameters and initial values. The PCA indicated that four factors explained 22% of variance in the data. The first principal component, was clearly related to photosynthesis of PL. It accounted for 10% of variance and was correlated with the variables VmaxS, VmaxL, and PL, NO_3, NH_4. The second principal component was related to the zooplankton state variables, ZL and ZS.

Based on the sensitivity analysis, the parameters selected to estimate from the observed data were VmaxS, VmaxL, λP, MorZP0 and VD2N0. Data from the A-line (off Hokkaido, Japan - outside the Oyashio region) was used with a conjugate gradient method to calculate the local minimum of the cost function, which is defined as the squared differences between observed and simulated data. After estimating these parameters, the time-dependent features of each compartment of the NEMURO/FORTRAN Box model were calculated.

Endnote D1

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APPENDIX E: BASS/MODEL WORKSHOP TO *REVIEW ECOSYSTEM MODELS FOR THE SUBARCTIC PACIFIC GYRES*

Workshop objectives

The BASS/MODEL workshop on higher trophic level modeling (March 5-6, 2001, Honolulu, U.S.A.) recommended a 1-day workshop to evaluate the results of the inter-sessional workshop and initiate hypothesis testing using the models developed.

This follow-up BASS/MODEL workshop was held October 5, 2001, immediately preceding the PICES Tenth Annual Meeting in Victoria, British Columbia, Canada (see Endnote E1 for attendance). The objectives of the workshop were to:

- assess the results of the March 2001 workshop;
- review progress on model development and updated models; and
- begin to develop scenarios to test key hypotheses.

Review of baseline models

The two ECOPATH/ECOSIM baseline models developed at the March 2001 workshop on higher trophic level modeling should be viewed as work in progress. Estimates of biomass, productivity to biomass, consumption rate to biomass and diet composition were compiled from the literature and from research data provided by PICES member countries. In general, information available for 1990 (or 1990-1993) was used such that the two models could be viewed as representative of the early 1990s conditions. In total, 56 species groups (with three detrital groups) were included in the models, however some species were not common to both regions. Minke whales, common dolphin, Japanese sardines and anchovies were present in the Western Subarctic Gyre (WSA) model, but not in the Eastern Subarctic Gyre (ESA) model. Conversely, elephant seals were present in the ESA model only. Many of the estimates are at best only guesses. Some observations were derived from coastal ecosystems and therefore may not be applicable to gyre ecosystems.

In general, the total biomass estimated for the WSA was higher than for the ESA. Major differences between the two model regions include higher biomasses of flying squid and Pacific pomfret in the ESA, higher biomass of chaetognaths in the WSA, and higher salmon biomass in the WSA (pink salmon) than in the ESA (sockeye salmon). Marine mammal biomass estimates were identical for each region since they were derived from basic-scale North Pacific estimates. No biomass estimates of forage fish and micronektonic species groups were available from the literature or from research survey data, so these were evaluated by top-down balancing of each model. Biomass estimates for lower trophic level plankton groups were derived from outputs of the NEMURO model that had been calibrated for Ocean Station P in the ESA.

Productivity values were derived from mortality rates. Consumption rates were obtained from diet composition and laboratory descriptions of calories/gram for prey species. Both production and consumption estimates were weighted by residence time for migratory species. The estimates for lower trophic levels (*e.g.* large zooplankton) were taken from other ECOPATH models and, in some cases, from the NEMURO model.

All information on diet composition was poor. Marine mammal diets were not as detailed as fish diets. Salmon diets were specific and detailed with many stomachs sampled over large areas and seasons, however, only summer estimates were available for the WSA. The major difference between the WSA and ESA were the seasonal differences in the diet of salmon since WSA included sockeye salmon in May. Early spring diet estimates for the early 1990s were not available for the ESA. Physical forcing inputs to the NEMURO model can be generated to produce phytoplankton and zooplankton outputs.

Maximum photosynthetic rates, zooplankton growth efficiencies and microbial loops can be modified and initiated to provide various climate change scenarios. These outputs can be used in ECOSIM.

