(Re)Constructing Food Webs and Managing Fisheries

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Abstract
The construction and analysis of a food web is an ecosystem approach that augments classical fisheries management. Food web analysis delineates important ecosystem linkages representing species interactions such as predator-prey relationships; from these linkages emerges a better understanding of ecosystem resiliency, resistance, connectivity, energy transfer efficiency, mass flux, and energy partitioning. In turn, with an understanding of food web dynamics, critical fisheries issues, including the relative importance of fishery and natural mortality, identification of critical life stages, production surplus and partitioning, multispecies yield dynamics, and forecasting, the impact of fishery management scenarios can be more effectively examined. Unfortunately, elucidating a food web is not a trivial task. One of the more parsimonious, cost-effective, and fisheries-amenable methods of reconstructing (at least portions of) a food web is diet analysis. Incorporated as part of standard resource surveys, analysis of stomach composition can not only qualify the linkages of a food web, but can also quantify the magnitude and rate of energy and mass exchange. Examples of statistical analyses from northwest Atlantic diet data demonstrate the utility of this approach in constructing a food web that produces information useful in addressing key fisheries issues.

Introduction
Food webs are the skeletal and circulatory analogues of ecosystem "anatomy and physiology." That is, the predator-prey interactions that comprise food webs can ultimately determine the fate and flux of every population in an ecosystem, particularly upper level consumers of fiscal importance (Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985, Carpenter and Kitchell 1993, Christensen 1996). Numerous examples demonstrate the utility and insight that examining multispecies interactions have had
on fisheries management around the world (e.g., Andersen and Ursin 1977, Mercer 1982, Daan and Sissenwine 1991, Payne et al. 1992, Christensen and Pauly 1993, Walters et al. 1997, Pauly et al. 1998). While assessing fish populations with disregard to other species is known to be unrealistic, intellectually unsatisfying, and potentially misleading (sensu May et al. 1979, Murawski 1996), there persist challenges, be they scientific, institutional, philosophical or otherwise, that impede the implementation of multispecies and ecosystem approaches to fisheries management. Perhaps this is best expressed in a quote from Hilborn and Walters (1992: p. 448), which captures a pervasive attitude among fisheries scientists regarding food webs:

We believe the food web modelling approach is hopeless as an aid to formulating management advice; the number of parameters and assumptions required are enormous. Such large model-building exercises are perhaps of some utility in designing research programs, but will not help manage fisheries. The use of trophic relationships to estimate general yield potentials also seems unlikely to produce anything that fishery managers can use in the near future, although such relationships may become clearer in the long term as data are accumulated from a wide variety of fisheries.

I hope to demonstrate the contrary in this work, and will attempt to elucidate the utility that a classical food web approach can provide for fisheries management.

**What Is a Food Web?**

Food webs have been defined literally as road maps of species interactions, or as the relationship or connection between species, particularly trophic interactions (Pimm 1982, Cohen et al. 1993, Paine 1988). Implied are diagrams that graphically depict which species in a community interact, or serve as a schematic of energy flow in an ecosystem. DeAngelis (1992: p. 2) correctly separates the two major aspects of ecological systems into strict food web dynamics (the interactions between populations), in an ecological perspective, and energy and material flux (rates or magnitude of these interactions, expressed as units of energy or mass), in a thermodynamically balanced perspective. In this work I will primarily focus on the strict food web aspect of ecosystem dynamics, although this is highly interrelated with the flow of mass and energy. Although similar to the ECOPATH and ECOSIM (reviewed in Walters et al. 1997) approaches familiar to many fishery scientists, this approach, championed by May (1973), Cohen (1978), and Pimm (1982, 1991), focuses on summary statistics from a formal, ecologically oriented analysis that elucidates the structure of a food web and highlights major properties peculiar to a particular ecosystem. My goal is to relate these key ecological parameters to metrics and concepts familiar to fishery managers.
Materials and Methods

There are several ways to reconstruct and assess food webs, described in Table 1. Many of these methodologies are understandably cost- and time-prohibitive for most fishery agencies. However, one cost-effective and assessment-amenable method of reconstructing a food web is diet analysis. Augmented by other directed studies, this approach can provide a robust data set with which to analyze food webs. When incorporated as part of standard resource surveys, stomach analysis can qualify linkages and quantify the magnitude of these linkages across broad taxonomic, spatial, and temporal scales. If an agency is examining selected individual fish lengths, weights, ages, and maturities, then examining stomach contents is a natural extension of the existing sampling protocol.

The approach I used is based primarily upon stomach content evaluation, although I also relied on literature reports and body size and general biological inferences, particularly for prey of most invertebrates. I used the database on selected fish stomachs collected by the Northeast Fisheries Science Center (NEFSC) from 1973 to 1998. These data were collected in the spring and fall NEFSC surveys, covering the entire northeast U.S. continental shelf (ranging from Cape Hatteras to the Gulf of Maine). Stomachs were analyzed for total weight, prey volume (during 1981-present, weights prior to 1981), percent prey composition, and prey lengths if feasible to do so. These data are the primary source for the following analyses, and most species had more than 250 stomachs sampled.

I selected 75 “species” (i.e., groups of organisms at taxonomically feasible and functionally related levels) common in the northwest Atlantic. I included humans in this web. The lowest trophic level is highly aggregated (i.e., phytoplankton, detritus), yet there are 33 groups per species of invertebrates at the next trophic levels, as well as 35 species per groups of fish. Admittedly, this food web is vertebrate centric, and is, like all food webs, by default incomplete (DeAngelis 1992).

I first constructed an interaction matrix of the 75 pair-wise interactions, and assigned a –1, 0 or +1 if species A preyed on, did not interact with, or was eaten by species B, respectively. The presence or absence of a species in the diet of another species was the primary determinant of these values. A food web diagram was also constructed from these trophic linkages.

I then constructed an index of interaction strength matrix. This was based upon the assumption that percent frequency of occurrence of a prey item integrated predator spatial overlap, selectivity, and feeding rates for these prey items at varying abundances over the 25-year period across this broad geographic scale. This parameter was used to index the strength of trophic links between each of the 75 pairs. I calculated the mean interaction strength to assess how strongly connected the species in this community were.

I calculated standard food web metrics from these interaction matrices.
Table 1. **Common methods for reconstructing food webs, particularly species interactions and interaction strengths.**

<table>
<thead>
<tr>
<th>Approach</th>
<th>Comments</th>
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<tbody>
<tr>
<td>In situ observations</td>
<td>Observing or inferring a predatory event.</td>
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<tr>
<td></td>
<td>Video/photographic</td>
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<td></td>
<td>Spatial overlap-acoustics, trawls, etc.</td>
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<tr>
<td></td>
<td>Anecdotal evidence</td>
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<td></td>
<td>Directed observations</td>
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<tr>
<td>Experimental studies</td>
<td>Identifying and quantifying predation impacts.</td>
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<td></td>
<td>Laboratory rates-e.g. selection, consumption, etc.</td>
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<tr>
<td></td>
<td>Unplanned field manipulations</td>
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<td></td>
<td>Enclosures, translocations, removals, etc.</td>
</tr>
<tr>
<td>Diet analysis</td>
<td>Examining what has been eaten by a predator.</td>
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<tr>
<td></td>
<td>Stomach content evaluation-mass, volume, prey number</td>
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<tr>
<td></td>
<td>Composition (i.e. proportion) per prey type</td>
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<td></td>
<td>Selectivity indices, overlap indices</td>
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<tr>
<td></td>
<td>Mean stomach content, related statistics</td>
</tr>
<tr>
<td>Body size inferences</td>
<td>Relating morphometry with known feeding patterns.</td>
</tr>
<tr>
<td></td>
<td>e.g. Gill rakers</td>
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<td></td>
<td>Mouth gape</td>
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<td></td>
<td>Stomach length</td>
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<td></td>
<td>Aspect ratio</td>
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<tr>
<td>Microchemistry</td>
<td>Stoichiometry to infer diet.</td>
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<td></td>
<td>e.g. Fatty acids</td>
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<td>Bomb calorimetry</td>
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<td>Microconstituent analysis</td>
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<td>DNA, RNA probes</td>
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<td></td>
<td>Immuno-assays</td>
</tr>
<tr>
<td>Stable isotopes</td>
<td>Reconstructing trophic level position from predator tissue.</td>
</tr>
<tr>
<td></td>
<td>e.g. $^{15}$N</td>
</tr>
<tr>
<td></td>
<td>$^{13}$C</td>
</tr>
<tr>
<td>Ad hoc</td>
<td>Educated guessing in a situation with a lack of information.</td>
</tr>
<tr>
<td></td>
<td>Related literature values</td>
</tr>
<tr>
<td></td>
<td>Evidence from similar species, systems</td>
</tr>
<tr>
<td></td>
<td>Try to “think like a fish”</td>
</tr>
</tbody>
</table>


**Food Web Concepts**

The series of "standard" food web metrics merit revisiting to, at the least, clarify terminology. The first metric noted was simply the number of species \( S \). The number of interactions (or trophic links; \( L \)) was also counted. This number was then divided by the total number of possible interactions to determine the connectivity \( C \) of a system:

\[
C = \frac{L}{S(S-1)/2}
\]  

The number of interactions per species \( L/S \) was also calculated. Both \( C \) and \( L/S \) index the level of interactions, potential competition, trophic specialization, and overall inter-connectedness of a food web (May 1973, Pimm 1982, 1991; Cohen et al. 1993). The product \( S \times C \), when coupled with an assessment of overall web interaction strength (either mean interaction strength [May 1973] or eigenvalues of the interaction matrices [Pimm 1982]) gives an assessment of mathematical stability for a system. Here stability is defined as whether a population will return to equilibrium after a perturbation, realizing that there are both global and local stabilities (DeAngelis 1992, Pimm 1991). Associated with the idea of stability are concepts of: (1) equilibrium, defined as when time approaches infinity, a system becomes relatively constant (given local variability) near a "carrying capacity"; even though it is contentious as to whether equilibrium truly exists in biological systems, yet is often assumed for distinct time scales; (2) resilience, defined as how fast a system returns to equilibrium after a perturbation; (3) persistence, which is a measure of the strength of a system against departure from equilibrium, or how long component populations persist at certain levels before being changed to new equilibria; and (4) resistance, defined as the relative magnitude that a change in one population has on other populations in a system, measured as the ratio or percent change before and after a perturbation for all component populations (Pimm 1991, DeAngelis 1992). Recognizing the contentious nature of these concepts (e.g., Hastings 1988, Paine 1988, Pimm and Kitching 1988, Warren 1990), I will only address these items qualitatively.

The number of basal species (no trophic levels supporting these organisms), the number of top predators (defined here as a species having less than three predators), the number of species at trophic levels 2 and 3, and the total number of intermediate species (non-basal and non-top-predator species) were enumerated, as were the number of cannibals (species known to prey upon themselves), the number of cycles (when species A preys upon species B and vice versa), and the number of omnivores (defined as the number of species eating prey from more than one trophic level; Pimm and Lawton 1978). The modal food chain length was calculated to determine the most common number of trophic levels in this food web. Finally, the number of predators for a prey item, the number of prey
items for a predator, and the predator to prey ratio were calculated. This set of metrics details the specific properties of a particular food web and gives insight into the rate and flow of material and energy distribution in an ecosystem. Identifying the links between species is required to assess energy/mass partitioning, energy transfer efficiency, and surplus production of an ecosystem.

Results and Discussion

**What Does This Food Web Information Tell Us, and How Does It Relate to Fisheries?**

The first thing to note is that this is a relatively large food web, as most food webs average <20 species, and 95% of webs have <40 species (Table 2; Cohen 1989). I recognize the high degree of aggregation at lower trophic levels in this web, but 33 invertebrate groups is larger than most whole food webs (discussed in Goldwasser and Roughgarden 1993). The level of observation on the feeding habits for this number of species is unusually high, yet by no means exhaustive. This is a complicated system that has been observed rather frequently, yet needs continued attention, including focus on the multispecies system attributes and better quantification of species linkages.

The values for the connectivity and number of interactions per species (C and L/S, Table 2) demonstrate that this is a highly connected food web, as depicted in Fig. 1. If one examines the level of connectivity in this system in relation to the number of species, this food web is approaching the theoretical maximal connectivity (ca. 50%) and is an extremely distinct outlier in the decreasing hyperbolic curve of C vs. S (Pimm 1982, Warren 1990). Most food webs that have >50 species have a connectance of approximately 10%. I recognize that I was conservative in my assessment of interactions, and the high connectivity I report for this system may be an artifact of the grouping for invertebrates, the focus on fish, construction by using all known interactions (disregarding interaction strength when ascertaining linkages), and the inclusion of humans in the web. However, this invertebrate grouping is no worse than lower trophic levels in other webs, and again the number of groups at lower trophic levels is relatively more exhaustive than most other whole webs. The ratio of predators to prey is lower than the ECOWEB mean (Table 2), also suggesting that this web is not as vertebrate (or top predator) centric as others. The results from this food web may be an artifact of our sampling protocol, but more likely reflect true features of this system. Certainly, a higher threshold of species interaction other than presence in the diet of another species will lower the overall connectivity of this web, but unless this threshold is relatively high the connectivity will still be distinct from other food webs examined. The scale of the data, both temporally and spatially, is larger and longer than most food web analyses. The orders of magnitude in size...
### Table 2. Summary of food web statistics from the northwest Atlantic continental shelf community.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>NW Atlantic</th>
<th>ECOWEB mean</th>
</tr>
</thead>
<tbody>
<tr>
<td># Species ($S^a$)</td>
<td>75</td>
<td>19, 95% of webs &lt;40</td>
</tr>
<tr>
<td># Interactions ($L$)</td>
<td>2,557</td>
<td>–</td>
</tr>
<tr>
<td># Possible interactions</td>
<td>5,550</td>
<td>–</td>
</tr>
<tr>
<td>Connectivity ($C$)</td>
<td>46.1%</td>
<td>31.2%</td>
</tr>
<tr>
<td>$S \times C$</td>
<td>34.6</td>
<td>3.744</td>
</tr>
<tr>
<td># Interactions/Spp. ($L/S$)</td>
<td>34.1</td>
<td>1.72</td>
</tr>
<tr>
<td># Cannibals</td>
<td>20</td>
<td>–</td>
</tr>
<tr>
<td>% Cannibals</td>
<td>27%</td>
<td>–</td>
</tr>
<tr>
<td># Omnivores</td>
<td>48</td>
<td>–</td>
</tr>
<tr>
<td>% Omnivores</td>
<td>64%</td>
<td>27%</td>
</tr>
<tr>
<td># Top predators</td>
<td>8</td>
<td>–</td>
</tr>
<tr>
<td>% Top predators</td>
<td>11%</td>
<td>30.1%</td>
</tr>
<tr>
<td># Basal species$^b$</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td>% Basal species</td>
<td>3%</td>
<td>20.9%</td>
</tr>
<tr>
<td># Species at trophic level 2</td>
<td>33</td>
<td>–</td>
</tr>
<tr>
<td>% Species at trophic level 2</td>
<td>44%</td>
<td>–</td>
</tr>
<tr>
<td># Species at trophic level 3</td>
<td>31</td>
<td>–</td>
</tr>
<tr>
<td>% Species at trophic level 3</td>
<td>41%</td>
<td>–</td>
</tr>
<tr>
<td># Intermediate species</td>
<td>66</td>
<td>–</td>
</tr>
<tr>
<td>% Intermediate species</td>
<td>88%</td>
<td>49%</td>
</tr>
<tr>
<td># Cycles</td>
<td>70</td>
<td>–</td>
</tr>
<tr>
<td>% Cycles</td>
<td>3%</td>
<td>–</td>
</tr>
<tr>
<td>Modal chain length</td>
<td>4</td>
<td>2-3 (2.59)</td>
</tr>
<tr>
<td>Maximum</td>
<td>9</td>
<td>3.74</td>
</tr>
<tr>
<td>Minimum</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td>Mean # Prey/predator</td>
<td>17.5</td>
<td>2.21</td>
</tr>
<tr>
<td>Maximum</td>
<td>61</td>
<td>–</td>
</tr>
<tr>
<td>Minimum</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>Mean # Predator/prey</td>
<td>15.7</td>
<td>2.46</td>
</tr>
<tr>
<td>Maximum</td>
<td>38</td>
<td>–</td>
</tr>
<tr>
<td>Minimum</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td>Predator/prey ratio</td>
<td>0.894</td>
<td>1.18</td>
</tr>
<tr>
<td>Mean interaction strength</td>
<td>0.0697</td>
<td>–</td>
</tr>
</tbody>
</table>

The ECOWEB mean values are from 213 food webs analyzed in a similar fashion; – indicates not examined (Cohen 1989, cited in Goldwasser and Roughgarden 1993). See text for description of interaction strength.

$^a$Some grouping, particularly in lower trophic levels.

$^b$Taxonomic resolution very low.
Figure 1. Species and links of the northwest Atlantic food web. This tangled “bird’s nest” represents interactions at the approximate trophic level of each species, with increasing trophic level towards the top of the web. The left side of the web generally typifies pelagic organisms, and the right to middle represents more benthic/demersally oriented organisms.

2. Phytoplankton. 27. Polychaetes. 52. Winter Skate.
3. Calanus sp. 28. other worms. 53. Thorny Skate.
4. other copepods. 29. Starfish. 54. Ocean Pout.
6. Chaetognatha (i.e. arrow worms). 31. Sea cucumbers. 56. Yellowtail Flounder.
8. Euphasiids. 33. clams, mussels. 58. Summer Flounder.
9. Crangon sp. 34. Snails. 59. Witch Flounder.
10. Mysids. 35. Urchins. 60. Four-spot Flounder.
19. Mantis Shrimps. 44. Spotted Hake. 69. Toothed Whales, Porpoises.
20. Tunicates. 45. White Hake. 70. Seals.
23. other crabs. 48. Haddock. 73. Migratory Billfish.
across the ontogeny of these organisms will increase the number of connections relative to other systems. Finally, a limited number of marine food webs have been analyzed, thus the high connectivity of this system relative to theoretical expectations remains an intriguing aspect for further research.

Regardless of whether this food web revises connectance theory, two major points arise from the high connectivity observed for this food web: (1) there are a lot of generalists in this ecosystem, and (2) there is a high degree of diet overlap for these component organisms. A cursory glance at Fig. 1 shows the “bird’s nest” of interactions in this system, and the almost opaque quality of this diagram enforces the idea of ubiquitous overlap and connectedness in this food web. For simplicity, Fig. 2 depicts the food web for the major groups from a fishery perspective, yet even this simplification exemplifies the complexity of these interactions.

The mean number of predators per prey and mean number of prey per predator are also higher than the ECOWEB means (Table 2). In addition, 64% of the species in this food web feed omnivorously. Even splitting out the lower trophic levels would not ameliorate this high level of overlap and omnivory. Omnivory indicates opportunistic feeding. Thus, there is high potential for competition in this food web, particularly if fish feed opportunistically and switch diet preferences based upon relative abundance of prey. For example, there are 38 predators of sand lance (species 36 in Fig. 1) in this system. Therefore, many of the fish in this ecosystem are ecologically interchangeable (at least from the perspective of prey populations).

There also exists a high potential for indirect effects on other species in this system, given an impact on a particular species. When a system is as connected as this northwest Atlantic system (Fig. 1, Table 2), changes in predator or competitor populations may release a particular species or group of species from interaction pressure (i.e., the interaction strengths decline), allowing that species to drastically increase. For example, Fogarty and Murawski (1998) hypothesize that the notable increase in elasmobranchs on Georges Bank is due in large part to a decrease in competitive pressure from the gadoids that have been overfished. The potential for Markovian spirals increases with this level of connectance. As in the previous example, impacts on species A influence species B which directly impacts species C and also indirectly releases species K, a competitor of both species C and D, ad infinitum. That is, from a stability perspective, resistance may be low for this web. The challenge is then to predict what the future portions of biomass will be in this system, at least in qualitative trends, for various management scenarios. The large number of interactions contributes to the stochastic nature of this ecosystem, to the consequent uncertainty in the predictions, and hence to the magnitude of this challenge. The northwest Atlantic food web demonstrates the need to consider these species as a whole and not as individual populations, particularly noting the complexity and ubiquity of these interspecific interactions.
Figure 2. Simplified schematic of the northwest Atlantic food web depicting the major fish groups and their interactions with other major prey and predator groups.
Yield dynamics must take into consideration a multispecies perspective, else fishery managers will be surprised at the amount of predicted “surplus” production that is actually consumed by predators or inhibited by competitors.

Assessing interaction strengths for a food web is difficult, definitely an area for further improvement (Paine 1988, Cohen et al. 1993), and yet provides insight into energy and material partitioning within the web. Factors that alter interaction strength are abundance, overlap, and selectivity/avoidance of predators and prey. Fishing mortality (F) impacts the abundance of these populations, and thus directly impacts the strength of species interactions, which ultimately can propagate throughout a system indirectly affecting all species and how biomass and energy are partitioned (Carpenter and Kitchell 1993, Christensen 1996, Murawski 1996, Walters et al. 1997, Fogarty and Murawski 1998). That is, cascading impacts from F have the potential to directly or indirectly alter every population in a food web given a set of interaction strengths. In addition, natural mortality (M) can be much more significant than F for a given species in this system (Overholtz et al. 1991; Overholtz et al. 1999). Thus, if the major portion of mortality for a species is due to predation, fishery managers should be cognizant of this fact.

