

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:

$$\frac{dB_i}{dt} = GE_i \sum_{j \in \text{prey}} [f_{ij}(\bar{B})] - \sum_{k \in \text{pred}} [f_{ki}(\bar{B})] + PP(B_i) + IM(B_i) + BA(B_i) - EM(B_i) - F_i B_i - M_0 B_i$$

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 <i>et al.</i> (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.