Update of ECOPATH/ECOSIM models

Kerim Aydin reviewed the updated ECOPATH/ECOSIM baseline models. Figures E1 and E2 show composite images of the food webs for the Eastern and Western Pacific Subarctic Gyres. These models were initially constructed from data assembled at the March 2001 BASS/MODEL workshop and updated by including results of lower trophic level modeling by the MODEL Task Team and upper trophic level data from a wide range of sources on both sides of the Pacific.

Future adjustments to the models based on additional data presented at the Victoria workshop will be incorporated into the final versions of these models and presented at an inter-sessional BASS/MODEL workshop to be convened in April 2002. This will lead to a PICES Scientific Report

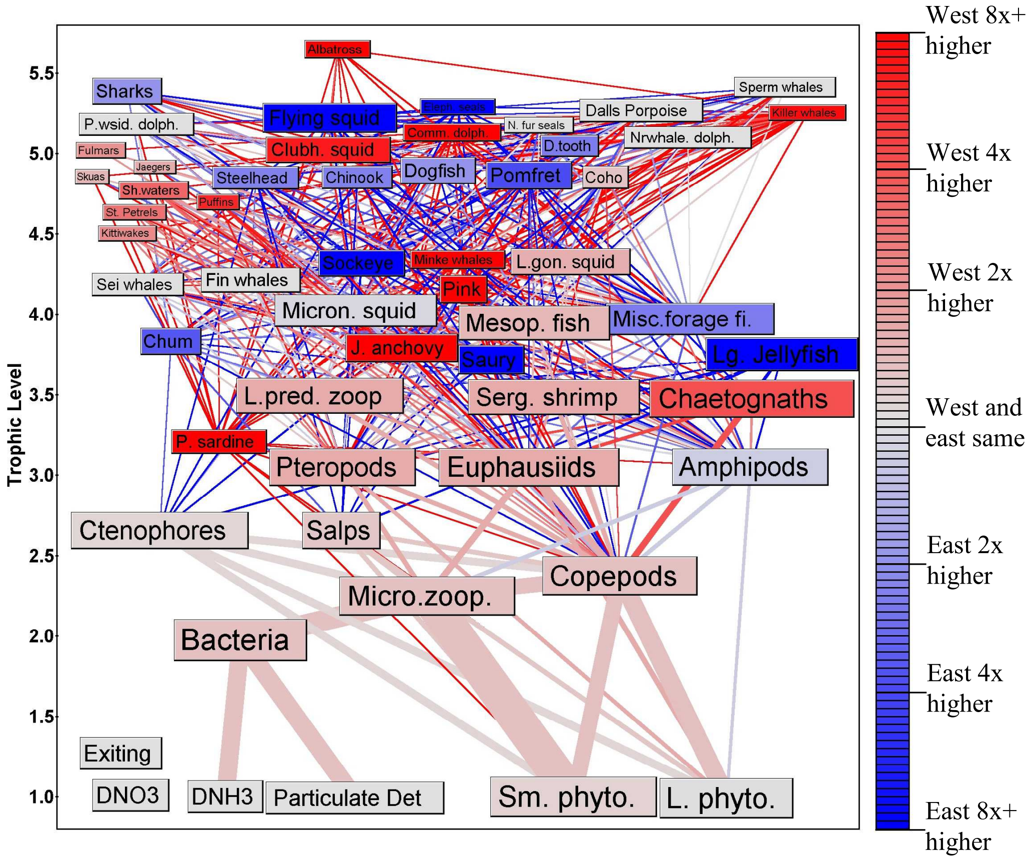

Fig. E1 A combined quantitative food web of the Eastern and Western Pacific Subarctic Gyres constructed from data assembled at the March 2001 BASS/MODEL workshop and presented at the PICES Tenth Annual Meeting. Species in both the Western and Eastern Gyres are shown. The area of each compartment is proportional to log of average biomass density (t/km^2), and the width of each connecting flow is proportional to the square root of the averaged yearly flow volume (t/km^2/year). Coloration shows the ratio of west *vs*. east biomass density and flow volume: where the ratio of west/east is higher (red) and where the ratio of east/west is higher (blue).