If we assume that the frequency of occurrence of a prey item in a predator diet is an index of interaction strength, then this web is weakly connected (Table 2). That is, although there may be numerous interactions, few are of sufficient magnitude to drive whole-system dynamics, similar to the results of Sissenwine et al. (1982). This may explain the lack of competitive exclusion for this high number of species, as the relative importance of many interactions drop out from the major energy and material pathways through this food web. This loosely connected web also reiterates the functional interchangeability of these species.

The structure of this food web, in terms of co-occurring species, is static (Sissenwine et al. 1984, Gabriel 1992). However, the functioning of this food web is dynamic. Interaction strengths examined at temporal or spatial intervals give greater insight into system functioning than a static, cumulative view (Schoenly and Cohen 1991). Species interactions are the pathways for the flux of material and energy from one population to another, and determine how biomass and energy are partitioned in an ecosystem. Addressing the dynamic nature of these interactions is not a trivial task, yet explains the “physiology” of an ecosystem. To illustrate this point, in the 1970s the major portion of this food web was comprised of gadoids and flounders (reviewed in Backus 1987, NEFSC 1995, and Fogarty and Murawski 1998). If one blacks out species 36-41, 49-55, and 64 in Fig. 1, the result is a historical representation of this ecosystem as depicted in Fig. 3a. That is, this was a vertically oriented system, with the preponderance of biomass in the gadoid and flounder species. Shift forward in time to the removal of foreign trawlers, the increase in the domestic groundfish fleet, and the subsequent decline of historically abundant gadoids
Figure 3. (A) Depiction of a "vertical" food web, where the majority of the energy and mass flux is to demersal and benthic organisms. Representative of the northwest Atlantic ecosystem in the 1970s. (B) Depiction of a horizontal food web, where the major pathway of energy and mass flux is captured in migratory pelagics. Representative of the current northwest Atlantic ecosystem.
and flounders. That is, human (species 75 in Fig. 1) impacts were so strong that one can effectively black out species 42-63. The remaining species on the left of Fig. 1 are predominately pelagic, resulting in the food web as it currently exists, concentrated primarily in a horizontal pathway of energy and mass flux (Fig. 3b). These migratory pelagics disperse energy across a wider geographic range instead of a more localized focus found in the demersal fishes. One potential hypothesis is that the current biomass of pelagics has replaced biomass of now-depleted groundfish (Fogarty and Murawski 1998). A corollary hypothesis is that even with a major decrease in F for the key demersal fish in this system, without an increase in the yield or otherwise overt removal of this pelagic biomass shunt, the demersal stocks may not rebound to historic levels since a significant portion of their energetic flux is intercepted by this dominant pelagic component. Similar qualitative scenarios can be examined using this basic, food web-based approach.

This food web contains 70 cycles, a relatively high number (Table 2). Recalling that a cycle is when species A consumes species B and vice versa, each cycle may indicate potential stock bottlenecks. For example, age 0+ gadoids are consumed by Atlantic mackerel, who are themselves consumed by these gadoids once the gadoids attain larger size classes (Fig. 1, Michaels 1991; Pers. comm., W.M. Michaels, NEFSC, and E.G. Durbin, URI). The strength of these cycles depends upon the relative biomass of each participant. Depending on the strength of each interaction, a particular species may be consumed by some of its major “prey” before it surpasses critical life history stages. Stock bottlenecks may also arise from predation, lack of prey due to increased competition, or direct fishing mortality on these life stages, yet the negative feedback loop of cycles is an overlooked mechanism that fishery managers need to consider when examining age structured population models, particularly recruitment processes.

Another important negative feedback loop in this food web is cannibalism. Over one-fourth of the species in this food web exhibit this phenomenon (Table 2). *Loligo pealii* (longfin squid), *Illex illecebrosus* (shortfin squid), copepods, *Melanogrammus aeglefinus* (haddock), *Pollachius virens* (pollock), *Gadus morhua* (Atlantic cod), *Merluccius bilinearis* (silver hake), *Urophycis regia* (spotted hake), *U. tenuis* (white hake), *U. chuss* (red hake), *Myoxocephalus octodecemspinosus* (longhorn sculpin), *Sebastes* spp. (redfish), *Scophthalmus aquosus* (windowpane flounder), *Squalus acanthias* (spiny dogfish), *Cynoscion regalis* (weakfish), *Pomatomus saltatrix* (bluefish), migratory scombrids, migratory sharks, birds, and *Lophius americanus* (goosefish) all exhibit cannibalism. Of these, silver hake (11%), pollock (9%), longfin squid (2.6%; 16% all cephalopods), shortfin squid (2.7%; 53% all cephalopods), goosefish (3.7%), and bluefish (7%) have a significant portion of their diet composed of individuals of their own species. Cannibalism is generally not a positive phenomenon for a stock other than as a density-regulating mechanism, and is particularly noteworthy when >10% of a fish’s diet consists of conspecifics. Aside from the vora-
ocious and opportunistic feeding nature of these fish, this implies that
different life stages of a fish are functionally different species. Most fish
in this community exhibit ontogenetic shifts towards increasing piscivory,
particularly after 40-50 cm, and the cannibalism demonstrated by these
fish is by larger size classes on 10-25 cm individuals. Fishing mortality is
known to target larger size classes (Hilborn and Walters 1992). Thus, with
both cannibalism and cycles impacting smaller size classes, I hypothesize
that when both cannibalism and cycles are operating on small size classes,
the negative effects on already depleted stocks are intensified. A few indi-
viduals may reach sizes large enough to be piscivorous, in large enough
numbers to reduce incoming cohorts through cannibalism but in too few
numbers to limit their other prey populations. If those prey populations
consume the larval phases of the depleted stock, the negative feedback
becomes more intense. A cohort must then incur predation by its eventual
prey plus predation by its parents before it reaches maturity. Once it reaches
maturity, the cohort is smaller than its predecessor, and is even less likely
to reduce the prey population. The number of ensuing larvae is then con-
sumed by a larger number of prey, but is still subject to cannibalism.
Again, the interaction strength determines the importance of cannibalism
and the negative feedback loop described here. This secondary mecha-
nism of overfishing could have occurred in the gadoids on Georges Bank
after the early 1980s, and may still impacting part of this species com-
plex.

The modal chain length for this web is reasonable compared to the
ECOWEB average, considering that I included humans. This is slightly larger
than the estimate Pauly et al. (1998) present for this region, yet is still
lower than the five or six levels that were historically observed. When
fishing pressure removes larger size classes and alters the dynamics of
species interactions, forcing fish to feed upon lower trophic levels, yet
another negative feedback loop is initiated. Economic value of fish is typi-
cally inversely proportional to its trophic level, thus this food web impact
has far-reaching implications. That humans are also consuming more for-
age fish of lower trophic levels (Pauly et al. 1998) is alarming.

Quantitatively addressing the stability of the northwest Atlantic food
web is a moot point given the continual perturbations it has experienced
over the past several decades. Assuming this system is at least locally
stable (i.e., composition of community biomass is relatively static on a
short time scale; e.g., 2-3 years), then two points stand out. One is that
with the high degree of interactions in this web, the resilience is going to
be very high. That is, to return to historical equilibrium, presuming that
(1) it existed, (2) it resembled a state where cod and other gadoids were
predominant in this community, and (3) we can manipulate it to do so, will
take a long time. Second, even if we reduce the human-induced perturba-
tions of the system in the future, we may find that the system has already
been perturbed beyond its historical limits and may have shifted to a new
local equilibrium. Measuring the persistence of this system is difficult,
but we have clearly exceeded earlier persistence limits as indicated by changes in component populations ranging across several orders of magnitude (NEFSC 1995). How the populations in this, and similar, ecosystems will fluctuate stochastically from one local equilibrium to another remains a major, if not the key management challenge for our nation’s resource managers. Enhanced understanding of complex systems via a lucid examination of food webs is one useful way to meet this challenge.

Acknowledgments

I thank all members of the Food Web Dynamics Program of the NEFSC, past and present, for their dedicated effort at collecting, auditing, and maintaining this food habits database of unprecedented scale and scope. I thank F. Almeida, W. Gabriel, L. Garrison, M. Fogarty, M. Terceiro, and other reviewers for constructive comments on earlier versions of this manuscript. I also thank W. Overholtz, F. Almeida, M. Fogarty, R. Brown, G. Begg, P. Rago, M. Sissenwine, S. Murawski, J. Collie, L. Maden, R. Rountree, and L. Garrison for stimulating conversations about this food web that sparked many of the ideas presented in this paper. This work was supported by NOAA, NMFS, NEFSC, and NOAA’s Coastal Ocean Program, Georges Bank Study. Finally, I assert Solo Deo Gloria.

References


A Multivariate Approach to Monitoring Changes in Species Composition of a Demersal Fish Community

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Extended Abstract

While extensive biomass surveys routinely gather information on the abundance of commercial and noncommercial fishes, information from these surveys is often analyzed on a species-by-species basis only. A more “holistic” analysis of community data is usually the domain of community ecology. Various approaches have been used to describe communities at different sites, to relate community structure to underlying explanatory factors, and to assess changes in community structure over time.

We describe a multivariate approach to derive indices of species composition based on trawl catch data from any number of stations. Our primary goal is to describe if and how the species composition of a community changes across some environmental gradient, across space, or over time, based on samples from the community at different points in space and time. Specific objectives are (1) to develop robust indices which summarize the major patterns of variation in species composition, (2) to model the indices as a function of environmental variables, (3) to identify the major trends over time in these indices, and (4) to interpret the indices in terms of species composition by relating them back to underlying species abundances.

The suggested approach follows a sequence of steps which keeps species abundance data and environmental data separate until appropriate indices of species composition are obtained. The indices are subsequently related to environmental gradients:

1. Sampling sites are selected from a clearly defined area and time frame in accordance with the goals of the study.
2. Species to be included in the analysis are selected and possibly combined into species groups at an appropriate level of aggregation. Rare species may be eliminated or, alternatively, can be aggregated at higher taxonomic levels.

3. After constructing a site-by-species matrix of abundances the data are transformed in order to reduce the influence of a few very abundant species. Field et al. (1982) recommend a fourth-root transformation which in its effect is similar to a log-transformation, but has the advantage that it is invariant to scale changes when used with the Bray-Curtis index of dissimilarity.

4. From the matrix of transformed abundances, Bray-Curtis dissimilarities among each pair of sites are computed.

5. Based on the Bray-Curtis dissimilarities an ordination using non-metric multidimensional scaling (NMDS) is performed. We recommend choosing a criterion for goodness of fit in advance and do the ordination using as many axes as is necessary to achieve the criterion. Goodness of fit is assessed using Kruskal’s stress criterion, a measure of discrepancy between the distances in ordination space and the underlying Bray-Curtis dissimilarities.

6. Because the orientation of axes is arbitrary, the solution is rotated using principal components such that the first axis corresponds to the axis of maximum variation. We suggest using the scores for each site along each rotated ordination axis as indices of species composition. Each index can be interpreted as representing a different, independent aspect of species composition.

7. The indices are subsequently related to appropriate explanatory variables, either in an exploratory sense to identify variables that are most strongly related to species composition, or to test hypotheses regarding species composition. The principal advantage of using indices of this kind is that they are statistically well behaved and allow us to conduct hypothesis tests regarding species composition. Furthermore, multivariate indices provide more sensitive indicators of change in community structure and can identify general trends that may not be apparent when using univariate measures (Austen and Warwick 1989).

8. Apart from relating the indices to environmental variables, we suggest a straightforward approach to interpret indices in terms of the underlying species compositions using scatterplots and rank correlations. Plotting the abundance of a species against each index is used to identify individual species that are strongly related to an index, and to assess the nature of the relationship. We found that species were almost always monotonically related to indices. In such cases we
recommend that important associations be defined simply in terms of the magnitude of the observed rank correlations.

The approach is illustrated using data from shrimp trawl surveys conducted by the Alaska Department of Fish and Game and the National Marine Fisheries Service in nearshore areas of the central Gulf of Alaska. For this example we used data collected between 1976 and 1995 in four nearshore areas around Kodiak Island. Species abundance data were transformed as described above and the NMDS ordination was conducted in 5 dimensions to achieve a satisfactory fit (Kruskal's stress = 12%). Only results for the first axis, the major mode of variation in species composition, are described here.

The first axis primarily reflected interannual variation; i.e., most of the variation in species composition in this data set occurred over time. There was a much stronger difference over time than among areas or along other gradients. The index, adjusted for depth effects, showed a strong decreasing trend with a sharp drop after 1980, but there were significant differences among the four areas (Fig. 1).

A group of five taxa (shrimp, Pacific herring, capelin, Pacific sand lance, and Pacific tomcod) showed a strong positive association with the first index, as defined by rank-correlations greater than 0.35 (plus group). In contrast, a minus group consisting of arrowtooth flounder, flathead sole,
Pacific cod, and walleye pollock was negatively correlated with the first index. Thus, the sharp decrease in the first index was shown to be related to a strong decrease in catch per unit of effort (CPUE) of the plus group, and a simultaneous increase of the flatfish and gadid species in the minus group (Fig. 2).

Using the outlined approach we were able to clearly demonstrate a pronounced shift in species composition that occurred in the nearshore areas of Kodiak Island in the early 1980s as well as significant differences in timing among different areas. The proposed index of species composition based on Bray-Curtis dissimilarities and NMDS ordination provides a sensitive indicator of variation in community composition and can provide a powerful link for statistically relating species composition to environmental variation and for testing hypotheses regarding species composition.

References


OSMOSE: A Multispecies Individual-Based Model to Explore the Functional Role of Biodiversity in Marine Ecosystems

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Abstract
Considering the management of marine resources as the management of an ecosystem integrating different interactive components has enriched our understanding of fisheries dynamics. Indeed, the dynamics of marine exploited communities do not only reflect the effects of fishing mortality and of hydroclimatic conditions but is also the result of multiple interspecific interactions. An individual-based model OSMOSE (Object-oriented Simulator of Marine biOdiverSity Exploitation) is developed in Java programming language to explore the functional role of biodiversity in the exploitation of multispecies systems. By its flexibility, individual-based modeling permits implementation of different levels of biodiversity. In OSMOSE, species are age- and size-structured and modeled as interacting in the bosom of a spatial trophic web. Each species can be the predator or the prey of another species depending on its stage of its life cycle. Two simple rules form the basis of the trophic model. There is first a criterion of body length for the selection of prey and secondly a law of spatio-temporal co-occurrence. Thus, the fishes would prey regardless of the taxonomic identity of their prey and, moreover, predation and competition can vary with time, according to species abundances and changes.
Introduction

With the increase of the number of both species and trophic levels being exploited, multispecies approaches have gone through a large expansion in fisheries science (e.g., Mercer 1982, May 1984, Daan and Sissenwine 1989, Pauly et al. 1998). Two main types of approaches have so far been developed.

The first multispecies investigation consisted of extending to several species the monospecies models that were classically used in fisheries science. This approach encompasses the multispecies Schaefer model (May et al. 1979, Kirkwood 1982, Ströbele and Wacker 1991) and the Multispecies Virtual Population Analysis (MSVPA; Andersen and Ursin 1977, Helgason and Gislason 1979, Pope 1979). The multispecies Schaefer model is a system of several differential equations of Schaefer including a few linear terms of interspecies interactions. Some variants exist in the expressions of species dynamics and interactions, in particular for the case of a two species predator-prey system, the pioneer study of which is the one of Lotka-Volterra. Indeed, three functions are investigated: the growth rate of a predation-free prey population, the functional and the numerical responses of the predator (Holling 1959, Hassel and Varley 1969, Arditi and Ginzburg 1989, Yodzis 1994). The MSVPA lies on the estimation of the predation rate mortality of exploited species by partitioning the food of each stock into the different potential prey in relation to their biomass and a suitability coefficient. This latter has to take into account the size suitability of the prey, the degree of species habitats overlap, and the chance a predator has to encounter a prey.

The second type of multispecies approach is more concerned with the emergent properties of multispecies assemblages or ecosystems without explicitly detailing the species processes that are at stake. Three reasons which could motivate this approach are: (1) Practical reasons since investigating aggregated levels requires a less exhaustive information. It is illustrated by the use of the MSY concept for the total exploited fish biomass in a given ecosystem (Brown et al. 1976, FAO 1978); i.e., the equilibrium production of a multispecies assemblage is a parabolic function of fishing effort and the MSY corresponds to the exploitation of this assemblage up to half its virgin biomass. (2) There is a need to search for other ways than classical fisheries approaches to estimate the marine biomass production and to understand the trophic structure of marine ecosystems. To this end, Christensen and Pauly (1992) and Pauly et al. (1998) developed the trophic model ECOPATH. In this compartment approach, the species are segregated into a certain number of groups that are linked together with matter flows. Two mass conservative equations describing the equilibrium production and consumption of each species group form the basis of ECOPATH. (3) The analysis of both catch and scientific trawl survey data has allowed to bring to the fore the existence of noteworthy conservative patterns at the scale of the ecosystem. A widespread observation in fish-
eries science, and in other ecological fields as well, is the relative stability of ecosystems total production compared to individual species production (e.g., Sutcliffe et al. 1977, Beddington 1984, Murawski et al. 1991). Another observed property is the relative uniformity in the shape of marine ecosystem size spectra; i.e., the distribution of biomass concentration is a slightly decreasing function of organism size (Sheldon et al. 1972, Pope and Knights 1982, Murawski and Idoine 1992, Rice and Gislason 1996). This conservative property, despite the fluctuations observed in species abundance, suggests that the interactions within a species assemblage tend to spread the biomass over the whole range of organism sizes, that is to fully occupy the production potential of a given system (Kerr and Ryder 1989).

Two main multispecies approaches can then be distinguished, the first lying on the coupling of species dynamics with interaction modules, the second paying particular attention to the macroscopic properties of the ecosystem. Two main ideas can be drawn from these different approaches: First, they almost all refer to trophic interactions, and second, the different studies agree to conclude that interspecific interactions help the key to understanding the emergent features at the ecosystem level. Nonetheless, the processes that link the dynamics at the levels of the species and the ecosystem are not clearly defined. On the one hand, the coupled species dynamics provide a partial vision of the ecosystem (few species are considered) and on the other hand, the aggregated approaches do not make clear the interspecies interactions that give rise to the investigated macroscopic behavior. The complexity of fisheries systems can be at the origin of both the modeling difficulty and the difficulty in linking both approaches. This complexity has been defined by Pimm (1979) and Kikkawa (1986) as the number of pairs of interspecific interactions in the system. In addition, for Goodman (1975), the complexity of ecosystems is synonymous with trophic diversity which can be measured by species richness. Accordingly, it appears that the notion of biodiversity and its derivatives can link the different scales of multispecies studies and could be the key to understanding ecosystem dynamics. For these reasons, an alternative multispecies approach has been developed that enables one to take into account ecosystem biodiversity and to explore its influence on the macroscopic attributes which are of interest for the management and the assessment of marine systems, namely their stability, resistance, and resilience.

**Functional Role of Biodiversity**

**Relationship Between Ecosystem Biodiversity and Stability**

In terrestrial ecology, the nature of the relationships between the diversity of the organisms living in an ecosystem and the properties of this
latter, in particular the relationships between diversity and stability, are among the most investigated, experimentally and theoretically as well. MacArthur (1955), Odum (1969) or more recently Hammer et al. (1993) and Tilman (1996) draw a parallel between a better stability of the ecosystem with a greater species richness, thereby assuming that the energy flow in a complex trophic web, i.e., which presents a great number of interspecies links, would be less sensitive to disruptions since it can use more different pathways through the system. In contrast, at the local level, a higher species richness would decrease the stability of species abundances by these phenomena of abundance compensations following, for example, climate perturbations (Tilman 1996). Fisheries ecologists have also been aware of the close links that could exist between the biodiversity of the resource and its stability, in the sense defined by MacGillivray and Grime (1995); i.e., the capacity of an ecosystem (1) to resist to a change while maintaining a function to a certain level (resistance), and (2) to recover normal levels of a function after perturbation (resilience). In their simulations of multispecies systems, Wilson et al. (1991) have observed that in the case where the biological and demographical parameters of the populations are similar, the species dynamics are chaotic but such that the production peaks are in phase: thereby, the system biomass varies greatly. In contrast, when the population parameters are such that there is a functional diversity within the species, the total biomass of the system becomes stable. This “diversity-stability” hypothesis is the most common in ecology although some experimental studies have led to its rejection. With the idiosyncratic hypothesis, Lawton (1994) discusses the possibility that no particular relationship exists between the species diversity and the properties of the system. The resulting controversies raise some questions about the relevance of species richness as the study variable and consequently about the functional equivalence of the species in an ecosystem. Other hypotheses have then been proposed as alternatives to the “diversity-stability” hypothesis. The “rivets” hypothesis suggests that the resistance of an ecosystem can decrease with the number of species even though the system performance (biomass production, for example) does not seem to be affected. But the consequences of a perturbation can be sudden and drastic. This hypothesis has been introduced by Ehrlich and Ehrlich (1981) who compare the species of an ecosystem to the rivets of a plane. The progressive removal of the rivets up to a certain threshold would cause the ecosystem to collapse. The authors suppose that some species extinctions can go unnoticed in terms of system performance because redundancy may exist within the system, thus generating a non-linear relationship between diversity and stability.

**Redundancy Hypothesis**

The redundancy hypothesis proposed by Walker (1992) is in a way the logical development of the rivets hypothesis and considers that some species are capable of extending their functions in the ecosystem in order to
compensate certain decreasing abundance of similar species. In the core of this concept is the idea that the ecosystem is segregated into a certain number of functional groups, within which species would have functional analogs. Some species can disappear with little effects on ecosystem processes as long as each functional group is represented. An important role of redundancy is to provide an insurance to the system. During an environmental change, a species can disappear since the biotic and climatic conditions do not correspond any more to its tolerance range. But other species belonging to the same functional group may be resistant to the perturbation and even increase their production as a consequence of competition. By extending this redundancy hypothesis, a keystone species would be a functional group without redundancy. Its loss would cause massive changes in ecosystem structure and may give rise to many other extinctions (Fig. 1). It is worth noticing that the keystone status can be attributed to or removed from a species following the evolution of the system. A redundant species can indeed become a keystone species if it becomes the last representative of its functional group and conversely.

Ecosystems containing the same number of species can have different functional structurations, thereby resulting in difficulties of analyzing, comparing ecosystems and in establishing clear relationships between species richness and the stability properties of ecosystems. Indices used for characterizing biodiversity also have to be nonambiguous. The number of species of a community, for example, is an insufficient measure to characterize the composition of a community. At equal density and species richness, two communities can have very different structures. The concept of "species diversity" thus substitutes for the simple one of species richness to allow for the relative species abundances. It corresponds to the cardinal measures of biodiversity (Cousins 1991), both Shannon and Simpson indices of which are the most used. The interest of these indices is to permit global comparison of either different communities or the successive states of the same community. But they do not convey the functional structures, namely the different modes of community organization. New measures are proposed, called ordinal measures (Cousins 1991), which do not consider the species in an equivalent way. The "taxonomic distance" effect can, for instance, be taken into account (Vane-Wright et al. 1991) with the hypothesis that the phylogenetic classification of the species reflects anatomical and morphological differences between species. Previously evoked is also a measure based on the size of individuals, namely the size spectra of the ecosystem. The underlying hypothesis is that the trophic organization of a system is linked to morphometric differences between species. The observed gap between the prey species ranges of different predators would most often stem from similar gaps in the dimensions of the organs involved in food intake (e.g., body size, jaws size). The existence of such relationships would thus allow viewing the size spectrum of a community as a global indirect expression of its functional structure.
To conclude, the notion of biodiversity can have major consequences in fisheries management. It seems indeed indissociable from ecosystems properties of stability since it can allow this latter to dispose of a certain margin of adaptability while facing some perturbations, especially those due to fishing mortality. An important investigation area would be to define some criteria enabling determination of the functional role of each taxonomic entity in the ecosystem (redundant or keystone species).

**OSMOSE: An Alternative Model for Diversified and Dynamic Trophic Web**

**Underlying Hypotheses**

In this context, OSMOSE (Object-oriented Simulator of Marine biOdiverSity Exploitation) has been developed to possibly account for two aspects which are supposed to be important in the functioning of marine multispecies communities: (1) the diversity of the components (e.g., species richness, biological parameter diversity, size diversity). Indeed, OSMOSE is devoted to investigating the functional role of biodiversity in ecosystem stability and subsequently to exploring the consequences of fishing activity on this biodiversity. (2) the possibility for the ecosystem trophic structure to vary. In the multispecies models previously mentioned, there is little place for adaptation and change, as the elements of the system can hardly learn or modify their behavior. As an example, the classical models represented by a more or less complex system of differential equations and describing

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*Figure 1. Theoretical structuration of ecological communities.*
various dynamics (stable, cyclic, or chaotic) are capable of functioning but not of evolving (Allen 1990). Indeed, the species dynamics are modeled from preestablished relationships of predation or competition. In this context, an attempt is made to model a dynamic trophic web by implementing the possibility for the predators to shift species in relation to species abundance conditions. As stated by Rice (1995), life-history omnivory has profound effects on system dynamics. For Cousins (1991), any species can be the prey of a predator if the predator encounters some individuals of this species, if the prey is not too large (size inadequacy for possible predation, escapement) and finally if the prey is not too small (null energy gain). In OSMOSE, the predation behavior is continuously conditioned by the first two conditions. The third condition will be respected only in the case where prey of adequate size are in sufficient abundance in the predator environment. Thus fishes would prey regardless of the taxonomic identity of their prey (see for example Bond 1979, Laevastu and Larkins 1981, Sissenwine 1984). This opportunism seems realistic in the case of animal preys for which the catches are mainly due to physical and mechanical processes. More specificity exists, due to chemical processes, for parasitism relationships or for example the search of food of terrestrial herbivores (Cousins 1991).

**An Individual-Based Simulation Tool**

The individual-based approach we have adopted enables, by its flexibility, taking into account a great number of species and, by its principle, managing predator opportunism by a simple law of spatio-temporal co-occurrence. Two biological principles form, indeed, the basis of this approach (DeAngelis and Gross 1992), namely: (1) the physiological and behavioral unicity of each individual which results from the combination of both its genetic inheritance and its environment, and (2) the localization principle which states that an individual is mainly affected by the only organisms that are located in its spatio-temporal vicinity. The biological entity which should correspond to a computer individual had first to be chosen. We had the choice between the species, the cohort, the shoal or the fish level. As individual size is potentially an important variable to set the predation process and to address the functional role of ecosystem biodiversity, the species is too aggregated a level to represent the unit of action and interaction of the model. Besides, for the individual entity chosen, the variables of interest for our study (biological parameters, fish size, predation behavior) have to be relatively homogeneous. As shoals are generally composed of fishes having the same size, the same food, the same spatial coordinates, and belonging to the same species it was not relevant to consider the fish level. In OSMOSE, the unit of interest is then the fish school. In object-oriented programs, as many objects as desired can be created from some molds called classes and can interact by means of messages. Written in Java, OSMOSE is an artificial ecosystem containing a certain number of object species (up to a hundred species) which are a set of age
classes which are in turn a collection of fish schools (Fig. 2). This hierarchical structure permits following some key features at different levels of aggregation. The object species are characterized by some input parameters as survival, growth, and reproduction ones (Table 1). These are parameters that can be easily collected from the literature or from the FishBase database (Froese and Pauly 1997).

**Description of the Modeled Processes**

The model represents annual dynamics of interactive species which are heterogeneously distributed in a rectangular lattice. To initiate the system, an abundance value is given to the age class 0 of each species. Then, a pseudo-cohort is formed from the following classical survival equation and is randomly distributed in the lattice:

\[
N_{a+1} = N_a e^{-M} \quad \text{with} \quad \begin{cases} N_a = \text{abundance of age class } a \\ M = 1 & \text{for } a = 0 \\ M = 0.2 & \text{for } 1 \leq a < \text{longevity} \end{cases}
\]

The mean lengths and weights at age for each species are calculated from the input von Bertalanffy parameters. Thereby, at time 0 and within an age class, all the shoals have the same values for the length and weight attributes. Once the system is initiated, the whole life cycle of fishes is modeled following the processes that occur in the course of one simulated year (Table 2). First the fishes are submitted to the so-called diverse mortality. For fishes older than age 1, this mortality is independent of feeding activity (predation and starvation). For age class 0, on the contrary, the starvation mortality is implicitly taken into account in this diverse mortality rate, the interannual variability of which, follows the one supposed for the ecosystem primary production (stable, cyclic, or chaotic). The subsequent stages are only applied to age-1 and older fishes. Following the foraging activity, the predation process occurs such that a predator can potentially feed on any species, provided that there is spatio-temporal co-occurrence and that the prey size does not exceed a certain threshold value. Laevastu and Larkins (1981) and Gislason and Helgason (1985) estimate the upper predator/prey size ratio at about 10%. Thus, as all fish go through the larval-juvenile stage, they can be at a given moment at the basis of the carnivore trophic levels. Thereby, two species can be simultaneously the predator and the prey of each other, according to their stage in the life cycle. On the other hand, fishes should consume about 3.5 grams of food per gram of fish and per year. This value represents an average calculated from different species values provided by Longhurst and Pauly (1987). From the ratio between the quantity of food the shoals achieve to consume and the one the shoals should consume, a predation success rate is calculated. One can notice that during this stage,
Figure 2. Hierarchical organization of OSMOSE.
Table 1. Input parameters of OSMOSE.

<table>
<thead>
<tr>
<th>INPUT PARAMETERS</th>
<th>SYMBOL</th>
<th>DETAIL</th>
</tr>
</thead>
<tbody>
<tr>
<td>GROWTH parameters</td>
<td>$L_\infty$</td>
<td>Von Bertalanffy growth model parameters</td>
</tr>
<tr>
<td></td>
<td>$a_0$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$K$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$c$</td>
<td>Allometry parameter (g.cm$^{-3}$)</td>
</tr>
<tr>
<td>REPRODUCTION parameters</td>
<td>Maturity age</td>
<td>(years)</td>
</tr>
<tr>
<td></td>
<td>$\alpha$</td>
<td>Relative fecundity (number of eggs spawned per g. of mature female)</td>
</tr>
<tr>
<td>SURVIVAL parameters</td>
<td>Longevity</td>
<td>(years)</td>
</tr>
<tr>
<td></td>
<td>$D$</td>
<td>Diverse mortality rate (free of predation and fishing, in year$^{-1}$)</td>
</tr>
</tbody>
</table>

Table 2. The processes modeled in OSMOSE during one time step (year).

<table>
<thead>
<tr>
<th>PROCESS</th>
<th>DESCRIPTION</th>
<th>LEVEL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural mortality without predation</td>
<td>$N_{\text{surv}} = N_\alpha e^{-D}$</td>
<td>Age class</td>
</tr>
<tr>
<td>Poraging</td>
<td>Moving towards higher densities of potential preys</td>
<td>Shoal</td>
</tr>
<tr>
<td>Predation</td>
<td>- Size criteria for prey selection</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Spatio-temporal co-occurrence</td>
<td>Shoal</td>
</tr>
<tr>
<td>Predation success rate S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Starvation mortality</td>
<td>When S&lt;30%, the probability for a fish to die is a negative exponential function of S</td>
<td>Shoal</td>
</tr>
<tr>
<td>Growth</td>
<td>Von Bertalanffy model: $\Delta L = L_0 (1 - e^K D) e^{-X_\alpha - p}$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Depending on $S$, $\Delta L=10%$.</td>
<td>Shoal</td>
</tr>
<tr>
<td>Reproduction</td>
<td>$N_0 = \alpha SB$</td>
<td>Species</td>
</tr>
</tbody>
</table>

$=$simulation time in years, $\alpha=$age in years, $N=$fish number, $D=$dive Mortality rate in year$^{-1}$, $L=$fish length in m, $\alpha=$relative fecundity in number of eggs per g. of mature female, $SB=$spawning biomass in g.
the predation mortality of fish is taken into account in a completely explicit manner. Depending on the predation success rate, a phenotypic plasticity is then implemented each year for fish mortality (starvation), growth and indirectly for reproduction (Table 2). In other words, the more the fish feeds, the more it grows, the less it dies and the more it reproduces. It is worth noticing that in OSMOSE, the key stages of the fish life cycle are explicitly modeled. For example, the stock-recruitment relationship observed in the simulator stems from explicit density-dependent processes such as predation or starvation mortalities. Also, the three functions investigated in Lotka-Volterra type predator-prey systems (namely the growth rate of a predation-free prey population, the functional and the numerical responses of the predator) emerge in OSMOSE from simple microscopic predation behaviors.

Conclusion

OSMOSE provides a possible alternative to other multispecies models by enabling investigation of the spatial dynamics of a great number of interacting species without making any a priori hypothesis on the food web architecture. OSMOSE is still in progress but different simulations can from now on be envisaged. The model will be generically implemented with the study of different types of exploitation inspired from the main world fisheries. The fisheries can be classified on the basis of the type of exploited resource as it was proposed by Larkin et al. (1984): the number of species caught (in the order of magnitude of about ten or of a hundred), habitat (e.g., pelagic, demersal), the number of exploited trophic levels. Besides, the existence of different strategies of exploitation allows establishment of a transverse typology. For example, target fisheries can be distinguished from nondiscriminating fisheries. The first exploitation type is illustrated by the North Sea fishery which can be represented by a set of diversified fleets targeting one or a small set of species of commercial interest (Gulland and Garcia 1984). For the second fishing strategy, a great number of species is exploited by a uniform fishing fleet. These fisheries would possess a more important operational flexibility (Garrod 1973). They can seasonally or annually shift species assemblages in order to stabilize their income despite the resource variability. By means of a comparative approach of these different typologies, OSMOSE will permit testing of different hypotheses concerning the functional role of marine ecosystem biodiversity. For this purpose, the main interest of this model is to provide as output the ecosystem size spectra, which is suspected to be an important indicator of ecosystem structuration, accordingly to the various observations and theoretical developments that have been mentioned in this article. With OSMOSE, an attempt will be made to link the notion of species redundancy with the distribution of fish sizes in an ecosystem. Moreover, the spatialized size spectrum is provided in OSMOSE and can be used to study the effect of marine refuges on fish population dynamics. Consisting of
closing some fishing areas in order to preserve ecosystem (functional?) biodiversity, this management strategy is increasingly advocated but we still lack, on the one hand, criteria to determine the spatio-temporal limits of the refuges, and on the other hand, experience to judge the consequences of this type of measure. The virtual laboratory OSMOSE may permit exploration of the conditions within which these spatio-temporal restrictions can be useful.

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Ecosystem Considerations and the Limitations of Ecosystem Models in Fisheries Management: Insights from the Bering Sea

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Abstract

Over the past 10 years there has been increasing criticism of management decisions that are based on single-species approaches and a call for the implementation of ecosystem approaches. The major criticism of single-species models is that they cannot predict changes in community structure. Unfortunately, our experience in modeling the Bering Sea shows that these same criticisms can also be leveled against ecosystem models.

We employed trophic mass-balance models (Ecopath and Ecosim) to examine some possible explanations for the changes that occurred in the Bering Sea between the 1950s and 1980s. We removed fish and mammals...
from the modeled system and tracked how other components of the ecosystem responded. Our mass-balance models indicate that neither whaling nor commercial fisheries were sufficient to explain the 400% increase in pollock biomass and other changes that may have occurred between the two time periods. The simulations further suggest that environmental factors, affecting recruitment or primary production, may be more important in determining the dynamics of the Bering Sea ecosystem than predator-prey interactions alone. These findings illustrate that mass balance models that do not account for the impact of climate variability on year-class strength cannot provide reliable estimates of trends in marine fish production. However, our models can show how predation and fishing can affect trophic interactions among species. As such, ecosystem models are a useful scientific tool to identify gaps in understanding and data needs, but are unlikely to ever replace single-species models. They may instead complement and provide parameters to single-species models. Ecosystem models such as ours are still in the early stages of development and will become increasingly more important as a management tool as they begin to incorporate spatial and oceanographic/climatic information.

Introduction

The Magnuson-Stevens Fishery Conservation and Management Act (1996) is the basis of fisheries management in U.S. jurisdictional waters. It maintains that fisheries are to be conserved and maintained to protect the marine ecosystem and to ensure the greatest overall benefit. It further encourages the application of ecosystem principles in fishery conservation and management.

To date, fisheries have not had good tools for understanding how fishing for one species will affect other components of the ecosystem. Fisheries scientists and managers are not yet able to replace single-species approaches with multispecies ecosystem approaches that can reliably predict shifts in species composition, abundance, and productivity. This is changing, however, as people begin to pool their collective knowledge into multispecies and ecosystem models. A number of models have recently been constructed for marine ecosystems around the world (e.g., see contributions in Christensen and Pauly 1993, Pauly and Christensen 1996), and their numbers keep increasing (see http://www.ecopath.org). However, ecosystem modeling is still in its infancy, leaving it unclear to what extent such models can guide ecosystem-based management.

A fundamental question for fisheries concerns how ecosystem models can be used to guide management decisions. Ecosystem models provide information on trophic linkages in a system and have the potential to show how fishing on one species might have unintended effects on other species in a system. Such models were applied to various regions of the North Pacific more than 20 years ago (Laevastu and Larkins 1981, Laevastu...
et al. 1982). However, in order to make progress in marine ecosystem management, scientists need to consider more fully how to sufficiently validate these models and communicate the results to managers in a meaningful way that can guide management decisions. This is the challenge we face in our attempt to model the large-scale changes that occurred in the eastern Bering Sea between the 1950s and 1980s.

**An Ecosystem Model of the Eastern Bering Sea**

We constructed an ecosystem model of the eastern Bering Sea using the Ecopath and Ecosim approach. Ecopath is a software package that describes an ecosystem at steady state using a mass-balance approach (Christensen and Pauly 1992, 1995). It is a relatively simple, but powerful method to model the biomass and fluxes of an ecosystem, and gain some insights into the relationships of the various species in the ecosystem. Ecosim can be applied to the Ecopath files, turning them into fully parameterized simulation models (Walters et al. 1997).

The area we delineated in the eastern Bering Sea encompasses the region covered by the Alaska Fisheries Science Center's bottom trawl surveys of the shelf and slope down to 500 m (Fig. 1). It included a wide range of marine habitats but was treated as a single homogenous area. (A spatially explicit model is being developed using Ecospace software.) Nearshore fauna and the northern portion of the Bering Sea were not considered. We constructed two models: one for the 1950s before large-scale commercial fisheries were under way, and another for the 1980s after many marine mammal populations had declined. Both were annual average models, which means that the biomass and species composition of summer and winter were averaged to provide a year-round annual average.

The main motivation for developing these models was to test the commercial whaling cascade hypothesis (i.e., that pelagic whaling in the eastern Bering Sea in the 1960s set up a chain of events that released prey, reduced predation, and increased the Bering Sea's walleye pollock carrying capacity; Merrick 1995, NRC 1996). How the ecosystem differed between the pre-whaling and post-whaling periods, and how the effects of fishing and whaling altered the dynamics of the Bering Sea were among the questions we posed. We also used the model to consider how changing current fishing quotas for pollock might alter the dynamics of other species in the ecosystem.

A complete description of the model and parameters used is contained in Trites et al. (In press). We split the hundreds of species that make up the Bering Sea ecosystem into 25 groups (Fig. 2). Information gathered from published sources included the numbers or biomass of each group of species living in the Bering Sea; their diets, rates of consumption, and production. The two primary data sources for groundfish biomass estimates were surveys or stock assessments conducted by the Soviet Union during the 1950s and the United States National Marine Fisheries Service
Figure 1. The eastern Bering Sea as defined in the ecosystem model. Total area is approximately 500,000 km².

(NMFS) during the 1980s. Population estimates for marine mammals came from Perez (1990), the NRC (1996) report, and the 1987-1988 Marine Mammal Protection Act annual report (NMFS 1988). Estimates for other species were drawn largely from stock assessments performed by NMFS scientists. Diet data for groundfish come primarily from the groundfish food habits database of NMFS while diet data for marine mammals come primarily from the 1996 NRC report and references therein. Several assumptions were made with respect to the 1950s model. For groups that had no abundance information from that time period, we assumed they had the same biomass as the 1980s period. We also made assumptions about the diet compositions of animals during that time period, particularly assuming that pelagic fish (herring, capelin, and others) were a more important prey than pollock in the 1950s.

The biomass estimates that we input to our mass-balance ecosystem models reflected our assumptions that most of the top predators (trophic level IV) declined from the 1950s to the 1980s (Fig. 3). They included Steller sea lions, seals, sperm whales, deepwater fishes, and other demersal fishes. The only top predators that were assumed to increase were large flatfish such as arrowtooth flounders. At the mid-trophic level (III), baleen whales and pelagic fishes were assumed to decline while small
Figure 2. Flow chart of trophic interactions in the eastern Bering Sea during the 1980s. All flows are in t per km$^2$ per year. Minor flows are omitted as are all backflows to the detritus.
flatfish, pollock, and walrus and bearded seals were assumed to have increased.

Pollock contributed over 50% of the total flow of energy through trophic level III during the 1980s compared to only 10% during the 1950s. In contrast, pelagic fishes contributed nearly 50% of the flow in the 1950s. At trophic level IV, no one species dominated the flow of energy during the 1950s. However, during the 1980s, large flatfish contributed over 60% of the total energy flow. Large flatfish and adult pollock that dominated the Bering Sea in the 1980s appear to be significant competitors of seals and sea lions. There are also significant overlaps in the diets of pollock and baleen whales.

Our dynamic simulation showed that removing whales from the 1950s model ecosystem had a positive effect on pollock, by reducing competition for food. However, whaling alone was insufficient to explain the 400% increase in pollock biomass that may have occurred between the 1950s and 1980s. Nor could commercial fisheries alone account for the observed changes. The magnitude of changes that occurred in the biomass of all the major groups in the eastern Bering Sea cannot be explained solely through trophic interactions and fishing removals. This suggests a need to examine our assumptions about the state of the Bering Sea in the 1950s, particularly with regard to pollock abundance.

We used our models to test various hypotheses about the effects of whaling, fishing and regime shifts on the Bering Sea (Trites et al., In press). Our models suggest that factors comprising a regime shift may have been at play in altering the Bering Sea between the 1950s and 1980s states, and may have been more important in affecting this northern ecosystem than trophic interactions and fishing removals. Important factors comprising the regime shift could be changes in temperature and/or current patterns that have differential effects on early life history survival of various species. In addition, our assumptions about low pollock abundance and the low importance of pollock in the diet of certain animals in the 1950s may be inaccurate. Shuntov (1972) reported that during the Soviet fishery investigations in the eastern Bering Sea from 1957 to 1964, walleye pollock was one of the most common Bering Sea fishes and was a staple food of large flatfish as well as other fishes.