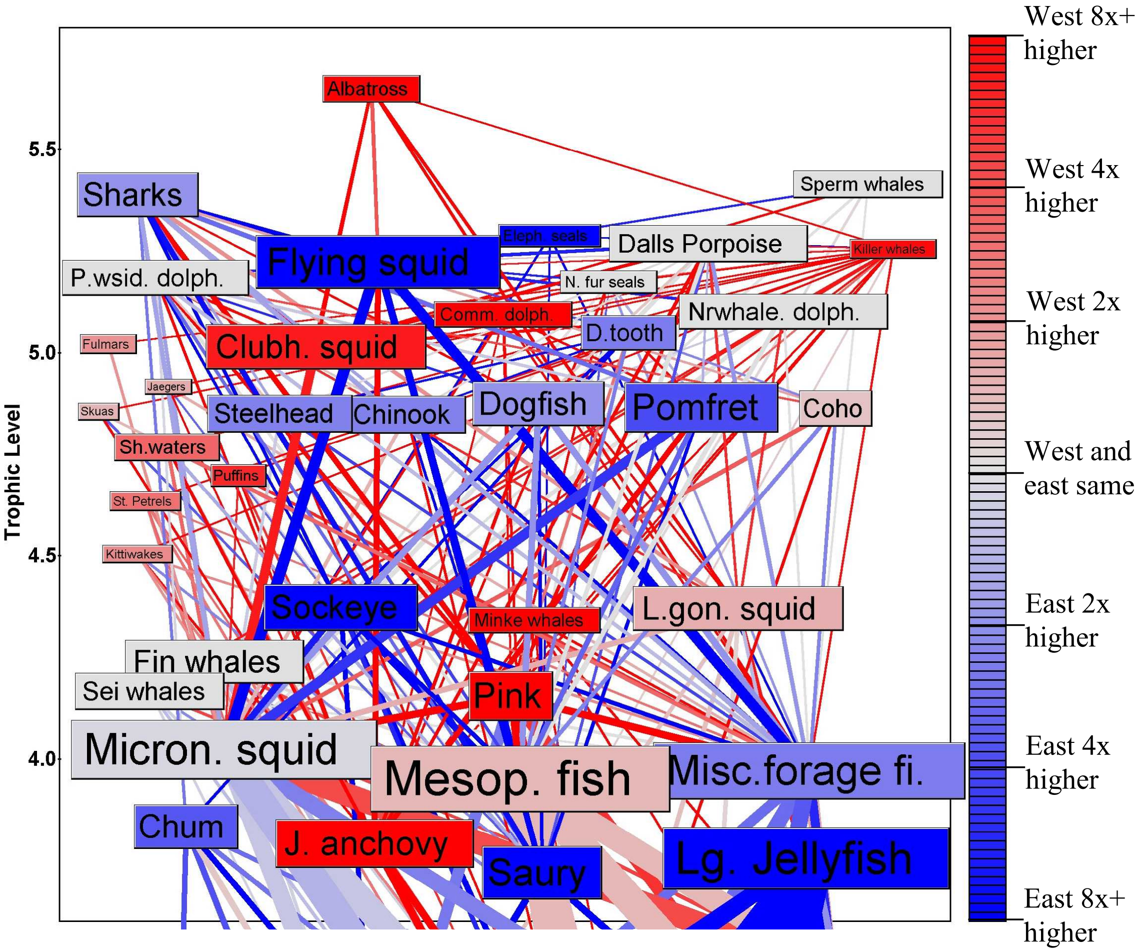

Fig. E2 An enlargement of the upper trophic level flows and biomass densities shown in Figure E1. Minor flows (the lowest 10% (cumulative) of prey mortality and predator diet) are removed for clarity. See Figure E1 for explanation of coloration.

to document the models and assess the overall state of knowledge of food web interactions and critical dynamic links in subarctic gyre ecosystems. In addition, the April 2002 meeting will focus on the potential to incorporate dynamic simulations of climate into these models.

This continuing synthesis highlighted some key areas for future research, for example, the exploration of dynamics of the intermediate trophic levels such as micronektonic squid, small forage fish, and mesopelagic fish (Fig. E2). The biology of these species is currently poorly understood and yet central to the functioning of the subarctic food web.