Our conclusions about the causative factors influencing the shifts in the Bering Sea ecosystem are in contrast to those for the Gulf of Thailand ecosystem. Christensen (1998) found that fishing rates alone could move this tropical ecosystem from one state to another (1960s-1980s: before and after the development of trawl fisheries). Future work to improve the Bering Sea 1950s model should include testing the possibility of a higher dominance of pollock than we assumed.

We examined three pollock fishing scenarios to explore how the Bering Sea ecosystem might be changed from its 1980s state. We considered the effects of reducing the biomass of adult pollock by 50%. We also considered what might happen if pollock were overfished to the point that all
the juvenile and adult pollock were removed. Obviously, these two scenarios are hypothetical and do not reflect fishing policies that would be considered under the present fishery management regime. Finally, we considered how the Bering Sea ecosystem might look if pollock were not caught at all. All simulations were run over 30 years.

Our model suggests that increased fishing pressure on pollock has only a small effect on the equilibrium estimates of adult biomass due to a continuous replenishment from the juvenile stock (Fig. 4). At certain fishing levels, juvenile pollock may benefit from reduced cannibalism. System-wide effects are minimal, with the biomass changes of individual groups changing from less than 1% to about 30%, because the adult pollock stock does not change appreciably. However, the model predicts that equilibrium biomass levels of seals, sea lions, and piscivorous birds would increase due to an increase in the abundance of juvenile pollock.

Dynamic simulations of overfishing pollock to the point of extinction in the 1980s, predict the decline of seabirds that consume juvenile pollock. However, reducing the adult biomass of adult pollock by 50% would have a positive effect on seals, sea lions, and piscivorous birds because the abundance of juvenile pollock, which they consume, increases as cannibalism
by adult pollock is reduced. This result corroborates the conclusion previously made by Laevastu and Favorite (1988) for Bering Sea pollock: that fishing on the older, cannibalistic portion of the stock might increase juvenile survival and abundance.

Simulations in which pollock fishing is stopped in the 1980s result in a larger adult population and a smaller juvenile pollock population. Reducing the juvenile pollock population has a negative effect on seabirds and a small negative effect on marine mammals.

**Success and Failure of the Bering Sea Ecosystem Model**

We were unable to move from the assumed state of the Bering Sea in the 1950s to our more certain understanding of the Bering Sea in the 1980s using dynamic simulation of the trophic interactions and fishing removals. Our assessment was that environmental change (which we did not explicitly model) is one explanation for the changes in flatfish and pollock, and the decline of pelagic fishes. Uncertainty in the 1950s state is the other explanation.

We do not know at this point how well our models represent the Bering Sea ecosystem, nor do we have a straightforward means of quantifying the uncertainty of our results. However, we can do further testing to examine our assumptions of the 1950s model. We can also try to project the 1980s model forward in a way that matches present observations. Our models are based on the best available data and have been used in a simple and rigorous modeling framework (Ecopath) that has a number of checks and balances to ensure consistency. Thus, we feel that we can make inferences about some of the general and fundamental properties of the Bering Sea, despite our incomplete knowledge of the past and present. For example, we can identify some of the major flows of energy through the Bering Sea and better understand the trophic relationships of the different species living in the Bering Sea. Our model suggests that the Bering Sea is a system where cascading effects of changing one component tend to be sluggish and may be small compared to the magnitude of change that the environment can cause via its impact on recruitment or primary production. Whether fishing for pollock or other species results in the unexpected changes predicted by our model remains to be verified. It nevertheless highlights the strength of ecosystem approaches to understanding the whole system.

Our conclusions are broad and general and may not be particularly useful to people charged with setting fishing quotas or making other management decisions. However, our models are the first step in a series of models that will come later. Splitting more groups of species into immature and mature stages, and adding habitat and spatial/migratory relationships (Walters et al. 1998) will all improve this model. Ecosystem
Figure 4. Equilibrium biomass for Bering Sea species following changes to the fishing mortality of adult pollock in the 1980s model. Arrows mark the instantaneous rate of fishing (F per year) during the 1980s. The top left panel shows changes in the biomass and catch of baleen whales under different levels of F. The other five panels show the relative change (%) that would occur to other species in the ecosystem model to compensate for changes in the abundance of adult pollock.
models will also need to explicitly consider seasonal and environmental factors influencing carrying capacity and recruitment of dominant species. These are being extensively studied by the National Oceanic and Atmospheric Administration’s (NOAA) Fisheries Oceanography Coordinated Investigations program (Kendall et al. 1996) and the Southeast Bering Sea Carrying Capacity program (http://www.pmel.noaa.gov/sebscc/).

Criticisms that have been leveled against single species models can be equally raised against multispecies ecosystem models such as ours. Neither type of model does a particularly good job yet of predicting large decadal shifts in abundance, productivity, or species composition. It is unlikely that ecosystem models will ever replace single-species models. Instead, ecosystem models will likely complement single-species models and provide a context and/or parameters for them. They should prove to be another addition to the scientific and management toolbox.

As a management tool, ecosystem models are not yet very useful. They still need to prove themselves by being able to reconstruct the past or by making realistic predictions about the future. They also need to convey uncertainty. However, as a scientific tool, ecosystem models such as ours are very useful. They can help to identify gaps in understanding and data needs. They can also guide the choice of experiments to highlight our understanding (Walters et al. 1997). Finally, and perhaps most important, they are a tool to bring diverse groups of people together to share their knowledge about small pieces of the ecosystem and increase the collective knowledge about the whole system.

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References


A Mass-Balanced Model of Trophic Flows in Prince William Sound: Decompartmentalizing Ecosystem Knowledge

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Abstract

Just as real-world food webs contain complex interactions among species, so too must scientists and others interact to describe food webs in realistic ways. The most useful ecosystem models are constructed through collaboration among a wide range of experts. Collaboration among Prince William Sound (PWS), Alaska, researchers resulted in a mass-balanced Ecopath model of trophic flows including all ecosystem components (explicitly or implicitly). This study was conducted to describe functional interactions among components, and to reveal thermodynamic constraints of these interactions, thus enabling further refinement of contributed estimates as well as dynamic simulations of ecosystem perturbations.

Since the 1989 Exxon Valdez oil spill (EVOS) in Prince William Sound, and adjacent areas, research teams focused on the status of particular biological components of the PWS ecosystem, changes to those components, and the effects of EVOS. Some research groups investigated the effects of EVOS on larger segments of the PWS ecosystem, but a system-wide analysis was not undertaken until the current model was constructed. Estimates of basic population parameters were lacking for several biological components of the ecosystem, but the Ecopath approach enables refinement of knowledge of uncertain groups based on the constraints of interrelationships among groups. The whole-system model described herein can be used by managers, schools, or local communities for learning, knowledge refinement, or simulation of environmental disturbances such as oil spills or increased fishing. Ecopath modeling through multiway collaboration is presented as a broadly accessible tool for restoration and resource planning with the potential to be highly community-based.
Only fluency across the boundaries will provide a clear view of the world as it really is.
E.O. Wilson, Consilience: The Unity of Knowledge, 1998

Introduction
It is increasingly apparent that single-species approaches to fisheries management fail in all but the most fortuitous circumstances (Wilson et al. 1994, Roberts 1997; also see Laevastu et al. 1996). This realization provides increased impetus for resource managers to adopt a more ecologically sophisticated logic. For example, components of ecosystems interact with each other, the actions of resource users affect nontarget components of ecosystems, resource users can influence the "biotic integrity" of an ecosystem (NMFS 1998), and natural changes in certain ecosystem components can cause changes in other components, which are often unpredictable. Incorporation of such whole-ecosystem considerations into resource decision-making is called "ecosystem-based management," in which human activities are managed within the context of a naturally dynamic and integral ecosystem (Langton and Haedrich 1997, NMFS 1998; also see Juda 1996, Okey and Harrington 1999).

Such nice ideas are not challenging to discuss; the real key to achieving ecosystem-based management in decision-making forums is the application of integrative analytical tools. The first tool needed is one that describes interactions of the components of a defined ecosystem, and the constraints that might exist among those components. For example, thermodynamic (energy flow) constraints can limit the sizes of populations, either absolutely or in conjunction with other limiting factors like predation or recruitment. The second analytical tool needed for the transition to ecosystem-based management is one that can be used to predict the effects of changes in one ecosystem component on other components. These tools should be comprehensive enough to provide a cohesive picture of the defined ecosystem, in as accurate a manner as possible, while retaining adequate simplicity to enable a wide range of interested parties to comprehend and use the model. Most importantly, these tools can function optimally when parallel collaborative structures enable maximum flow of ecosystem knowledge.

A mass-balanced trophic model of the Prince William Sound ecosystem was constructed using the user-friendly Ecopath software, with the collaborative contributions of a working group of experts from the region. This is a static model that includes all biotic components of the PWS ecosystem, either implicitly or explicitly, in a possible scenario of interrelationships (trophic energy flows among components). The data in the model were then analyzed in dynamic simulation routines called Ecosim and Ecospace to predict indirect effects of simulated perturbations on the biotic system. This modeling approach is discussed in the methods section below.
The purpose of this paper is to point out the natural necessity for broad collaboration to achieve (1) realistic descriptions of whole ecosystems, and (2) functional policies and "ecosystem-based management" of human activities (defined in Okey and Harrington 1999). We illustrate this necessity for collaboration by describing the methods used to construct the PWS model. This paper is about collaboration, not Ecopath modeling per se.

Our premise is that human knowledge of the ecosystem is, to a large degree, compartmentalized among individuals, research teams, institutions, and other groups. This is especially true within the modern milieu of western culture and science. We suggest that the most realistic description of an ecosystem can be constructed by de-compartmentalizing knowledge through collaborative efforts such as the one described herein, and through everyday communications and working relationships. Furthermore, traditional ecological knowledge of native communities may prove invaluable for achieving a fuller understanding of ecosystems, as this knowledge may be less compartmentalized, albeit generally less quantifiable.

The science conducted subsequent to the EVOS has been criticized for failing to maximize opportunities for knowledge gathering as the result of political and legal constraints (Keeble 1991, Wheelwright 1994, Paine et al. 1996). Our efforts to construct a balanced trophic model of PWS revealed that reliable estimates of basic information such as biomass, production and consumption rates, and diet composition are lacking for many groups. One explanation for this paucity of information is that EVOS research was not guided by a system-wide analytical framework. Another is that some components of the ecosystem have simply not been studied in depth because the ecosystem is complex. Notwithstanding these alternative explanations, a considerable amount of information has been collected about the biota within Prince William Sound during the years since the spill (Spies et al. 1996). Moreover, significant efforts have been made to describe, in detail, larger functioning segments of the PWS ecosystem to reveal system-level effects of EVOS (Cooney 1997, Duffy 1997, Holland-Bartels et al. 1997). These programs are the source of much of the available knowledge of the PWS ecosystem, but a comprehensive, system-wide synthesis had not been undertaken until the current model was constructed (see contributions in Okey and Pauly [1998] for a more detailed description of the model).

The mass-balanced trophic model of Prince William Sound was constructed to integrate and synthesize what is being learned from the various research and monitoring projects within the Exxon Valdez oil spill (EVOS) restoration program, and to enable insight into "the effects of the oil spill and the long-term restoration and management of injured resources and services from an ecosystem-level perspective," as desired by the EVOS Trustee Council (1996:53). A collaborative synthesis of compartmentalized information can optimize ecosystem-level insights into the impacts of EVOS and other anthropogenic stressors. Moreover, the EVOS Trustee
Council stated that existing PWS data sets “need to be integrated in a simple [cost-effective] model to benefit long-term resource management,” and “the restoration program will increasingly focus on an integrated, ecological approach.” The goals of our study are to achieve these stated objectives.

**Methods**

**The Ecopath Model of Prince William Sound**

The balanced trophic model of PWS was constructed to describe the most likely flow scenario during the period from 1994 to 1996. A quantitative description of the whole trophic structure of PWS and adjacent waters and the relationships among the different species and groups inhabiting the area will place the results of individual EVOS projects into a realistic context and enable marine resource policy planning on an ecosystem level (multispecies as opposed to single species). The PWS model has unique potential as its 50 defined ecosystem components makes it, by far, the most explicit Ecopath model to date. There are many possible examples of its use; a PWS Ecopath model can be used to reveal of shifts in trophic structure in the wake of the oil spill that might be hindering the recovery of seabirds and marine mammals. Likewise, a quantitative analysis of the relationships between seabird foraging and hatchery-released fish will help to identify the ecological role of the hatchery program. Also, it may help track pollutants as they move through the food web (Dalsgaard et al. 1998). The versatility of the Ecopath system allows it to produce a fast and cost-effective overview of any part of the system. The basic idea of this project is that the use of a mass balance model such as Ecopath will allow easy identification of areas of trophic flux that will be of interest to those involved in policy making and restoration.

**Constructing the PWS Model**

The collaborative process of constructing a balanced trophic model of the PWS ecosystem consisted of four components: (1) a scoping period to identify ecosystem components and experts, (2) workshops, (3) coordinated e-mail and telephone communications, and (4) an edited volume that provided a venue for authored contributions. Initial identification of components and contributors was accomplished through inputs from EVOS program scientists, conversations with other experts, and our knowledge of the PWS marine ecosystem and the scientific literature.

Three meetings occurred over a 9-month period: a preparatory working lunch held in conjunction with the 1998 EVOS restoration workshop in January 1998; a model specification workshop during March 2-4, 1998, at which invited experts provided initial estimates of biomass, production, consumption, diet composition, migration, and spatial distributions; and an evaluation workshop on October 5, 1998, at which participants evaluated the balanced model and initial analyses to refine strategies of future model iterations and analyses.
At the model specification workshop, parameters were contributed within the context of modifying a pre-existing, preliminary model of PWS, constructed from existing literature sources (Dalsgaard and Pauly 1997, Pauly et al. 1998b). This format of building upon an existing, simpler model served three purposes: (1) anticipating skepticism regarding construction of a realistic whole-ecosystem model, (2) avoiding pressure for commitment by contributors early in the process, and (3) ameliorating a seemingly daunting challenge by refining an existing model rather than starting from scratch.

Facilitated communication among working group participants was crucial to keep participants coordinated within the context of the whole interactive ecosystem, and the edited volume of authored sections enabled many experts to contribute data and invest time without sacrificing recognition. Table 1 shows that contributors from a broad range of affiliations contributed to the integration of knowledge about a broad range of ecosystem components.

Contributors provided estimates for each of the following parameters:

1. Biomass in wet weight units and expressed as density (t per km²) for PWS as a whole (9,059 km²).
2. The P/B ratio (production/biomass). In Ecopath-type models, this is equivalent to an instantaneous rate of total mortality (i.e., Z; per year).
3. The Q/B ratio (consumption/biomass). This is a population-weighted estimate of food consumption per unit biomass (per year), or ration for an average-sized individual.
4. Exports from the system consist of catches (here in t wet weight per year) and animals leaving the system.
5. Information for a group in which diet fractions add up to 1.

When available, contributors provided seasonal means allowing for consideration of seasonal oscillations. They were also asked to quantitatively indicate increasing or decreasing trends as well as uncertainty by providing confidence intervals or likely minimum and maximum values.

**Temporal Simulations with Ecosim**

Beyond the uses of static representations of the PWS ecosystem, the data in Ecopath files were used in dynamic simulations using the Ecosim approach of Walters et al. (1997). Ecosim models allow rapid exploration of the predicted consequences of natural or anthropogenic disturbances on all components of an ecosystem simultaneously over a specified time period (typically 10 years). These could include changes in fishing, anthropogenic disturbances like another oil spill, or natural changes in agents of physical forcing. Other changes in resource use or potential management actions can likewise be simulated.
Hypothetical Scenarios for Simulating Perturbations

After the balanced trophic model of PWS was constructed, hypothetical “what if” scenarios were simulated using Ecosim. These scenarios were contributed by B. Spies, B. Wright, and A. Gunther at the model specification workshop:

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

Spatial Simulations with Ecospace

The recently developed Ecospace routine (Walters 1998, Walters et al. 1998) was used to simulate changes in spatial distributions of Prince William Sound groups starting with information on habitat preferences and spatial distributions of habitats and organisms provided by contributors (also see Okey 1998). Ecospace simulates dynamic, two-dimensional redistribution of ecosystem components based on trophic interactions (flow) among organisms, their relative preferences for spatially specified habitats,
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<th>Ecosystem component</th>
<th>Contributor</th>
<th>Affiliation</th>
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<tr>
<td>Cetaceans</td>
<td>Craig Matkin</td>
<td>North Gulf Oceanic Soc., Homer</td>
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<td>Sharks</td>
<td>Lee Hulbert</td>
<td>NMFS Auke Bay Laboratory</td>
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<td>Pinnipeds</td>
<td>Kathy Frost</td>
<td>ADF&amp;G Fairbanks</td>
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<td>Cetaceans and pinnipeds</td>
<td>Rod Hobbs</td>
<td>NMML, NMFS, Seattle</td>
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<td>Pacific halibut</td>
<td>Bob Trumble</td>
<td>IPHC, Seattle</td>
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<td>Adult arrowtooth flounder</td>
<td>Mark Willette</td>
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<td>Tom Dean</td>
<td>Coastal Resources Associates, Vista, CA</td>
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<tr>
<td>Miscellaneous fish groups</td>
<td>Tom Okey</td>
<td>UBC Fisheries Centre, Vancouver</td>
</tr>
<tr>
<td>Seabirds and raptors</td>
<td>Bill Ostrand, David Irons</td>
<td>USFWS, Anchorage</td>
</tr>
<tr>
<td>Adult salmon</td>
<td>Slim Morestead (consulted)</td>
<td>ADF&amp;G, Cordova</td>
</tr>
<tr>
<td>Juvenile salmon fry</td>
<td>Tom Kline</td>
<td>PWS Science Center, Cordova</td>
</tr>
<tr>
<td>Nearshore demersal fishes</td>
<td>Tom Dean</td>
<td>Coastal Resources Associates, Vista, CA</td>
</tr>
<tr>
<td>Sea otter</td>
<td>J. Bodkin, D. Monson, G. Esslinger</td>
<td>USGS-BRD, Anchorage</td>
</tr>
<tr>
<td>Squid</td>
<td>Jay Kirsh</td>
<td>PWS Science Center, Cordova</td>
</tr>
<tr>
<td>Forage fishes</td>
<td>Evelyn Brown</td>
<td>UAF Institute of Marine Science</td>
</tr>
<tr>
<td>Deep epibenthos</td>
<td>Tom Okey</td>
<td>UBC Fisheries Centre, Vancouver</td>
</tr>
<tr>
<td>Adult Pacific herring</td>
<td>John Wilcock (consulted)</td>
<td>ADF&amp;G, Cordova</td>
</tr>
<tr>
<td>Sea ducks</td>
<td>Dan Esler</td>
<td>USGS-BRD, Anchorage</td>
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<tr>
<td>Juvenile Pacific herring</td>
<td>Robert Foy</td>
<td>UAF Institute of Marine Science</td>
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<tr>
<td>Jellyfish</td>
<td>Jennifer Purcell</td>
<td>Horn Point Lab, Cambridge, MD</td>
</tr>
<tr>
<td>Small benthic infauna</td>
<td>Stephen Jewett</td>
<td>UAF Institute of Marine Science</td>
</tr>
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<td>Nearshore zooplankton</td>
<td>Robert Foy</td>
<td>UAF Institute of Marine Science</td>
</tr>
<tr>
<td>Offshore zooplankton</td>
<td>Ted Cooney</td>
<td>UAF Institute of Marine Science</td>
</tr>
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<td>Deep large infauna</td>
<td>Tom Okey</td>
<td>UBC Fisheries Centre, Vancouver</td>
</tr>
<tr>
<td>Shallow small epibenthos</td>
<td>Tom Dean</td>
<td>Coastal Resources Associates, Vista, CA</td>
</tr>
<tr>
<td>Shallow large infauna</td>
<td>Tom Dean</td>
<td>Coastal Resources Associates, Vista, CA</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>Peter McRoy (consulted)</td>
<td>UAF Institute of Marine Science</td>
</tr>
<tr>
<td>Macroalgae and eelgrass</td>
<td>Tom Dean</td>
<td>Coastal Resources Associates, Vista, CA</td>
</tr>
<tr>
<td>Forage fish diets</td>
<td>Molly Sturdevant</td>
<td>NMFS Auke Bay Laboratory</td>
</tr>
<tr>
<td>Birds eating herring eggs</td>
<td>Mary Anne Bishop</td>
<td>Pac. NW research station, USFS, Cordova</td>
</tr>
<tr>
<td>Recreational catches</td>
<td>Scott Meyer</td>
<td>ADF&amp;G, Homer</td>
</tr>
<tr>
<td>Commercial catches</td>
<td>Bill Bechtol</td>
<td>ADF&amp;G, Homer</td>
</tr>
<tr>
<td>Preliminary model of PWS</td>
<td>J. Dalsgaard, D. Pauly</td>
<td>UBC Fisheries Centre, Vancouver</td>
</tr>
<tr>
<td>“What if” scenarios</td>
<td>B. Spies, B. Wright, A. Gunther</td>
<td>AMS, NMFS Juneau; AMS</td>
</tr>
</tbody>
</table>
and their movement rates and vulnerability to predators in the various specified habitats.

**Results**

Workshop participants helped define the ecosystem and its components, they contributed estimates for the input parameters listed above, and they provided information on spatial and temporal changes. Figure 1 shows the trophic levels and the relative biomasses of biotic components of PWS based on the contributed estimates to the trophic flow model (trophic flows are left out of Fig. 1, as they are too numerous to display in this format). This model and its graphical representation represents a likely scenario of energy flow, based on the assumption of equilibrium in the system.

The structure of trophic flows provides an indicator of knowledge flow and a guide for researcher interactions when refining the parameter estimates for a group. Figure 2 identifies all of the direct flows connected to a single group in the model (in this case, adult Pacific herring). Ideally, the parameter estimates for a given group are derived empirically and have a high degree of accuracy and precision, but in reality, there are varying degrees of uncertainty among groups. Inconsistencies in energy flow between connected groups are indicated when the Ecopath model is unbalanced. These highlighted inconsistencies enable researchers to revisit the data and refine the model in a systematic way. This refines the realism of the overall model as well as estimates for individual groups. If a particular group is “unbalanced” within the model (i.e., when the ecotrophic efficiency is greater than 1; “ecotrophic efficiency” is the proportion of production by a group that is either consumed or exported), this may indicate that biomass or production/biomass values for the group are underestimates, or that consumption by other groups has been overestimated. Thus, the researcher for a group can use trophic flow connections as a guide to collaborative interactions in order to refine the information for a group.

Ecosystem components extracted from other trophic positions reveal unique trophic flow patterns that indicate different knowledge flow structures for refinement and learning. The relative magnitudes of trophic flows are not shown in these figures, but optimal knowledge flow structures would also account for magnitude of flows.

One Ecosim simulation is presented as an example of the usefulness of the collaborative approach; Fig. 3 shows functional responses of some groups to an aggressive fishery on sandlance in PWS, as trajectories of biomass changes. The model predicts that both seabirds and avian predators (birds that eat seabirds) would decline in response to such a fishery, while other groups would increase.
Figure 1. Components of the balanced trophic model of Prince William Sound, Alaska, displayed on a trophic level scale. Box size represents the log relative standing biomass of each component. Trophic flows are not displayed here, as there are too many connections for this format.

Figure 2. A mid-trophic-level component (adult Pacific herring) extracted from the overall food web along with directly connected components. Known trophic flows among components serve as indicators of knowledge flow among experts to optimize refinement of information about the group and its interrelationships (e.g., refine model input parameters).
When the same Ecosim scenario is used in the Ecospace routine, components are redistributed in two-dimensional, habitat-specified space at the relative biomasses revealed by the Ecosim run. Thus, a comparison of the “equilibrium” and “sand lance fishery” scenarios reveals different predictions of spatial distributions as well as temporal trajectories.

**Discussion**

Trophic interactions in an ecosystem are also flows of energy, which vary in rate and magnitude among connections (between the various components) and in time and space. We contend that ecosystems can be best understood when flows of ecosystem knowledge closely resemble flows of energy. Pathways to optimize knowledge flow for one ecosystem component should be based on the trophic flows immediately surrounding that component. Ecosystem-based trophic models, like Ecopath, integrate previously disparate ecosystem information through a system of knowledge flow that resembles trophic flow. This method was used to synthesize a cohesive picture of an apparently compartmentalized ecosystem.

Several EVOS-funded projects, notably the Alaska Predator Ecosystem Experiment (APEX), the Nearshore Vertebrate Predators (NVP) project, and the Sound Ecosystem Assessment (SEA) project, are devoted to the biology and ecology of distinct groups of organisms, sometimes including their prey, their predators, or both. As a result of these programs, the resolution of information is high for some ecosystem components. However, resolution is low for other components. Use of an Ecopath model allows all components of the defined ecosystem to be included and balanced (while accounting for imports and exports). This approach enables modification and verification of distinct components, as well as insights into whole ecosystem structure and function. Within the Ecopath framework, the precise information gained from the large investments in some research programs results in increased knowledge of less-studied components. This knowledge refinement is optimized through an appropriate knowledge flow structure.

This approach can be used to gain a better understanding of individual resource components and their potential trajectories in an ecosystem context, in addition to ecosystem structure and function. These trophic flow models can also be used to accurately map the fate and transport of contaminants within a food web (Dalsgaard et al. 1998).

A mix of reluctance and enthusiasm was encountered during our attempts to initiate a collaborative synthesis of ecosystem knowledge in Prince William Sound using the Ecopath approach. Some of the initial reluctance was linked with skepticism about the Ecopath approach. However, feedback from participants indicates a higher degree of enthusiasm and acceptance of the approach, as well as increased interaction and discussion among research groups, now that a face-to-face workshop was conducted.
Aside from technical skepticism about a particular analytical approach, reluctance to collaborate in an ecosystem context, in general, is linked to aspects of human behavior, such as social group dynamics and perceptions of territory. Behaviors reinforcing reluctance to collaborate are natural and adaptive, but offset by other motivations that reinforce collaboration. Based on our experience with this synthesis, we suggest that reluctance to collaborate can be overcome by redefining working communities and territories to resemble ecosystem structure. We also suggest that this can be done through workshops, collaborative reports, and other venues of knowledge flow patterned after energy flows in ecosystems.

The initial PWS model was constructed through the collaboration of members of the scientific community in the region, and it is planned to

Figure 3. Ecosim simulation of the response to an aggressive sand lance fishery showing biomass declines in seabirds (which prey on sand lance), juvenile salmon, and avian raptors (which depend on seabirds and salmon). Eulachon, a competitor of juvenile salmon and a prey of seabirds, increases as seabirds decline. Aggregation of seabirds into one group masks the magnitude of declines in seabird species that are particularly dependent on sand lance. The functional responses predicted by Ecosim integrate the relative trophic forces in an ecosystem. These functional responses, rather than the absolute magnitude of responses, are useful for resource decision making and research planning. This sand lance example is a relatively simple one; some simulations predict more broad and dramatic responses.
also integrate traditional knowledge from native communities. The representation of knowledge and the knowledge flow structures of these communities, however, differ in fundamental ways from the knowledge structure of the scientific community. Examination of these differences will aid in the development of optimal collaborative structure for understanding the ecosystem.

Some overlap exists between these two knowledge systems, and thus, some opportunity exists for integration, as elegantly demonstrated by Johannes (1981) in the South Pacific. The potential of incorporating traditional knowledge is further underscored by the richness of information attainable by examining lists of local common names, as discussed by Palomares et al. (1999). We suggest that tremendous potential exists for the integration of traditional ecosystem knowledge into current science and management structures through the type of collaborative modeling approach outlined in this paper, and using analytical tools like the Ecopath approach to constructing trophic models of historical ecosystems to be used as benchmarks. This has been discussed by Haggan (1996, 1998) and Pitcher (1998), and has been achieved by contributors to Pauly et al. (1998a). Failure to include traditional knowledge in such a process certainly limits the realism of the model, as well as its ultimate effectiveness as a management tool.

One potential outcome of Ecopath modeling activities in PWS is community-based resource management and policy development. By this we mean resource management that functions well because it is appropriately, and constructively, influenced by stakeholder communities and other trustees. The future success of oil spill restoration and resource management planning will be optimized through the participation of stakeholders, especially when venues for participation are functional, educational, and collaborative. We suggest that community-based management naturally occurs in parallel to ecosystem-based management that is achieved through knowledge flow structures that resemble ecosystem structures, as explored during this collaborative approach.

A great deal can be learned from Ecosim simulation models to aid resource managers in making decisions that affect the development of these communities. Perhaps even more importantly, the outputs and implications of Ecosim model runs are easily grasped by anyone because of the friendly user interface and graphics that are clear and intuitive. To encourage the process of ecosystem-based management, the model of PWS will be widely disseminated among the public as well as among managers. A CD-ROM version of the PWS model is available for distribution to interested organizations and institutions, including schools through the Exxon Valdez Oil Spill Trustee Council and appropriate trustee agencies. This CD-ROM also includes a local/traditional language database of the marine organisms of PWS and beyond. In addition, a locally enriched, customized version of “FishBase,” the global, computerized encyclopedia of
fishes, will also be made available on the worldwide web (see MacCall and May 1995 and www.fishbase.com).

In this paper we have outlined an iterative process. Knowledge about trophic interactions must exist before optimal knowledge flow structures can be indicated by trophic structure. Knowledge flow structures suggested by this process can then be used to refine the input parameter estimates, and thus increase the realism of the model. As the realism of the model increases, the tool becomes more useful for resource assessment and management, as well as research scoping and planning. At the same time, interest in the approach increases within the communities that are aware of the model. This in turn continues to increase model realism and applications. In this sense, the Ecopath approach has the potential of becoming a focal point for a living synthesis of ecosystem information.

Acknowledgments

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References


Applying Ecosystem Management to Fisheries in the Strait of Georgia

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Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada

Abstract

The Strait of Georgia is located between Vancouver Island and mainland British Columbia. It is one of the most important marine ecosystems in the Pacific, as most British Columbians live within 10 km of its shores and it is a major rearing and nursery area for a number of important species of fishes. Various components of the dynamics of this ecosystem have been identified over the past 50 years. However, the connection between fish dynamics and ecosystem dynamics remains poorly understood. Recent studies have shown that major changes in the composition of fish species can occur naturally in response to shifts in the climate and ocean environment. In the Strait of Georgia, these regime shifts affect the matching of copepod movement into the surface waters with the first feeding stage of larval hake and herring. As these two species are the dominant fishes in the Strait of Georgia, changes in their biomass will affect the dynamics of the populations of other species. We propose that the key process that regulates fish abundance is related to the factors that regulate the timing of the vertical migrations and abundance of copepods. According to our hypothesis, copepods are the component of the zooplankton community that link the fundamental processes of microscopic plant production through the association of light and nutrients with the survival of larval fish. We suggest that effective management of the fish populations in the Strait of Georgia requires an understanding of how climate and ocean changes affect ecosystem dynamics. A first step toward ecosystem management could be the production of species ecosystem management charts. We provide examples of these charts for Pacific herring, Pacific hake, and coho salmon. The charts included in this paper may ultimately be shown to require major changes. It is the process of identifying the key factors affecting species abundance that is important in the initial stages of ecosystem management.
It may be as challenging to find methods to communicate the information among experts as it is to acquire the relevant information. There is considerable speculation in our approach, but we propose that it provides a framework to begin to manage single species in the context of their ecosystems.

**Introduction**

The Strait of Georgia is the center of recreational and commercial activity in British Columbia. The Strait, which is located between Vancouver Island and the British Columbia mainland (Fig. 1), is one of the most important juvenile salmon rearing areas in the Pacific Ocean. The Canadian portion of the strait is 220 km long, 33 km wide, and has a surface area of about 6,900 km² (Thomson 1981). The maximum depth is 421 m and the average depth is 155 m. The area south of the Strait that is in United States water is known as the San Juan Islands and Puget Sound. This area is shallower and influenced oceanographically by winds and tides. The Fraser River contributes about 80% of the freshwater runoff into the strait (Thompson 1981). The surface salinity averages about 31‰ which is 2.8‰ less than the average salinity (33.8‰) found off the west coast. The Strait of Georgia is a semi-enclosed sea that is connected to the Pacific Ocean in the north by Johnstone Strait and in the south by Juan de Fuca Strait. These two narrow passages affect the movement of water in and out of the Strait of Georgia, resulting in reduced salinity and a temperature profile that is influenced on the surface by the Fraser River and on the bottom by inflowing deep water from offshore. The total volume of freshwater discharge reduces the surface salinity particularly in the summer. Water circulation, mixing, and stratification in the strait are largely influenced by its freshwater discharge, together with tides and wind. The more general estuarine circulation (Thomson 1981) was described about 35 years ago. The fresh water that is added to the Strait must eventually leave on the surface. The replacement by bottom water from offshore is about 1,000 times richer in nitrates (NO₃) than surface water (Harrison et al. 1994). This nutrient-rich bottom water is eventually mixed into the surface, providing nutrients for phytoplankton that become food for other organisms. The Fraser River discharge starts to increase in March; reaches a maximum in June; gradually decreases in July, August, and September; and remains near minimum levels throughout the rest of the year. From March to September, the discharged fresh water is mixed with seawater in the Strait and most of the mixture forms as a large plume extending over as much as one-third of the southern area of the Strait. This plume, and specifically the edge of the plume, is an area of high productivity that attracts large numbers of young salmon and herring as well as their predators.

Wind mixing is the dominant physical mechanism that entrains nitrates from the nitrate-rich deep water into the surface layer in the Strait of Georgia. Modeled impact of wind events on nitrate fluxes (St. John et al.
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1993) in the southern Strait, showed that nitrate entrainment in the surface layer was reduced when runoff from the Fraser River was high as greater energy was required to break down the more buoyant surface layer. Increases in primary production lagged behind the wind mixing events and were lower and occurred earlier when runoff was high. An earlier spring bloom occurred because the increased stability of the more buoyant surface layer resulted in a shallower depth of mixing for plankton and effectively increased the light available for photosynthesis at a time light limits plankton growth (St. John et al. 1993). Variations in river runoff have also been shown to affect the nutrient supply to the surface waters (Harrison et al. 1994). When Fraser River flows were reduced, wind mixing was more effective and productivity increased. It is this period from April to September when production is periodically nutrient-limited (Parsons et al. 1981) that we believe is important for salmon survival (Beamish and Mahnken 1998).

Li et al. (1999) modeled the salinity and volume fluxes in the Strait of Georgia as a function of Fraser River runoff. The model calculations identified a rapid response in the circulation trends to changing trends in Fraser River flows. The influence of sea level wind patterns was not incorporated into the model but the authors noted that short-term persistent wind events would result in interannual variability in the modeled response to Fraser River runoff. A dramatic decrease in river flow would, according to the model, result in an increase in surface salinity within about 1 year. Other studies of the factors affecting the daily and seasonal oceanographic conditions within the Strait of Georgia have been described by a number of investigators (Hutchinson and Lucas 1931; Waldichuck 1957; Thomson 1981, 1994; LeBlond 1983; Crean et al. 1988; Harrison et al. 1994), and all identify the Fraser River as having a major influence on the oceanography of the Strait of Georgia.
In this study, we consider the variability in the ocean ecosystem that occurs about a mean trend that changes over decadal scales in response to climate shifts (Beamish et al. 1999b). It is this shift from one "state" to another that we think is of primary importance in the concept of ecosystem management. We identify decadal-scale trends in Fraser River flows and in sea surface temperatures, both of which affect the productivity of fishes.

Fraser River flows have been monitored since 1912 and are customarily reported as flow in cubic meters per second measured at Hope, British Columbia. The trend (Fig. 2) shows a general increase in flows beginning in the late 1940s and extending through to 1976 (the highest on record). Since 1976 the flows have generally remained low. In contrast, 1997 was the second highest annual discharge this century but 1998 will be one of the historic low values. Major shifts in trends occurred in the mid-1940s and in 1977. If the annual Fraser River discharge, expressed as m$^3$/s, is shown as ±1 standard deviation from the time series mean (Fig. 2), the period beginning in the late 1940s through to 1976 is a period of extreme high flows. Periods before and after were characterized by average to below average flows (Fig. 2). The years of extreme discharge tend to occur the year following a La Niña (Table 1) but there were years in the 1960s of higher discharges that did not follow a prominent La Niña. There also is a tendency for extreme low discharge years to follow El Niño years, but again there were extreme low discharge years that did not follow El Niño years.

There was not a major change in the trend of annual flows in the 1990s, but there was a significant increase in the volume of discharge in April (Beamish et al. 1999a; Fig. 3). Beginning about 1989, flows in April increased which indicated an earlier beginning of the spring freshette (Fig. 3). There also has been an increase in sea surface temperatures (Fig. 4). Our data series indicates a distinct period from 1969 to 1977 with an average of about 10.4ºC; from 1978 to 1991 with an average of about 11.3ºC; and a recent warming beginning about 1992 with an average of 11.6ºC. Thus the overall surface temperature has increased about 1.2ºC in the last 2 decades. In general the pattern of flows of the Fraser River and the patterns of temperatures (Beamish et al. 1999a) reflect the trends seen in the Aleutian Low Pressure Index (Beamish et al. 1999b) which indicates that global climate processes affect the ocean environment in the Strait of Georgia.

Moore (1991), Moore and McKendry (1996), and Mantua et al. (1997) showed that there were trends in the amount of runoff from large rivers on the west coast of North America that were related to trends in climate. Moore (1991) showed that the depth of the snowpack in the Fraser River basin declined by 22% over the same period that Fraser River flows declined by 28%. Beamish et al. (1999a, 1998c) showed that decadal scale changes in climate were related to shifts in the migratory behavior of coho salmon and synchronous decreases in marine survival. These previous
Figure 2. Average annual discharge from the Fraser river (m³/s). Flow year is April 1 to March 31 of the following year. The dashed line is the cumulative sum trend (Beamish et al. 1998d). The cumulative sum of the anomalies provides a simple visual picture of the trends in the index. The method of accumulating sums or CuSum (Murdock 1979) is a way of studying trends by including information from past data points. The calculation is a simple addition of a data point to the sum of all previous data points. Each data point may have a constant subtracted from it, to enhance visualization of trends in the series. The constant is usually the mean of the entire series. If there is a trend in the data there will be a trend in the CuSum graph. In recent years there was an increasing trend in discharge that changed in 1977 to a declining trend.
Table 1. Relationship of extreme low and high Fraser River discharge years to La Niña and El Niño events.

<table>
<thead>
<tr>
<th>High discharge year</th>
<th>La Niña year</th>
<th>El Niño year</th>
<th>Low discharge year</th>
</tr>
</thead>
<tbody>
<tr>
<td>1964</td>
<td></td>
<td>1965</td>
<td></td>
</tr>
<tr>
<td>1962</td>
<td></td>
<td>1963</td>
<td></td>
</tr>
<tr>
<td>1954</td>
<td></td>
<td>1951/1953</td>
<td></td>
</tr>
</tbody>
</table>

Figure 3. Average April discharges from the Fraser River (m$^3$/s). The CuSum trend (dashed line) shows an abrupt change in the late 1980s.
studies identify a relationship between the dynamics of the ocean ecosystem in the Strait of Georgia and climate. The long-term or regime changes that may alter the survival pattern of a particular year class are important, as these impacts need to be distinguished from fishing effects. In this report, we cannot examine the relationships of the population dynamics of all major species, but we briefly review the state of the key species and relate the dynamics of three species to the dynamics of the ecosystem.

**Major Fisheries**

The current state of the major fisheries in the Strait of Georgia is summarized in Table 2 and Fig. 6. Other fisheries and other important biota have not been included in this report but additional descriptions are available in Ketchen et al. (1983).

The most abundant resident fish species is Pacific hake (Table 2). The abundance has increased slightly in recent years (Saunders and McFarlane 1997) and may now exceed 65,000 t or more than 300 million fish. This estimate is considerably lower than the earlier estimates because revisions in target strength have reduced all previous estimates (Saunders and McFarlane 1997). Most Pacific hake spawn in the Strait of Georgia.
Table 2.  **Key fish species and condition of stocks in the Strait of Georgia.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Condition</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coho salmon</td>
<td>Wild stocks are in very low abundance. In recent years about 3 million juveniles rear in the strait until fall, then leave. Ocean age 1 juveniles have not returned in recent years.</td>
<td>Major recreational and commercial fisheries now closed.</td>
</tr>
<tr>
<td><em>Oncorhynchus kisutch</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chinook salmon</td>
<td>Wild stocks are in low abundances but stable.</td>
<td>Major recreational fisheries are restricted and the commercial fishery is closed.</td>
</tr>
<tr>
<td><em>O. tshawytscha</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sockeye salmon</td>
<td>Declining from historical high levels to below long-term average.</td>
<td>Transitional-juveniles remain in the strait less than 2 months.</td>
</tr>
<tr>
<td><em>O. nerka</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pink salmon</td>
<td>Declining from historical high levels to below long-term average.</td>
<td>Transitional-juveniles remain in the strait less than 3 months.</td>
</tr>
<tr>
<td><em>O. gorbuscha</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific herring</td>
<td>Historical high levels of abundance but individual size declining. Recent catches in the last 5 years averaged 16,000t with a stock size of 80,000 t.</td>
<td>Largest commercial fishery for roe of all British Columbia herring stocks.</td>
</tr>
<tr>
<td><em>Clupea pallasi</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific hake</td>
<td>Historical high levels of abundance and largest resident biomass in the Strait of Georgia. May be over 1 billion fish or 75,000 t.</td>
<td>Small commercial fishery during 1980s; averaging 8,000 t during 1990s.</td>
</tr>
<tr>
<td><em>Merluccius productus</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walleye pollock</td>
<td>Probably at high levels of abundance, possibly 15,000 t or 65 million fish.</td>
<td>Small commercial fishery (less than 2,000 t).</td>
</tr>
<tr>
<td><em>Theragra chalcogramma</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lingcod</td>
<td>Very low abundance.</td>
<td>A restricted recreational fishery and the commercial fishery closed.</td>
</tr>
<tr>
<td><em>Ophiodon elongatus</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific cod</td>
<td>Very low abundance.</td>
<td>Commercial fishery closed.</td>
</tr>
<tr>
<td><em>Gadus macrocephalus</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inshore rockfishes</td>
<td>This group of rockfish consists of about 6 species of importance for the fisheries. The combined abundance is low and declining.</td>
<td>Valuable commercial and recreational species.</td>
</tr>
<tr>
<td><em>Sebastes</em> sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spiny dogfish</td>
<td>Probably at average levels of abundance of 60,000 t or 35 million fish.</td>
<td>Small commercial fishery.</td>
</tr>
<tr>
<td><em>Squalus acantias</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>English sole</td>
<td>Very low abundance relative to pre-1980s abundances.</td>
<td>Not actively managed.</td>
</tr>
<tr>
<td><em>Pleuronectes vetulus</em></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
from late February to late March. Most spawn for the first time at an age of 3 years and live for up to approximately 15-20 years. Hake in the Strait of Georgia are resident and feed mainly on euphausiids. In April, they also can be a major predator of herring (McFarlane and Beamish 1985); however, there is no evidence that they are an important predator of salmon. The increase in abundance in the 1990s has been associated with a large decline in individual length and a continuous series of strong year classes.