Another key direction for future work lies in developing methods to integrate gyre processes with boundary currents and near-shore processes. Specifically, concurrently examining the dynamics of boundary current species such as the Pacific sardine and Japanese anchovy in relation to the dynamics of the salmon-dominated subarctic gyre ecosystems that were simulated by these models, will increase our understanding of North Pacific-wide climate systems and their interrelations with coastal systems.

Recent improvements to NEMURO model

Bernard Megrey reviewed recent progress and improvements on the NEMURO lower trophic level modelling efforts.

Diagnostic calculations

Several diagnostic calculations were added to the NEMURO model. These included production/ biomass (P/B) ratios for phytoplankton and zooplankton, food consumption/biomass (C/B) ratios for small, large and predatory zooplankton, and ecotrophic efficiency (a measure of how much primary production transfers up the food web to the zooplankton species and ultimately to higher trophic level species).

Validation to Station P

The NEMURO model was parameterized for Ocean Station P and output was compared to data collected from that site. Results were favourable. NEMURO provides reasonable C/B and P/C ratios. Annual primary production from the model (149 gC/m^2/yr) is only 6% higher than the best current estimate (140 gC/m^2/yr) by Wong *et al.* (1995). Average chlorophyll concentration from the model (0.42 mg/m^3) is only 5% higher than the long-term value (0.4 mg/m^3) measured by Wong *et al.* (1995). An f-ratio (assuming that the production of the large phytoplankton is primarily fuelled by "new" nitrogen) is in a good agreement with the estimate by Wong *et al.* (1995): 0.23 and 0.25 respectively.

Zooplankton vertical migration

Results without ontogenetic migration of predatory zooplankton (ZP) show a large diatom bloom around day 73 (Fig. E3, top panel). The prevailing view is that there is no spring bloom at Station P. Thus the bloom is an artifact of the "box" nature of the model. Adding ZP migration, decreases biomass of phytoplankton by a factor of 2 (Fig. E3, bottom panel) and generates more reasonable diagnostics. The estimates of ecotrophic efficiency are not significantly affected.

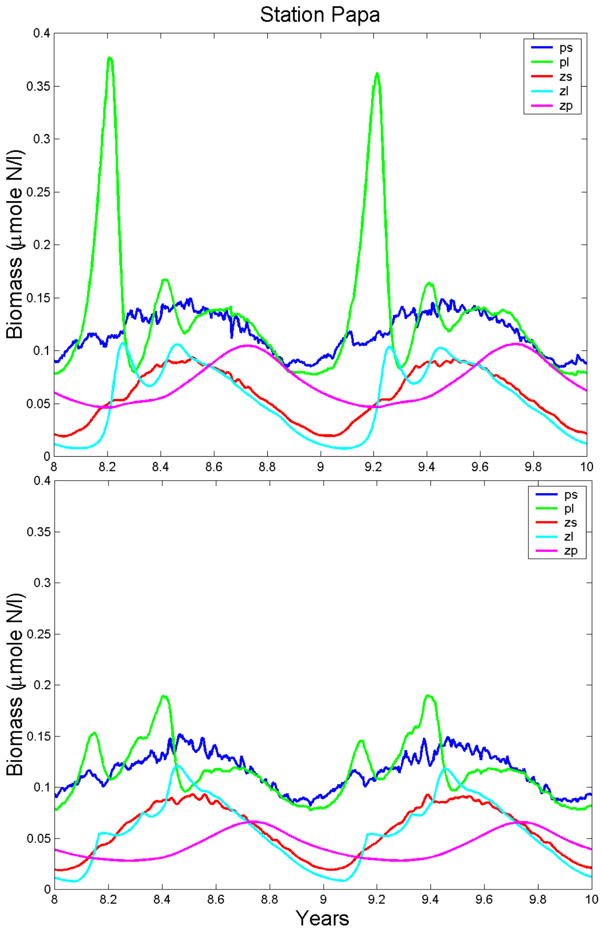

Fig. E3 Comparison of NEMURO output with (bottom panel) and without (top panel) ontogenetic migration of large zooplankton.