 Associated with Pacific hake populations are walleye pollock (Table 2). They are considerably less abundant than Pacific hake but feed on similar organisms. The Strait of Georgia stock is at the southern limit of pollock distribution in the subarctic Pacific. Abundance was relatively stable during the early 1980s and declined during the late 1980s, but has increased since 1994 (Saunders and Andrews 1997). There currently is a small fishery at approximately 1,000 t.

 Pacific herring stocks in the Strait of Georgia are currently at or near historical high levels of abundance (Schweigert et al. 1998). Most Pacific herring spawn in the strait in late winter. The juveniles remain for about 1 year and migrate out of the strait to the west coast of Vancouver Island. Thus, relatively large numbers of juveniles feed in the Strait of Georgia in their first year of life. The number that leaves the Strait has been speculated to be about one-half of the year class. These fish return to spawn in the Strait at age 3, but there is considerable doubt about the location of the migrants when they are not in the Strait. The current estimated abundance of mature fish of approximately 75,000 t (at 100 g/fish) is equivalent to about 750 million adult fish. However, only approximately half of the fish remain and feed over the summer.

 Lingcod and Pacific cod abundances are extremely low relative to past abundances. Both species feed primarily on other fishes, although the juveniles feed on plankton in the first few months after hatching. Rockfish species are aggregated into groupings labeled “inshore rockfish” (about six species). These fish tend to be slow-growing and long-lived. In general, they are in low abundance, relative to previous abundances. They are important for the recreational and commercial fisheries, but in recent years the total catch of “inshore rockfish” species was less than 500 t. Spiny dogfish are in large abundance and are predators of a number of other fishes (Beamish et al. 1992). Despite their long life and predatory habit, they are extremely slow-growing and do not consume large numbers of other fish. They also tend to feed mainly on plankton for the first 10-20 years of life. They are an important component of the ecosystem, but their impact on the dynamics of other species remains uncertain.

 Historically, the flatfish fishery was a major groundfish fishery in the Strait of Georgia (Ketchen et al. 1983). Although several species were harvested, English sole was the main species in the catch. Catches declined abruptly in 1981 and have remained at low, but stable levels ever since (Fargo 1994). There is no regulation of catch levels, but there are restrictions on fishing locations and fishing effort.
Pacific salmon are the group of fishes of most interest to managers and biologists. Six species of salmon, including steelhead (*Oncorhynchus mykiss*), enter the Strait of Georgia. Historically, only coho and chinook salmon remained in the Strait over the winter and only a small percentage of these survived the first winter (Healey 1980, Sandercock 1991). The movement into salt water and movement out of the Strait varies among species, with sockeye salmon spending the least amount of time (Groot and Cooke 1987). Chum salmon now remain in the Strait longer than in the past (Beamish and Folkes 1998), and probably in greater numbers. The greater abundance and longer resident time may be a result of releases from hatcheries in Canada and the United States. Despite the low abundance of coho and chinook salmon older than ocean age 0, there may be more juveniles entering the Strait now than in the past as a result of releases from hatcheries (Beamish et al. 1995a,b).

It is important to have some approximation of the abundance of juvenile salmon (ocean age 0) of all species that feed in the Strait of Georgia to compare to abundances of other species. A difficulty with producing this estimate is the very high early marine mortality and the tendency for juveniles to migrate quickly out the Strait (Healey 1980). We used the procedures described in Beamish et al. (1998b) to produce abundance estimates of the various species. The swept volume estimates are believed to be minimal, but they provide a general indication of abundance that can be used to compare to the estimated abundances of other species during the summer feeding period. We estimated the abundance of coho, chinook, and chum salmon in September of 1997 and pink and sockeye salmon in June and July of 1998. Recognizing that most sockeye salmon and possibly a large proportion of pink salmon may have left the strait by June and July (Groot and Cooke 1987) these estimates will be low. In general, the total abundances of all five species of Pacific salmon range around 10 million individuals (Table 3) and possibly as high as 20 million. Abundances decline substantially by late fall (Beamish et al. 1999a), but the abundances in Table 3, probably approximate juvenile salmon abundance during the summer. The important observation is that the abundances of juvenile salmon are substantially smaller than the abundance of hake and herring.

**Plankton and Larval Feeding**

We collected fish larvae in 50 m or 200 m oblique plankton tows in the central portion of the Strait of Georgia, using 56 cm diameter bongo nets, with a 250 µ nitex mesh towed at 1 m/s while the vessel speed was 2 knots. Each sample was preserved in 5% formaldehyde solution and sorted in the laboratory at a later date. Volume of water strained was determined from a flow meter within the net. The complete sample was examined for fish larvae. In this paper, we report the gut contents of the first 30 larvae that had stomach contents. It was necessary to open the stomachs of hake
to determine if there were contents even though the body wall appeared to be transparent. Calanoid copepods found in the gut were generally transparent and fragmented, making the identification difficult. Often, prosome length and width were the only parts measured. Whole copepods were counted and identified when possible, but identifications were difficult because some parts were missing. We confirmed our identifications by exchanging samples with another laboratory.

In 1997 and in 1998, virtually all larval hake had absorbed their yolk sacs by April 1. Over 90% of the gut contents of hake and herring in both years were copepods including copepod eggs (Tables 4 and 5). In 1997, the dominant food items were juvenile and adult *Pseudocalanus minutus* (Table 4). In 1998, there were more *Neocalanus plumchrus* (about 70%) than *P. minutus*, and all *N. plumchrus* were juveniles (Table 5). Many of the *P. minutus* had well-developed genital segments averaging approximately 1.3 mm in total length. Juvenile stages (C3, C4, and C5) were also present in the guts. It is possible that in 1997, our ability to detect larvae with stomach contents was not as reliable as in 1998. The results, therefore, show the contents and are not used to estimate the percentage that were feeding. We recorded the mean size of the larval fish to confirm that these specimens were at the first feeding stage.

Plankton samples were collected either separately or in association with the larval fish diet study using the nets and procedures described earlier. Plankton analysis was carried out by subsampling catches and estimating the numbers of organisms per 100 m³ filtered, using the flow meter in the plankton net to estimate the total volume filtered. In 1996 and 1997, the abundance of *P. minutus* in the surface waters increased about 10 days before the maximum abundance of *N. plumchrus* (Fig. 5). For both these species, the increase in abundance was greatest at the end of March and the first week of April. Adult *P. minutus* were present in the first samples collected in February with maximum abundance from mid-March to early April. *N. plumchrus* abundance maximums followed *P. minutus* but *N. plumchrus* reached much higher densities. After June, adult

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**Table 3. Approximate abundance of juvenile Pacific salmon in the Strait of Georgia in the summer.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Sampling period</th>
<th>Habitat depth (m)</th>
<th>Abundance</th>
<th>Error limits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coho</td>
<td>Sep 1997</td>
<td>0-45</td>
<td>2,762,000</td>
<td>1,451,000-4,073,000</td>
</tr>
<tr>
<td>Chinook</td>
<td>Sep 1997</td>
<td>0-45</td>
<td>3,097,000</td>
<td>2,379,000-3,816,000</td>
</tr>
<tr>
<td>Chum</td>
<td>Sep 1997</td>
<td>0-15</td>
<td>3,635,000</td>
<td>1,134,000-6,137,000</td>
</tr>
<tr>
<td>Pink</td>
<td>Jun-Jul 1998</td>
<td>0-15</td>
<td>3,434,000</td>
<td>1,836,000-5,032,000</td>
</tr>
<tr>
<td>Sockeye</td>
<td>Jun-Jul 1998</td>
<td>0-15</td>
<td>684,000</td>
<td>173,000-1,120,000</td>
</tr>
</tbody>
</table>
Table 4. Contents of stomachs of larval Pacific hake and Pacific herring at first feeding, April 1997.

<table>
<thead>
<tr>
<th>Date</th>
<th>Species</th>
<th>Total</th>
<th>Number examined</th>
<th>Number of stomachs</th>
<th>Average length (mm)</th>
<th>Neocalanus plumchrus</th>
<th>Pseudocalanus minutus</th>
<th>Copepod eggs</th>
<th>Copepod parts or other species</th>
<th>Other items (non-copepods)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr 8</td>
<td>Hake</td>
<td>13</td>
<td>13</td>
<td>3</td>
<td>4.2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>74</td>
<td>74</td>
<td>37</td>
<td>8.5</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>≤50</td>
<td>0</td>
</tr>
<tr>
<td>Apr 26</td>
<td>Hake</td>
<td>164</td>
<td>30</td>
<td>5</td>
<td>4.8</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>8</td>
<td>4</td>
<td>2</td>
<td>17.9</td>
<td>0</td>
<td>1</td>
<td>8</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Apr 26</td>
<td>Hake</td>
<td>264</td>
<td>40</td>
<td>14</td>
<td>5.1</td>
<td>0</td>
<td>7</td>
<td>50</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Apr 26a</td>
<td>Hake</td>
<td>253</td>
<td>48</td>
<td>26</td>
<td>4.7</td>
<td>0</td>
<td>5</td>
<td>58</td>
<td>15</td>
<td>1</td>
</tr>
</tbody>
</table>

* 200 m tow.
Table 5. Contents of stomachs of larval Pacific hake and herring at first feeding, April 1998.

<table>
<thead>
<tr>
<th>Date</th>
<th>Species</th>
<th>Total</th>
<th>Number examined</th>
<th>Number of stomachs</th>
<th>Average length (mm)</th>
<th>Neocalanus plumchrus</th>
<th>Pseudocalanus minutus</th>
<th>Copepod eggs</th>
<th>Copepod parts or other species</th>
<th>Other items (non-copepods)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr 6</td>
<td>Hake</td>
<td>154</td>
<td>37</td>
<td>30</td>
<td>4.4</td>
<td>9</td>
<td>1</td>
<td>0</td>
<td>91</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>NC</td>
<td>79</td>
<td>30</td>
<td>11.3</td>
<td>0</td>
<td>0</td>
<td>36</td>
<td>33</td>
<td>8</td>
</tr>
<tr>
<td>Apr 6</td>
<td>Hake</td>
<td>566</td>
<td>27</td>
<td>27</td>
<td>4.4</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>37</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>NC</td>
<td>489</td>
<td>30</td>
<td>10.8</td>
<td>2</td>
<td>0</td>
<td>28</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Apr 23</td>
<td>Hake</td>
<td>329</td>
<td>123</td>
<td>30</td>
<td>4.1</td>
<td>10</td>
<td>7</td>
<td>2</td>
<td>19</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>NC</td>
<td>169</td>
<td>30</td>
<td>12.4</td>
<td>0</td>
<td>1</td>
<td>87</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Apr 23</td>
<td>Hake</td>
<td>271</td>
<td>89</td>
<td>30</td>
<td>4.3</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>NC</td>
<td>146</td>
<td>16</td>
<td>12.8</td>
<td>1</td>
<td>1</td>
<td>21</td>
<td>13</td>
<td>0</td>
</tr>
</tbody>
</table>

NC = Not counted.
N. plumchrus were not found in the surface waters, but there was a second peak in the abundance of P. minutus in the southern Strait in June and in the north in August. We show average densities for the Strait in Fig. 5. In 1997 P. minutus density was higher than N. plumchrus in the north and the reverse was true in the south. The copepods Calanus pacificus and Metridia pacifica were also present and in some sampling locations their abundance in 1997 was similar to P. minutus and N. plumchrus. In 1996, small numbers of M. pacifica were found in the samples.

Bornhold et al. (1998) studied the juvenile development of N. plumchrus in the Strait of Georgia. As the naupliar stages migrate to the surface they develop through to the first copepodite stage about the time they reach the surface. The copepodite stage C5 is the stage of maximum biomass and the stage that signals a return to deeper waters. In addition to sampling the surface 50 m for plankton composition in the mid-1990s, Bornhold et al. (1998) reexamined data from three other plankton studies, dating from 1967. They observed that the date that 50% of the N. plumchrus were at C5 stage in the surface 50 m changed from about May 17 in 1967 to April 21 in 1997. From 1981 to 1997, the change was from about April 26 to April 21, or less than 1 week. Overall, they identified a change in timing of 25-30 days in 30 years, with the greatest change occurring in the first 15 years between 1967 and 1981.

Figure 5. The average number of N. plumchrus (solid circles) and P. minutus (open squares) in the top 50 m of the Strait of Georgia, from eight sampling sites throughout the strait. The increases in abundance occur in late March and early April, with P. minutus increases preceding N. plumchrus.
We noted that in our study, *P. minutus* was an important food item for larval hake and herring in both 1997 and 1998. *N. plumchrus* was an important item in 1998, but less common in our identifications in 1997. However, as mentioned, the representativeness and accuracy of the 1997 analyses may not be equivalent to the 1998 analyses. It is clear that *P. minutus* is an important component of the diet, and its earlier appearance than *N. plumchrus* in the plankton samples may indicate that it also is more abundant in the surface waters earlier in the year.

**Spawning and Abundance Changes for Hake and Herring**

Hake biomass remained stable at approximately 60-70 kt during the 1980s and the 1990s. From the late 1970s through the 1980s the average size was 42 cm for males and 44 cm for females age 4 and older. Since 1990, the numbers of hake increased as a consequence of five strong year classes. Associated with the increase in numbers has been a decrease in length to 36 and 37 cm (age 4 and older) for males and females, respectively. Therefore, although biomass has remained relatively stable, numbers have increased threefold. Pacific hake spawn late February to early April with peak spawning occurring in the midwater depths exceeding 200 m in mid- to late March. Large midwater spawning concentrations are found in the south-central Strait of Georgia. Eggs hatch in shallower water, often in about 5-6 days. Larvae begin feeding 4-6 days after hatching. Extensive studies of the timing of hake spawning have not been conducted, thus we do not know if the mean spawning date has changed.

Herring spawn in tidal and subtidal waters around the Strait of Georgia. Eggs hatch within 8 days and larvae start to feed within 4 days of hatching. Herring spawn throughout the Strait of Georgia from mid-February to late March (Hay and McCarter 1998). The duration of spawning has decreased since the mid-1980s, but the date of maximum spawning has not changed from mid-March (Hay and McCarter 1998). Herring abundance has approached historical high levels since 1990 and is estimated to be 75 kt. This high abundance has been maintained throughout the 1990s by above-average year classes in 1990, 1991, 1992, 1995, and 1996 (Schweigert et al. 1998).

**Natural Regulation of the Strait of Georgia Ecosystem: A Hypothesis for Ecosystem Management**

The details of the mechanisms that affect the dynamics of the Strait of Georgia ecosystem are obviously complex. However, we propose that the key process that regulates fish abundance is related to the factors that regulate the timing of the vertical migrations and abundance of copepods.
Figure 6. (Top) Trends in catch of Pacific cod, lingcod, flatfish (mostly English sole), and Pacific hake in the Strait of Georgia. (Bottom) Catches of coho salmon in the Strait of Georgia from the recreational fishery (Xs) and the commercial and recreational fishery combined (open squares). Actual abundances were not determined; however, fishing effort was virtually unrestricted over this period.
According to our hypothesis, copepods are the component of the zooplankton community that link the fundamental processes of microscopic plant production through the association of light and nutrients with the survival of larval fish. It is no coincidence that most fishes in the North Pacific reproduce in the winter immediately before copepods move from the diapause state in deeper water (Conover 1988) into the surface waters, which ensures that eggs hatch about the time copepods are available for food.

The availability of copepods immediately after yolk-sac resorption by larval hake and herring is the fundamental mechanism that we propose is the lever that shifts the dynamics of this ecosystem. The dynamics of the fish community in the Strait of Georgia respond to the timing shifts in copepod vertical migration through the abundance shifts of Pacific hake and herring, as these are the dominant fish species in the Strait.

Throughout the North Pacific, including the Strait of Georgia, the calanoid copepods are dominant within the zooplankton biomass (Mackas and Tsuda 1999). The life history of copepods places them in the key position in the Strait of Georgia ecosystem. Copepods that dominate the zooplankton biomass have a seasonal migration from a winter residence in deeper water to the surface water in the spring. The juvenile copepods complete their growth in the surface waters before returning to deep water in the late spring and summer (Miller et al. 1984). In the Strait of Georgia, most N. plumchrus reproduce in these deepwater areas in January and February (Fulton 1973). As the fecundity appears to be around 1,000 eggs (Mackas and Tsuda 1999), it can be argued that their abundance is regulated more by the habitat conditions than number of offspring as is common with plants and animals that produce large numbers of seeds and babies (Colinveaux 1978).

We propose that the connection to the decadal shifts in climate and the changes in the abundance trends of fishes in the Strait of Georgia is through changes in the vertical migration of copepods into the surface. Changes in the timing have been shown for the North Pacific (Mackas et al. 1998, Mackas and Tsuda 1999) and as previously mentioned for the Strait of Georgia (Bornhold et al. 1998). Off the west coast of British Columbia, the movement into and out of the surface waters by N. plumchrus has advanced by 50-60 days (Mackas et al. 1998) and in the Strait of Georgia by 25-30 days (Bornhold et al. 1998). Thus, the timing of copepod migration becomes an important reference point for the management of fishes as it provides information about the relative success of hake and herring spawning.

**Ecosystem Management Charts**

If the dynamics of the Strait of Georgia ecosystem is regulated as we propose, it is possible to identify the key processes that regulate abundance in a simplified chart. We call these ecosystem management charts. These
charts are developmental, as the relationships are both poorly studied and poorly understood. However, the charts identify the associations of the dynamics of fish populations with environmental factors and other fishes. The charts are intended to provide a broader scope for management by specifying the possible causes of abundance changes and helping to separate fishing impacts from natural changes. The charts are also useful for research planning as they highlight important relationships that need clarification. We suggest that these charts facilitate the development of ecosystem management. Initially, the chart may greatly oversimplify relationships, but the long-term objective should be to maintain simplicity. The difference between the initial and more advanced charts may not be the number of associations, rather a better appreciation of the importance of the key relationships. In this first attempt we identify the key linkages for three species in the Strait of Georgia.

**Coho Salmon Ecosystem Management Chart**

Coho salmon abundance is regulated naturally by the carrying capacity in the ocean and by the number of juveniles (smolts) produced in fresh water. The number of smolts produced is a function of freshwater habitat conditions and the number of spawning adults. The number of spawning adults is related to the amount of fishing mortality and to the marine survival. Currently, in the Strait of Georgia, about 77% of the population is from hatchery-reared smolts and fry (Beamish et al. 1998a). Thus, the total abundance is only partly affected by fishing effects on wild stocks. Marine survival is a function of early predation-based mortality and growth-related mortality that is proposed to occur in the fall and winter (Beamish and Mahnken 1998). According to our proposed relationship, stock and subsequent recruitment of wild stocks is linear for small stock sizes but recruitment is not a function of stock size at larger abundances. At these larger abundances stock size is regulated by the ocean environment.

The management chart for coho salmon (Fig. 7) identifies only the principal mechanisms currently regulating coho salmon abundance. According to the chart, coho salmon abundance is regulated primarily through the timing of copepod production, fishing effects, and the availability of suitable freshwater habitat for wild coho salmon. Because the wild spawning biomass or escapement is supplemented by large additions of hatchery fish, the interannual changes in total abundance are currently regulated by the ocean environment and not by fishing. Favorability of the ecosystem for coho salmon will be reflected in the “condition” of coho salmon in the fall which is a reflection of availability of food in summer according to the critical size and critical period hypothesis of Beamish and Mahnken (1998). Persistent poor condition would indicate poor overwinter survival. The regime response which determines the mean carrying capacity of the system for coho salmon is reflected in the timing of copepod production
Figure 7. Coho salmon ecosystem management chart. The chart identifies the relationships that may be most influential in the regulation of abundance. The three key areas are fishing, climate-ocean environment, and associated species. Climate, as a regime, affects Fraser River flows, which may affect primary productivity in the Strait of Georgia. Climate also affects the freshwater habitat, but the principal impact of climate is on the timing of copepod migration into the surface waters. The timing of this migration affects the survival of key competitors for food of coho salmon during their summer feeding period. Growth during the summer affects survival in the winter and fall and eventually determines brood-year strength. Predation is important but adult abundance is determined through growth. Fishing is important if removals restrict the ability of a stock to replenish itself. A manager needs to know if the regime is productive or less productive for coho salmon and this would be determined using climate indices and timing of copepod migration. In favorable regimes, more smolts would be required to achieve the maximum productivity. In less favorable regimes, the manager needs to be sensitive to the impacts of associated species and other coho salmon. In less favorable regimes, adding more coho salmon smolts or other potential competitors may also increase competition for food resources, which are less available.
as this will affect the abundance of Pacific hake and Pacific herring which compete for food with juvenile coho salmon. A suggested ecosystem management approach by managers would be to determine the relative strength of hake and herring year classes which affect competition for food of coho salmon, monitor the condition of coho salmon in the fall, and ensure that fishing and hatchery effects combine to produce the number of juveniles appropriate for the current regime.

**Herring Ecosystem Management Chart**

Herring in the Strait of Georgia migrate to offshore waters after spending about 1 year in the Strait (Hourston and Haegele 1980). There are some resident stocks and the timing and amount of movement apparently varies among years (Hourston 1982). As herring mature offshore, they migrate back into the Strait of Georgia to spawn and return offshore after spawning. It may be important to determine the mechanisms involved in order to understand how future climate and ocean changes will affect stock dynamics. It is clear that this migration complicates any interpretation of how the dynamics of the Strait of Georgia affect the abundance trends of herring. Our ecosystem management chart incorporates the offshore residence as a general predation component.

We propose that the year-class strength is determined initially by the availability of copepods for the larval herring (Fig. 8). It is also possible that salinity and temperature may affect survival as spawning and hatching occur in the shallow, intertidal areas. However, at this time we are not considering egg mortality to be a major source of interannual larval mortality. There is no question that larval mortality is a function of predation, but again, we propose that it is copepod availability that is the key factor regulating the initial year-class strength. We consider that predation in the first marine year becomes important during the summer and fall and during the offshore residence. It is well known that herring are a principal food item of a number of species (Hourston and Haegele 1980). It is less well known that it has not been possible to relate surveys of age-0 herring with subsequent recruitment, possibly indicating that predation mortality is also an important factor regulating the abundance of adults. Fishing impacts directly affect the abundance of spawning adults, but we do not consider that fishing currently affects recruitment as long as a minimal or “cut-off” biomass is maintained.

Ecosystem management of herring would require knowledge of the vertical migration timing of two copepods: *N. plumchrus* and *P. minutus*. A general classification such as early, average, or late may be appropriate in the initial stages of ecosystem management. Late copepod migration would indicate the possibility of poor larval herring survival and an early migration to the surface would indicate that larval survival will be high.
Figure 8. Herring ecosystem management chart. The chart identifies the key relationships that currently affect the abundance of herring in the Strait of Georgia. Climate will affect Fraser River flows and possibly the level of primary production in the strait, but the main impact of climate is the timing of copepod migration into the surface waters. Earlier movement into the surface waters makes food more available for larval herring at the time of first feeding. Herring abundance is regulated naturally through predation on all age classes, but predation does not restrict the ability of the population to replenish itself. The migration of herring out of the Strait of Georgia increases the predation impact. The current level of fishing would not affect abundance levels as indicated by the increasing abundance trends. Managers would need to know the favorability of the regime as indicated by the timing of copepod migration and any changes to a regime as indicated by the climate indices. Some form of abundance survey would identify trends, but declines could be for natural reasons if there was a change from a favorable to a less favorable regime.
Figure 9. Hake ecosystem management chart. This is the simplest of the three charts. Hake abundance is regulated by timing of copepod migration, similar to herring. As earlier migration is more favorable, more food is available at the time of first feeding of larval hake. The large abundance and high fecundity of hake ensures that a very large number of eggs are produced. Thus abundance is closely related to larval survival. Hake abundance is regulated naturally through cannibalism. Currently, fishing levels have an impact on the number of adults that consume juvenile hake. Increasing fishing effort would probably result in a higher survival of juveniles if the current regime persists.
Hake Ecosystem Management Chart

Hake, as the dominant species in the Strait of Georgia, has the simplest ecosystem management chart. Hake abundance is entirely dependent on the timing of the copepod reproduction cycle and cannibalism (Fig. 9). Early migration of copepods to the surface favors improved hake larval survival resulting in a strong year class. The natural regulation of hake abundance is proposed to be through cannibalism. Fishing at the current levels, in the current regime, would have little impact on the abundance of hake. Consequently, increasing fishing in an attempt to reduce competition for a species such as coho salmon would have no effect unless high amounts of hake were removed. However, because the natural regulation of hake abundance is through cannibalism the removal of large numbers of adults may reduce cannibalism resulting in even larger adult biomass a few years later and even greater competition.

Conclusion

This study combines a basic understanding of the oceanography, productivity process, and life history strategies of key fishes in the Strait of Georgia to develop an approach to ecosystem management. The oceanography of the Strait of Georgia is affected by Fraser River flows which are strongly affected by decadal-scale trends that we call regimes. Within these regimes there is considerable interannual variability (Moore and McKendry 1996, Mantua et al. 1997). The Strait of Georgia is also affected directly by wind patterns and intensities. All of these influences alter the ecosystem dynamics but according to our proposal, the principal factor regulating the dynamics of fishes is the timing of the copepod life cycle. Copepods migrating to the surface in the spring provide food for first-feeding larval fish and have immediate impacts on their marine survival. The early, average, or late migration of copepods to the surface alters the relative abundances of hake and herring and their abundances affect the survival of the resident fish species through the changes in availability of food. Changes in the abundance of the fishes reported in the paper have in the past been thought to be the direct result of fishing effects. Although excessive fishing pressures would be expected to reduce abundances, the regime concept implies that trends in abundances will change for natural reasons. Thus, the recorded changes in abundance of all species in the Strait of Georgia may not simply be associated with fishing. The fish abundances at any particular time may be adjusting to new states, as there is inertia within the population dynamics that affects the rate of change. Thus, changes in fish abundance may appear to be gradual. Fishing will have direct impacts on the ability of a stock to replenish itself if the abundance is lower than a minimal level. Abundances higher than this level are mostly regulated by environmental factors. This minimum level needs to be determined for each regime and for each species. The concept of regimes
means that the dynamics of the ecosystem can change. By identifying when large-scale climate shifts occur (Beamish et al. 1998d), it is possible to warn managers to reassess the dynamics of particular species. Regime shifts are not cycles or oscillations, but changes in state. The response to changes may have to be measured, rather than forecasted. Modeling attempts are useful as long as it is recognized that key components may be missing.

In the Strait of Georgia there were changes in the pattern of Fraser River flow that would affect the dynamics of the ecosystem in 1977, 1989, and possibly in 1996. It is difficult to study the changes earlier than the mid-1970s, but the trend of Fraser River flow also changed in the late 1940s, at the same time that indices of global climate changed (Mantua et al. 1997, Minobe 1997, Beamish et al. 1999b). The importance of the regime concept is the requirement to check ecosystems after a regime change to ensure that past relationships remain unchanged. For example, since 1989, there has been a trend to earlier Fraser River flows and higher sea levels (Beamish et al. 1999a) that have had profound effects on the behavior of coho salmon in the Strait of Georgia.

We propose that the key to starting ecosystem management is the ecosystem management chart. These charts identify the major mechanisms that affect the abundance of a particular species. The charts are clearly developmental, but they do show that changes in abundance can be a function of several variables, all of which must be considered when management is proposed. The charts in association with models such as Ecopath 3.0 (Christensen and Pauly 1996) also identify the key research issues required to improve management. Having discussions about the relative importance of the relationships in the charts is an important part of the process. The charts included in this paper may ultimately be shown to require major changes. However, it is the process of identifying the key factors affecting species abundance that is important in the initial stages of ecosystem management. It may be as challenging to find methods to communicate the information among experts as it is to acquire the relevant information. The charts are intended to provide a focus for the process of ecosystem management. They retain the identity of single species, but they attempt to incorporate essential impacts of the environment and associated species.

Acknowledgments

We very much appreciate the assistance of a number of colleagues over the years who have studied the Strait of Georgia ecosystem. The list is too extensive to identify everyone, but we want to mention Ray Scarsbrook, Bill Andrews, Mike Smith, and Chrys-Ellen Neville. Carol Cooper identified plankton and larval stomach contents. The captain, officers, and crew of the W.E. Ricker provided excellent support. The project was funded from the high priority project fund of DFO management, Ottawa.
References


Keystone Predators in the Central Pacific

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Abstract
We evaluated the potential of keystone predator effects among the guild of sharks, tunas, and billfishes at the apex of pelagic food webs in the central North Pacific ecosystem. The Ecopath approach was used as the basis for a dynamic model (Ecosim) that simulates the ecological effects of environmental change and/or fishery exploitation patterns. No single fish species of the highest trophic levels appears to have a profound and uniquely important role in the organization and structure of the central Pacific ecosystem. Instead: (1) The most important components among the guild of apex predators appear to be those such as yellowfin and skipjack tunas which have greater biomass than other apex predators, highly diverse diets, and rapid turnover rates. (2) Intraguild cannibalism and substantial diet overlap are common in these systems. The apparent complexity and importance of cannibalism invites more extensive data collection. (3) Simulated depletions of shark or tuna populations exhibit ecological changes similar to those observed when management or fishery exploitation effects are intense. (4) The ecological effects of longline
fisheries are diffuse and diverse. If we are to affix a keystone predator label in this ecosystem, it is that due to fisheries exploitation.

**Introduction**

By removing so many of the sea’s keystone predators, we are weakening an entire tier at the top of the food chain. This may have dire biological consequences throughout the ecosystem, far beyond the social, economic and moral costs of depleted fisheries. —*Hinman 1998*

The quote above summarizes a question and a concern expressed in a variety of reports (Apollonio 1994, Botsford et al. 1997). The problem was addressed by Pauly et al. (1998), whose analysis of fishery effects demonstrates a general reduction in the average trophic level for both marine and freshwater fishes harvested over the past several decades. The conceptual framework for this issue derives from keystone predator effects in a rocky intertidal community (Paine 1966), followed by a wide application in community ecology (Power et al. 1996) and extended to the ecosystem level in development of the trophic cascade hypothesis (Carpenter and Kitchell 1993). In other words, there is a growing body of evidence that changes in the tops of food webs are expressed at all trophic levels in a wide variety of aquatic ecosystems.

A recent review (Power et al. 1996) of the keystone predator and keystone species literature sought precise and predictable descriptions of keystone effects but concluded that a unifying ecological principle was not apparent and more research was necessary. However, that review did produce the general, operational definition of a keystone predator as: “one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance.” That concept and definition will suffice for the present.

Our study focused on the ecological role of apex predators in food webs of the Central North Pacific. As suggested by Hinman (1998), we wondered if one or more of those fishes served as a keystone predator. Unlike Atlantic stocks, central Pacific tuna and billfish stocks do not yet appear to be overfished (Stroud 1989, Shomura et al. 1994). Ecological effects stemming from the development of these fisheries have not been evaluated.

In this paper we develop an Ecopath model for the food web characteristic of the central Pacific pelagic system. Harvests in the model are those of the Asian and U.S. longline, purse seine, pole and line, and drift gill-net fisheries circa 1988 which include an assemblage of sharks, billfishes, tunas, mahimahi, and flying squid (Ueyanagi et al. 1989, Boggs and Ito 1993). The Ecopath model is employed in Ecosim to evaluate the
relative importance or keystone predator role for each of a suite of predator species sited at the apex of this food web.

**Methods**

**Model Structure and Inputs**

Our analyses are based on the Ecopath model initially developed by Polovina (1984) and subsequently modified (Christensen and Pauly 1992) in applications to scores of ecosystems (Christensen and Pauly 1993). At this writing, Ecopath models have been developed for approximately 90 different systems (Pers. Comm., D. Pauly, Fisheries Centre, University of British Columbia, Vancouver, B.C.). Recent applications include analyses of the linkage between primary production and fish production for the world’s oceans (Pauly and Christensen 1995) and estimates of changes in trophic structure due to fishery exploitation in both marine and freshwater systems (Pauly et al. 1998).

Derivation and application of the Ecopath model are detailed in Pauly et al. (1993) and will be only briefly summarized herein. The pertinent software and documentation are available without cost at the University of British Columbia Fisheries Centre website (http://www.fisheries.com). The core component of an Ecopath model is the balance of production and losses for each component of an ecosystem and expressed in the equation:

\[
\text{Production} + \text{Immigration} - \text{Predatory losses} - \text{Non-predatory mortality} - \text{Harvest} - \text{Emigration} = 0 \quad (1)
\]

In other words, the system is set to steady state based on estimates of rates for each of the terms in Equation 1. This equilibrium condition allows analyses of flows between trophic levels and a means for estimating the relative importance of individual state variables (e.g., species) or processes (e.g., detritivory, selective predation). An important element of this process is that the ratio of production to biomass (P/B) is equal to the sum of all sources of mortality: those due to predation, exploitation, and other causes. Thus, in Ecopath, the system is set to equilibrium based on the levels of mortality, biomass, and production at one point in time.

Walters et al. (1997) developed the Ecosim model as a way to simulate dynamic effects of changes away from the initial steady-state condition defined by an Ecopath model. In Ecosim, any change in exploitation rates is reflected in development of a new steady-state condition. User inputs can alter the initial conditions for exploitation rates, predator-prey interactions, and/or external changes in the environment as applied to any of the state variables in the Ecopath model. Ecosim then calculates the time course for consequent change in all other state variables and the new equilibrium condition. Derivation of the Ecosim model is detailed in Walters
et al. (1997). The software is also available at http://www.fisheries.com, including a version with population size structure and density-dependent or compensatory responses in growth rates and a new model (Ecospace) that sets the Ecosim dynamics in a spatial context.

In its simplest configuration, Ecosim represents dynamic change for each biomass state variable (B) with a differential equation of the form:

$$\frac{dB}{dt} = \text{Food Consumption} - \text{Predatory losses} - \text{Non-predatory losses} - \text{Harvest}$$

The consumption and loss rates are predicted over time as functions of prey and predator biomasses, using functions that explicitly account for “bottom-up” versus “top-down” control effects by representing prey as exchanging between behaviorally unavailable versus available states. Low exchange rates into predator-vulnerable states cause the model to exhibit bottom-up trophic control structure, while high exchange rates result in classic predator-prey control patterns (e.g., trophic cascades).

Because all Ecopath variables are embedded in a food web, effects of changes in one may be expressed in any and all others. Their dynamics depend on the linkages stated in the trophic flow matrix and in the parameters used to define each. For example, organisms with large P/B values (e.g., phytoplankton or zooplankton) respond rapidly to perturbation and achieve new steady-state values quickly. Those with low P/B values (e.g., sharks), which are indicative of K-strategy life histories or low turnover rates, respond slowly and with substantial lags. Both Ecopath and Ecosim include a diversity of options and alternative functions available to the user. In both cases, we employed the initial or default conditions provided with the software.

The trophic structure developed for the central Pacific model is presented in Fig. 1. Resolution is high at the top of the food web but aggregation is required for lower trophic levels where hundreds of species may be represented by one state variable (e.g., phytoplankton). We distinguish between adult and juvenile stages for all apex predators because intraguild cannibalism is a common feature of diets for these fishes. Separation of adult and juvenile stages was based on sizes at maturity or sizes at which each of the adult stages becomes vulnerable to longline gear. We scaled all state variables in biomass units per area and bounded the system as that represented for epipelagic waters from latitudes of 0ºN to 40ºN and longitudes of 140ºE to 140ºW.

The basic inputs for an Ecopath include estimates of biomass, P/B, total annual consumption/biomass (Q/B), fishery harvests and other exports from the system, and ecotrophic efficiency (EE) which is defined as the proportion of the total annual production that is harvested, exported, or preyed upon. If one of those is unknown, the Ecopath software balances the ecosystem budget and provides an estimate for that value. For this analysis, we used biomass as the unknown and estimated values for
Figure 1. A food web diagram of the Ecopath model for the central Pacific.
each of the other Ecopath inputs. Values for P/B roughly correspond with estimates of total mortality as derived from stock assessments (Shomura et al. 1994) or were estimated from life history characteristics and generation times which are reasonably well known for many of the organisms represented in this model. We note that many tropical marine fishes have very rapid growth rates, particularly in juveniles (Prince et al. 1989).

For Q/B values, we used the estimates of daily ration for tunas (Olson and Boggs 1986) and sharks (Stillwell and Kohler 1992) and then increased or decreased those for other predators based on their relative growth rates. For example, metabolic costs and growth are lower in adult billfishes than in yellowfin tuna and much higher than in sharks, so estimates of annual prey consumption rates (Q/B in Ecopath terms) for billfish were estimated to be much lower than for yellowfin tuna, and much higher than in sharks. Parameter values for lower trophic levels were chosen to meet P/B requirements while keeping P/Q (transfer efficiency) within reasonable bounds. These informal approximations produced a model for pelagic predators with a realistic range of productivity and consumption values related to a variety of life history strategies (Table 1). For this model, we assumed an ecotrophic efficiency value of 0.9 for most trophic levels as recommended by the Ecopath manuals. For adult apex predators, we assumed an ecotrophic efficiency value of 0.5 to represent a greater component of natural mortality not due to predation.

A second set of inputs to Ecopath represent the trophic interactions. For each predator, the relative components (% of biomass) of the diet composed of each prey is entered in the matrix. Our diet matrix is summarized in Table 2. Sources for these inputs were synopses of biological data (e.g., Bayliff 1980, Palko et al. 1982) modified to correspond with the simplified model food web. Hundreds of prey types have been identified for these predators and their generalist food habits are clearly opportunistic. The diet matrix includes differences between predators based on relative habitat use. For example swordfish, blue shark, albacore, and bigeye tuna are seasonally more abundant at higher latitudes where prey such as flying squid are dominant. Epipelagic predators such as blue marlin and skipjack tuna were assumed to prey more on epipelagic micronekton than deep-swimming bigeye tuna and albacore. The consumption of juveniles by adults (including cannibalism, since diet study identifications were often limited to family levels) was also based on habitat overlap. For example, skipjack and yellowfin tuna are more abundant in tropical waters and were assumed to be more important in each other’s diets than in the diet of the more temperate albacore tuna.

Modeling Protocol

Based on diet information, Ecopath constructs a food web and assigns each component to an average trophic level (Fig. 1). For this analysis, each
Table 1. Parameter estimates for the central Pacific Ecopath model.

<table>
<thead>
<tr>
<th>State variable</th>
<th>Biomass</th>
<th>P/B</th>
<th>Q/B</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue marlin</td>
<td>3.3</td>
<td>0.3</td>
<td>4.0</td>
<td>0.15</td>
</tr>
<tr>
<td>Other billfishes</td>
<td>1.9</td>
<td>0.5</td>
<td>5.0</td>
<td>0.16</td>
</tr>
<tr>
<td>Other sharks</td>
<td>1.2</td>
<td>0.1</td>
<td>1.5</td>
<td>0.05</td>
</tr>
<tr>
<td>Swordfish</td>
<td>3.6</td>
<td>0.4</td>
<td>5.0</td>
<td>0.15</td>
</tr>
<tr>
<td>Blue shark</td>
<td>16.0</td>
<td>0.15</td>
<td>2.1</td>
<td>0.08</td>
</tr>
<tr>
<td>Albacore tuna</td>
<td>7.9</td>
<td>0.5</td>
<td>12.0</td>
<td>0.18</td>
</tr>
<tr>
<td>Bigeye tuna</td>
<td>7.7</td>
<td>0.8</td>
<td>16.0</td>
<td>0.32</td>
</tr>
<tr>
<td>Yellowfin tuna</td>
<td>14.4</td>
<td>1.2</td>
<td>18.0</td>
<td>0.48</td>
</tr>
<tr>
<td>Skipjack tuna</td>
<td>12.2</td>
<td>2.0</td>
<td>20.0</td>
<td>0.74</td>
</tr>
<tr>
<td>Juvenile billfishes</td>
<td>3.7</td>
<td>7.0</td>
<td>40.0</td>
<td>0.02</td>
</tr>
<tr>
<td>Mahimahi</td>
<td>1.1</td>
<td>5.0</td>
<td>20.0</td>
<td>0.90</td>
</tr>
<tr>
<td>Juvenile swordfish</td>
<td>6.9</td>
<td>6.0</td>
<td>35.0</td>
<td>0.01</td>
</tr>
<tr>
<td>Juvenile blue shark</td>
<td>5.8</td>
<td>0.5</td>
<td>4.0</td>
<td>–</td>
</tr>
<tr>
<td>Juvenile other sharks</td>
<td>6.0</td>
<td>0.5</td>
<td>4.0</td>
<td>–</td>
</tr>
<tr>
<td>Juvenile skipjack</td>
<td>79</td>
<td>5.0</td>
<td>25.0</td>
<td>0.04</td>
</tr>
<tr>
<td>Juvenile albacore</td>
<td>34</td>
<td>2.0</td>
<td>25.0</td>
<td>0.01</td>
</tr>
<tr>
<td>Juvenile bigeye</td>
<td>23</td>
<td>3.0</td>
<td>30.0</td>
<td>0.01</td>
</tr>
<tr>
<td>Juvenile mahimahi</td>
<td>46</td>
<td>10.0</td>
<td>50.0</td>
<td>0.02</td>
</tr>
<tr>
<td>Juvenile yellowfin</td>
<td>89</td>
<td>3.5</td>
<td>35.0</td>
<td>0.01</td>
</tr>
<tr>
<td>Flying squids</td>
<td>67</td>
<td>10.0</td>
<td>50.0</td>
<td>0.15</td>
</tr>
<tr>
<td>Lance</td>
<td>879</td>
<td>0.5</td>
<td>2.9</td>
<td>–</td>
</tr>
<tr>
<td>Squids</td>
<td>294</td>
<td>5.0</td>
<td>25.0</td>
<td>–</td>
</tr>
<tr>
<td>Flying fishes</td>
<td>399</td>
<td>2.0</td>
<td>10.0</td>
<td>–</td>
</tr>
<tr>
<td>Fish nekton</td>
<td>2,090</td>
<td>1.5</td>
<td>6.0</td>
<td>–</td>
</tr>
<tr>
<td>Epipelagic micronekton</td>
<td>2,190</td>
<td>10.0</td>
<td>50.0</td>
<td>–</td>
</tr>
<tr>
<td>Mesopelagic micronekton</td>
<td>2,742</td>
<td>7.0</td>
<td>35.0</td>
<td>–</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>4,108</td>
<td>100.0</td>
<td>0.0</td>
<td>–</td>
</tr>
</tbody>
</table>