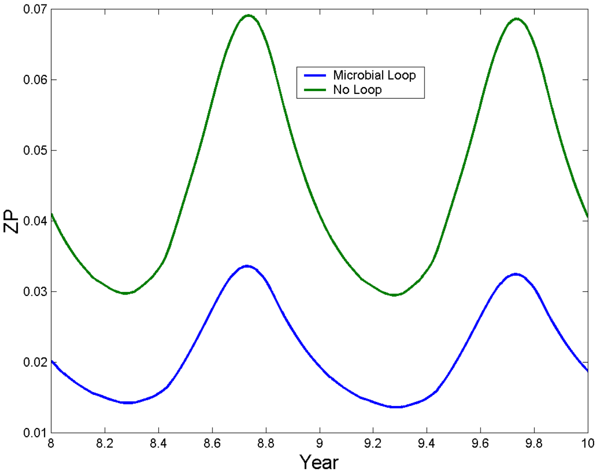

Fig. E4 Comparison of NEMURO output with and without the microbial loop approximation.

Microbial loop

Inclusion of a microbial loop had only a small impact on the standing stocks of small and large zooplankton (Fig. E4). Predatory zooplankton decreased by about one half, reducing potentially available biomass for fish production. These differences are due to the decreased net trophic efficiency of the system because a large portion of the primary production passes through a microbial community before entering the zooplankton community.

Recent progress

MODEL Task Team also conducted a sensitivity analysis and data assimilation for Station A7 (WSA) and added carbon fluxes to the LTL model.

The most recent improvements to the NEMURO model include:

- Acquired SST time series from Station P 1951-1988;
- Acquired equations to permit calculation of light at the surface;
- Modified primary production equations to explicitly include mixed layer depth (MLD) to permit simulation of regime shift scenarios.

Hypothesis testing scenarios

The following scenarios were suggested:

- ➢ Examine impact of changes in primary and secondary production on each gyre. Do they respond similarly or differently?
- ➢ Examine seasonality of changes in each system;
- ➢ Examine the role of primary production increases on sockeye salmon abundance;
- ➢ Examine role of predation in the regulation of population abundance:
    - o shark/salmon
    - o marine mammal/salmon
- ➢ Examine role of marine birds in each gyre;
- ➢ Examine role of forage fish in each gyre;
- ➢ Examine species competition for prey, *e.g.* pink/sockeye salmon; pomfret/squid, etc.

Recommendations

1. Convene a joint BASS/MODEL workshop in April 2002 to continue hypotheses testing of the models developed at the 2001 inter-sessional workshop and refined at the Tenth Annual Meeting;
2. Parameterize the WSA model, in particular finalize the boundary to exclude the transition area;
3. Calibrate and validate the NEMURO model to Station A7, which is more appropriate for the Western Subarctic Gyre;
4. For both the Eastern and Western Gyre models, incorporate time series (from the NEMURO model) for light, SST, etc., to generate primary productivity and zooplankton time series;
5. Hypotheses to be tested should be developed prior to the 2002 inter-sessional workshop and should focus on climate change scenarios;
6. Complete final data synthesis (including marine birds and mammals) prior to the 2002 inter-sessional workshop;
7. Following the inter-sessional workshop, prepare the two baseline models for publication in the PICES Scientific Report Series, including the results of hypotheses testing, and a data inventory;
8. PICES provide a means of accessing these models, and other workshop products on the web;
9. BASS/MODEL/REX Task Teams convene a joint session with GLOBEC at the PICES Eleventh Annual Meeting to examine *"Approaches for linking basin scale models to coastal ecosystem models"*;
10. Given the limited data on diet of many species inhabiting the gyres, PICES should encourage researchers to collect and collate diet data for species in these areas and sponsor the development of "Diet database" which would be peer-reviewed and citable.

Endnote E1

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APPENDIX F: BASS/MODEL WORKSHOP ON *"PERTURBATION ANALYSIS" ON SUBARCTIC PACIFIC GYRE ECOSYSTEM MODELS USING ECOPATH/ECOSIM*

Background

At the PICES Sixth Annual Meeting (October 1997, Pusan, Republic of Korea) the BASS Task Team sponsored a symposium on *Ecosystem Dynamics in the Eastern and Western Subarctic Gyres*. The purpose was to bring together available information on the two gyres in a comparative framework. Topics included: 1) ocean responses to climate forcing, 2) nutrients and primary production, 3) structure of the lower trophic levels, mesozooplankton communities and epipelagic nekton, 4) mid-water fishes, and 5) the importance of these areas to marine birds and mammals. Papers presented at the meeting were published in 1999, in a special issue of *Progress in Oceanography* (Vol. 43, No. 2-4).

A series of follow-up workshops was convened to identify potential models which might have utility for examining gyre systems. This included: the BASS Workshop on *Development of a conceptual model of the subarctic Pacific basin ecosystem* (October 20-21, 2000, in conjunction with the PICES Ninth Annual Meeting in Hakodate, Japan), the BASS/MODEL Workshop on *Higher trophic level modeling* (March 5-6, 2001, in Honolulu, U.S.A.) and the BASS/MODEL

Participants of the PICES BASS/MODEL Workshop (left to right): Salvador Lluch-Cota (CIBNOR, Mexico, local host), Bernard Megrey (Alaska Fisheries Science Center, U.S.A.), Francisco Werner (University of North Carolina, U.S.A.), Gordon McFarlane, Jacquelynne King (Pacific Biological Station, Canada), Kerim Aydin (University of Washington, U.S.A.), Ian Perry (Pacific Biological Station, Canada) and Jeffrey Polovina (National Marine Fisheries Service, U.S.A.). Not in picture: Michio Kishi (Hokkaido University, Japan), Takashige Sugimoto, Ichiro Yasuda and Sachihiko Itoh (University of Tokyo, Japan).

Workshop to *Review ecosystem models for the Subarctic Pacific Gyres* (October 5, 2001, immediately preceding the PICES Tenth Annual Meeting in Victoria, Canada). At these workshops, the BASS and MODEL Task Teams examined the feasibility of using the ECOPATH/ECOSIM modelling approach as a means to organize our understanding of ecosystems of the subarctic gyres.

The BASS/MODEL Workshop to test the baseline models developed at the March 2001 workshop, and refined at the PICES Tenth Annual Meeting, was held April 21-22, 2002, in La Paz, Mexico (See Endnote F1 for attendance). Specific objectives of the workshop were:

- synthesize all trophic level data in a common format;
- examine trophic relations in both gyres using ECOPATH/ECOSIM; and
- examine methods of incorporating the PICES NEMURO lower trophic level model into the analysis.

Review of baseline models

ECOPATH baseline models and the NEMURO model have been previously reviewed (PICES Scientific Report Nos. 17 and 21). The two ECOPATH models produced at that workshop should be viewed as work in progress. Estimates of biomass, productivity to biomass, consumption rate to biomass and diet composition were compiled from the literature and from research data provided by PICES member countries. In general, information available for 1990 (or 1990-1993) was used such that the two models could be viewed as representative of the early 1990s conditions. In total, 56 species groups (with three detrital groups) were included in the models, however, some species were not common to both regions. For example, Minke whales, common dolphin, Japanese sardines and anchovies were present in the Western Subarctic Gyre (WSA) model but not in the Eastern Subarctic Gyre (ESA) model. Conversely, elephant seals were present in the ESA model only. Many of the estimates are at best only guesses. Some observations were derived from coastal ecosystems and therefore may not be applicable to gyre ecosystems.

In general, the total biomass estimated for the WSA was higher than for the ESA. Major differences between the two model regions include higher biomasses of flying squid and Pacific pomfret in the ESA, higher biomass of chaetognaths in the WSA, and higher salmon biomass in the WSA (pink salmon) than in the ESA (sockeye salmon). Marine mammal biomass estimates were identical for each region since they were derived from basic-scale North Pacific estimates. No biomass estimates of forage fish and micronektonic species groups were available from the literature or from research survey data, so these were evaluated by top-down balancing of each model. Biomass estimates for lower trophic level plankton groups were derived from outputs of the NEMURO model that had been calibrated for Ocean Station P in the ESA.

NEMURO is a lower trophic level model (LTL) developed by the PICES MODEL Task Team during a modelling workshop held in Nemuro, Japan, in January 2000 (for details see Eslinger *et al.* (2000) and Megrey *et al.* (2000)). NEMURO simulates the annual dynamics of phytoplankton, zooplankton and nutrient concentrations for two locations in the North Pacific, Ocean Station P (57.5°N, 175°W) and station A7 (41.30°N, 145.30°E) off the A-line, an oceanographic sampling line off Hokkaido Island, Japan.

Ten years of output from the NEMURO model was used to supply "bottom-up" forcing to the ECOPATH/ECOSIM models, configured for each subarctic gyre system. NEMURO output from Ocean Station P was used to force the ESA ECOPATH/ECOSIM model, and output from station A7 was used to force the ECOPATH/ECOSIM WSA model. The model connection was a static one-way linkage.

Hypothesis testing

The purpose of this approach was to provide a "picture" of the two subarctic gyres, and to facilitate our understanding of how these systems respond to natural and anthropogenic change. It is hoped that it will form the basis of future work which will attempt to link the subarctic gyre systems to coastal systems.

A number of hypotheses were discussed as appropriate proxies to test the response of the two gyres to various trophic level changes and climate change scenarios. These were further refined into "Perturbation analyses" and "Function fitting and forcing".

Perturbation analyses

- Bottom up pulse

  Rationale: Increasing primary production could elucidate any bottom-up effects.

- Removal of squid

  Rationale: There is considerable confidence in the salmon diet composition for both gyres and discernible differences in the relative proportion of micronecktonic squid, forage fish and mesopelagic fish between the two gyre models. Since neon flying squid and boreal clubhook are probably competitors for micronektonic squid and forage fishes, their removal may have implications for prey availability for salmonids.

- Removal of salmon

  Rationale: Assuming that salmon abundance is determined outside of the gyre system, changes in abundance will greatly affect other trophic levels if salmon is a driving force within the gyre system.

- Removal of sharks

  Rationale: Sharks were selected as representative of a higher trophic apex predator.

Function fitting and forcing

Rationale: We were interested in investigating the changes that were required in productivity in order to explain changes in salmon abundance. Forcing functions at different trophic levels could be calculated by fitting the function to known salmon abundance data. We selected three trophic levels for which to fit foraging efficiency functions to salmon abundance trends, and then using the function to perturb the models: small phytoplankton, neon flying squid and sharks.

The results of these analyses will be available shortly in a PICES Scientific Report.

Endnote F1

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- Sachihiko Itoh

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- Bernard A. Megrey (convenor)
- Francisco E. Werner
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APPENDIX G: PROPOSAL FOR A BASS WORKSHOP ON *LINKAGES BETWEEN OPEN AND COASTAL SYSTEMS*

Recent BASS/MODEL workshops synthesized data and examined trophic relationships in the Eastern and Western Subarctic Gyres. These workshops facilitated our understanding of how these systems respond to natural and anthropogenic change. Participants at these workshops suggested the next phase of this work, from the standpoint of understanding the gyres, would integrate coastal, marginal seas and boundary current dynamics and linkages between gyres. To begin the process, this workshop will examine current information of the oceanographic and biological linkages between open ocean and coastal systems in the North Pacific. Invited papers will be prepared by "teams" of investigators to assess existing information on linkages for various physical and biological components. Presentations will include reviews of physical oceanography, phytoplankton, zooplankton, migratory pelagics, mesopelagics, marine birds and marine mammals. In addition, contributed papers, especially those attempting to develop conceptual models of physical or biological mechanisms that link coastal to open ocean systems, are encouraged. Selected papers will be published in a special issue of *Deep-Sea Research II* (Elsevier). Participants wishing to have their work considered for this publication should indicate their interest at the time of abstract submission, and be prepared to bring a completed manuscript to the Annual Meeting.

Endnote G1

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