Units for biomass estimates are kg per km². Ratios of production/biomass (P/B) and consumption/biomass (Q/B) are estimated per year. Instantaneous annual fishery mortality is represented by F.
Table 2. Summary of the trophic interactions matrix used in the central Pacific Ecopath model for each predator. Diet composition (as percentage by mass) is listed in descending order of importance for the top four prey types.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Dominant prey types</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue marlin</td>
<td>Squids, juv. and adult skipjack, juv. yellowfin</td>
</tr>
<tr>
<td>Other billfishes</td>
<td>Squids, juv. and adult skipjack, juv. yellowfin</td>
</tr>
<tr>
<td>Other sharks</td>
<td>Squids, fish nekton, juv. skipjack and juv. yellowfin</td>
</tr>
<tr>
<td>Swordfish</td>
<td>Flying squid, squids, fish nekton, juv. apex predators</td>
</tr>
<tr>
<td>Blue shark</td>
<td>Flying squid, squids, fish nekton, juv. apex predators</td>
</tr>
<tr>
<td>Albacore tuna</td>
<td>Flying squid, squids, micronekton, fish nekton</td>
</tr>
<tr>
<td>Bigeye tuna</td>
<td>Flying squid, squids, fish nekton, mesopel.</td>
</tr>
<tr>
<td></td>
<td>micronekton</td>
</tr>
<tr>
<td>Yellowfin tuna</td>
<td>Fish nekton, flying fishes, micronekton, juv. skipjack</td>
</tr>
<tr>
<td>Skipjack tuna</td>
<td>Micronekton, fish nekton, juv. apex predators, squids</td>
</tr>
<tr>
<td>Juvenile billfishes</td>
<td>Juvenile skipjack, micronekton, fish nekton, juv. mahimahi</td>
</tr>
<tr>
<td>Mahimahi</td>
<td>Flying fishes, fish nekton, micronekton, juv. tunas</td>
</tr>
<tr>
<td>Juvenile swordfish</td>
<td>Micronekton, fish nekton, squids, juv. apex predators</td>
</tr>
<tr>
<td>Juvenile blue shark</td>
<td>Micronekton, fish nekton, squids, flying squids</td>
</tr>
<tr>
<td>Juvenile other sharks</td>
<td>Micronekton, fish nekton, squids, juv. sharks</td>
</tr>
<tr>
<td>Juvenile skipjack</td>
<td>Micronekton, fish nekton, squids, juv. tunas</td>
</tr>
<tr>
<td>Juvenile albacore</td>
<td>Micronekton, fish nekton, squids, flying squid</td>
</tr>
<tr>
<td>Juvenile bigeye</td>
<td>Micronekton, fish nekton, squids, flying squid</td>
</tr>
<tr>
<td>Juvenile mahimahi</td>
<td>Flying fishes, micronekton, fish nekton, squids</td>
</tr>
<tr>
<td>Juvenile yellowfin</td>
<td>Micronekton, fish nekton, squids, juv. mahimahi</td>
</tr>
<tr>
<td>Flying squids</td>
<td>Micronekton, fish nekton, squids, flying squid</td>
</tr>
<tr>
<td>Lance</td>
<td>Micronekton, fish nekton, squids</td>
</tr>
<tr>
<td>Squids</td>
<td>Micronekton, fish nekton</td>
</tr>
<tr>
<td>Flying fishes</td>
<td>Micronekton</td>
</tr>
<tr>
<td>Fish nekton</td>
<td>Micronekton</td>
</tr>
<tr>
<td>Epipelagic micronekton</td>
<td>Micronekton, phytoplankton</td>
</tr>
<tr>
<td>Mesopelagic micronekton</td>
<td>Micronekton, phytoplankton</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>-</td>
</tr>
</tbody>
</table>
of the fishes represented by trophic level 4 and above was considered as a potential keystone predator.

Paine (1966) derived the keystone predator concept by evaluating responses of a rocky intertidal community to experimental removal of a predaceous starfish species. We conducted an analogous test through Ecosim by simply creating a sudden and sustained tenfold increase in the fishing mortality ($F$) for each individual apex predator compartment at year 2, then allowing the model to run for a total of 30 years. In all cases, this was sufficient to allow establishment of a new steady state or an obvious, new trajectory. In all cases, the manipulated predator biomass dropped to very low levels (ecological extinction). As a final test, we removed fishery exploitation from the entire apex assemblage. This simulation tested the role of the fishery as the keystone predator.

We judged the relative responses to each test by examining the model output for qualitative and quantitative changes based on two general questions: Did one or more other predators increase in proportion to that one decreased by exploitation (competition effects)? Did other species change substantially and in response to the altered apex predator assemblage (predation effects and indirect effects)? In a general sense, we simply asked how much change occurred in the Ecopath food web when one of the apex predators was removed. Because this is a modeling study with all of its attendant assumptions and problematic parameter estimates, we were conservative in the interpretation of “change.” We aggregated responses at the most general level: no substantial change (<50%) and major increase or decrease (>50%). To facilitate interpretation, we present the simulation results by normalizing the response of each state variable. We divided the simulated biomass by the initial biomass level specified in the Ecopath model (i.e., 1.0), then graphed responses in time as they depart from the initial condition. This facilitates interpretation of relative responses, but the reader should be cautioned that initial biomass levels can be substantially different for individual state variables. For example, initial biomass of blue marlin is estimated at 3.3 kg per m$^2$ while that of blue shark is 16 kg per km$^2$ (Table 2), yet both are at the apex of the food web (Fig. 1).

**Results**

**Food Web Structure**

The food web diagram presented in Fig. 1 indicates the extensive connectedness in this system, the compromise of presenting a food web that represents as many as 1,000 species arrayed across many trophic levels, and interactions that summarize cumulative, annual feeding rates over the entirety of a large foraging arena. In keeping with the caution of Walters et al. (1997) we attempted to aggregate prey types with a minimum of vertical trophic overlap. Individual apex predator species and their juveniles were separated based on the practical grounds that understanding of basic
biological characteristics (e.g., diets, age at maturity, growth rates) and records of fishery harvest are not all-inclusive. Each of those selected at the species level includes sufficient knowledge that would allow us to recognize its unique characteristics. Other groupings represent separation of the epipelagic from mesopelagic forms and the fact that diel migration crosses those habitat boundaries. Aggregates called epipelagic or mesopelagic micronekton basically include organisms of the size range from small zooplankton to euphausids and includes both herbivores and omnivores. Fish nekton includes all forms small enough to serve as prey and not identified by a more specific recognition as juvenile apex predators. The category labeled “lance” includes mesopelagic fishes of similar, small size. Squids are aggregated as large (flying squids) and small (all other squids).

The highest trophic levels of the food web (Fig. 1) are occupied by adult blue marlin (Makaira mazara), blue shark (Prionace glauca), swordfish (Xiphias gladius), and two aggregated components that include rare species of similar trophic position and life history. Other shark includes forms such as the thresher shark (Alopias vulpinus) and mako shark (Isurus oxyrinchus), while the category of other billfish includes forms such as the black marlin (Makaira indica), striped marlin (Tetrapturus audax), and sailfish (Istiophorus platypterus). Together, these forms are characterized by trophic positions between level 4 and level 5, relatively low P/B values, and modest biomass, except for blue shark which is very abundant.

The next tier of apex predators, at about trophic level 4, includes adult tunas such as skipjack (Katsuwonus pelamis), yellowfin (Thunnus albacares), bigeye (Thunnus obesus), and albacore (Thunnus alalunga), plus adult mahimahi (Coryphaena hippurus), although the latter has a trophic position similar to that of juvenile swordfish and juvenile other billfish (Fig. 1). Each of this group has higher P/B ratios and, in the case of skipjack and yellowfin tunas, a substantial biomass.

Juveniles of apex predators occupy the region between trophic levels 3 and 4. As stated above, they are treated as separate entities in this model because of substantial evidence of intraguild predation and diet overlap with adult forms. Their P/B ratios, biomasses, and prey consumption rates are generally high. In estimating biomass for the juvenile tunas, we included the assemblage of smaller tuna species (e.g., Auxis sp.) and mackerels. Although the food web does not identify them as individual categories, the life history characteristics of smaller Scombridae are included as their surrogate, juvenile tunas.

Diet of central Pacific apex predators typically contain a huge diversity of prey types and substantial overlap among species. For example, the diet of adult blue shark includes 19 of the forms represented in Fig. 1 and those range in size from small squids to adult billfishes. The two most abundant tunas, skipjack and yellowfin, exhibit almost complete overlap in the diet proportions for each of the 12 prey types in their stomachs. Only adult mahimahi has a substantially different diet from that of other
apex predators in that flying fish are its primary prey. While the general similarity of diets is one of the fascinating features of this system, summarizing this diversity is a challenge because we see only modest evidence of the resource partitioning so elegantly elaborated in studies of freshwater systems and terrestrial food webs (Polis and Winemiller 1995). Instead of reporting the complete diet matrix developed in this Ecopath model, we present only the major prey types representative of the diets for each predator and their overlap with others (Table 2).

**Modeling Results**

Simulated deletion of each, individual apex predator produced a range of results that we aggregated as two general kinds of responses. One group of results evidenced strong effects on only a few other components of the food web. Another group of results indicated a much more extensive and diverse set of effects. For the highest trophic levels (blue marlin, blue shark, other billfish, other shark, and swordfish), removal of the apex predator produced only modest responses among other members of the food web. The response to blue shark removal is representative (Fig. 2). In this case, rapid (within 5 years) and sustained increases occurred in the other billfish group, in swordfish, and in mahimahi, while juvenile blue shark gradually declined. The strongest response was a delayed but exponential and continuing increase in juveniles of other sharks. Other components of the food web were little affected.

Removal of blue marlin or other billfishes produced similar effects: skipjack tuna, all juvenile tunas, and mahimahi increased while juvenile billfish and flying fishes decreased. Although these responses are apparent by our criteria (i.e., > 50%), they were modest and established a new equilibrium biomass within less than 10 years. Swordfish removal caused increases in adult albacore and mahimahi, but no substantial declines in other components. Removal of albacore or bigeye tunas produced similar effects: juvenile swordfish and adult mahimahi increased while flying fishes decreased in direct response to the increase in their major predator, mahimahi. On the other hand, removal of adult mahimahi produced no strong responses in other food web components as compensatory consumption by other predators prevented increase in flying fish abundance.

The second group of results are represented by strong responses expressed in a diversity of food web components. The keystone predator test for yellowfin tuna is indicative of that and is presented in Fig. 3. Removal of adult yellowfin caused rapid, strong (>2×), and sustained increases in the biomass of juvenile yellowfin, flying fishes, mahimahi, and juvenile billfishes. Juvenile skipjack and fish nekton declined, but the latter exhibited a slow and continuing response. Other components were little affected. Removal of adult skipjack tuna produced responses very similar to those from adult yellowfin.

Although not pictured in Fig. 1, the apex of this food web is actually that represented by longline fisheries. As a test of that prospect, we used
Figure 2. Responses of selected food web components to removal of blue sharks. Biomasses for each are normalized to their initial condition. The Ecosim model was perturbed at 5 years into a 30-year simulation by a tenfold increase in fishery mortality for blue shark.

Ecosim to remove the estimated levels of fishing mortality from each and all of the apex predators. The results of that trial are summarized in Fig. 4 and exhibit more substantial responses that any of those derived from removing any of the individual predators.

Most, but not all, of the adult apex predators increased in response to removal of the fishery. Rates of response corresponded with life history characteristics (rapid maturity, high P/B values) with the tuna species responding most quickly. Over time, blue marlin, swordfish, and blue shark biomasses came to dominate the assemblage with the most substantial change (>8x) exhibited by blue marlin, with blue shark continuing to increase at 30 years. Conversely, adult mahimahi declined quickly and remained at low levels. Juvenile skipjack and juvenile yellowfin demonstrated opposite responses. The latter increased initially, then declined to sustained and low levels. Other food web components were less affected. In the absence of fishing, this food web would have a greater overall abundance of large fishes and would be dominated by those of highest trophic position.
Discussion

Contrary to expectation, no one member of this apex predator guild can be considered a clearly demonstrable keystone predator. Simulations of removal demonstrate complex compensatory responses in this ecological context. None of the simulations produced results indicative of simple replacement processes. For example, removal of the abundant blue shark did not cause an increase in the group of other adult sharks which have similar life history characteristics and diets. Instead, the juveniles of other sharks became most abundant. Two explanations may be offered. One is to simply note that the complexity of this food web context makes simple expectations subject to question. That may be true, but has no explanatory power and does not advance our understanding. The second is that we have provided inadequate or insufficient inputs to the Ecopath model that underlies these simulations. Most likely among those prospects is the insufficient accounting for intraguild cannibalism that would control survival of young sharks. Although our diet matrix does include some cannibalism (juvenile sharks are 0.5% of diets for blue shark and other sharks),
this may underrepresent the importance of cannibalism because shark diets are not well studied. Given the low fecundity and slow maturation of these fishes, a modest increase in cannibalism rates could have profound ecological effects.

An alternative approach is to seek independent evidence of ecological changes that may have transpired in places where shark removal programs or intensive fisheries have selectively decreased the populations of adult sharks (Bonfil 1994). Shark removals or shark exclusions (large-mesh nets) have been conducted in a number of places with a universal, general result: increase in abundance of small sharks. As simulated in the keystone predator test using Ecosim, real world removal of large sharks produces increases in small sharks. This comparison provides the encouragement of independent evidence, but does not explain why juvenile blue sharks should decline. This version of the model treats adult and juvenile members of a species as independent entities. Adults may cannibalize their juveniles and they may compete for some prey types, but there is no direct stock-recruit linkage. Therefore, first principles would have it that removal of adult blue sharks should produce more juvenile blue sharks. The opposite occurred and its explanation is not obvious and, again, calls for reevaluation of the adequacy of biological information used to develop Ecopath inputs for these fishes. This conclusion (more

Figure 4. Responses of selected food web components to removal of fishing mortality for all apex predators.
study is necessary!) should not overshadow that fact that the model and its embedded assumptions produced a general result remarkably analogous to ecological changes documented in several places where shark removal programs have been conducted.

Two members of the apex predator guild, adult yellowfin and adult skipjack tunas, apparently have critically important roles in this food web. Their removal evoked substantial and sustained changes in the structure of the system. Their importance corresponds with the fact that they are major biomass components of the apex guild and with their relatively high P/B ratios. They are, by definition, important and highly responsive members of the system. Their diets and trophic position also assure an important role as they are among the prey for higher-order predators such as billfishes and sharks, competitors of all members of the guild, and predators on a diversity of lower trophic levels. In this complex system with high degrees of trophic interaction and diet overlap, these tunas are the most effective generalists. They are opportunistic predators and capable of rapid biomass increase. Their abundance confirms the advantages of those traits.

Independent evidence of the keystone role for yellowfin tuna is also available in those systems where exploitation has been and continues to be more intense than in the central Pacific. Longline fishing has been intense in the Gulf of Mexico and Caribbean Sea for many years with the large tunas, especially yellowfin tuna, as major target species. Commensurate with a decline in yellowfin landings, catch reports from those fisheries include a general increase in the abundance of smaller tunas and a recent, rapid increase in the landings of mahimahi (Hinman 1998). The Ecosim simulation (Fig. 3) forecasts similar responses for the central Pacific food web.

As made apparent by Fig. 4, the real keystone component of this system is that owing to fishing. We cannot evaluate the structure of these systems prior to the development of exploitation because of the conundrum that what we know of these fishes and their ecosystem derives from fisheries. Blue marlin demonstrates the most dramatic response to removal of exploitation. We could expect, therefore, that the abundance of large billfishes such as the marlin species and swordfish would be the first to show rapid declines as the fisheries began to develop.

Again, there is some independent evidence in support of that hypothesis. As the Japanese longline fleet developed and expanded into the central Pacific in the 1950s, catch rates for large billfishes were the first to decline (Stroud 1989). As the Hawaii-based swordfish fleet developed, the catch per unit of effort dropped very quickly to less than one-third of the initial rates (Boggs and Ito 1993) while total catches rose to a sustained level as new ships were added to the fleet. In other words, the advent of new fisheries had its first and most profound effect on large billfishes. Removal of fisheries should produce the opposite effect, and that is seen in Fig. 4.
Our analyses indicate that knowing more about the intensity of cannibalism, especially that by sharks, would provide major returns in our understanding of food web dynamics. We also assumed that the juvenile tuna groups would represent the equivalent of life histories for other, smaller members of the tuna group (Scombridae). Organisms such as the bullet mackerel (*Auxis rochei*) are at the nexus of food webs in the Eastern Tropical Pacific (Olson and Boggs 1986). Their analogues play an essential role in our model, but we have no direct measures of their actual abundance and dynamics. That will remain an important unknown in this and similar pelagic systems until an adequate stock assessment technology is developed. As an immediate alternative, our simulations suggest that increases in mahimahi catches may be a signal of changing ecological interactions derived from intensified exploitation of larger and less resilient species such as marlin, other billfishes, and/or yellowfin and bigeye tunas.

Trophic cascade effects are well known from lakes (Carpenter and Kitchell 1993), were recently documented for the North Pacific (Shiomoto et al. 1997), and appear in some applications of the Ecosim model (Walters et al. 1997). We see no evidence of trophic cascade effects in these manipulations of the central Pacific model. Two conclusions derive from that observation. First, the Ecopath model structure includes high resolution at the upper trophic levels but substantial aggregation for the lower trophic levels. Thus a manipulation at the apex predator level may be dispersed by compensatory responses among the many other components at high trophic levels. Second, the previous and current levels of fishery exploitation are such that a manipulation of exploitation levels of apex predators is not sufficiently strong to be transmitted from trophic levels 4 or 5 and through the food web to the phytoplankton. Trophic cascades derive from strong and sustained manipulation of food webs (Carpenter and Kitchell 1993). Although there were strong responses to simulated removal of fisheries from the central Pacific food web, they were obvious only among components at or above trophic level 3.

Our conclusions about keystone predator effects are based on a model that works in the singular currency of energetics. This is a unifying method, but it may be insufficient in that it underrepresents the prospect that alternative currencies (e.g., nutrients, behavioral interactions that apportion space) and alternative mechanisms (e.g., migrations, predator avoidance) may play major roles in the structure of this community. We do not know that and, given the spatial scales of the key interactions, we probably will not see better alternatives or experimental tests of those for some time to come. Better models may be a quicker way to create and test alternatives. Comparative studies (e.g., Atlantic vs. Pacific) offer another opportunity for rapid learning.

Like all models, Ecopath and Ecosim are simplifications that effect a compromise between the merits of simple, general theory and the constraints of overwhelming ecological detail. Ecopath has the merit of being based on the need for a balanced energy budget. That forces an empirical
accounting in its parameterization and the experience of Ecopath modelers has accumulated to the point where the software includes challenges and warnings about unrealistic estimates. This creates a stable basis for using Ecosim as a tool to evaluate alternative scenarios.

Obviously, there is substantial opportunity for increasing the extent and accuracy of the basic data requirements of the central Pacific Ecopath. But, we cannot and should not use “waiting for better data” as an excuse. The lessons from the Atlantic Ocean (Hinman 1998) and from global fisheries development (Pauly et al. 1998), teach us that ecological changes have and will continue to occur more rapidly than can be documented by field studies. There is some urgency to these matters because resource management policies for highly migratory stocks and those based on ecosystem principles must be developed in the near future (Botsford et al. 1997). The rate of change in these ecosystems is substantially greater than our rate of learning based solely on accumulation of empirical evidence.

The main lesson for fisheries managers is that the effects of longline gear are ecologically complex. Models such as that described herein afford one tool for evaluating that complexity in an ecosystem context. An important lesson for conservationists is that the status of these apex predator populations and their ecological context can only be known through monitoring of the fisheries. One consequence of the 1992 United Nations ban on drift gillnets in the North Pacific was that the Asian fleets no longer provide ready access to data from their longline fleets. Those fleets account for approximately 95% of fishery exploitation in the Central North Pacific. Conservation concerns for the future of billfishes, sharks, and some tuna stocks are important, but must be expressed with the understanding that restriction of longline fishers registered under the U.S. flag accounts for a very small fraction of the exploitation pressure and, more importantly, constrains or eliminates our most important source of information about the status of these apex predators and the pelagic ecosystem that supports them. The Hawaii-based longline fleet is our essential monitoring tool in the central Pacific. Research must rise to the challenge of understanding how fishery-derived data can be extended to the ecosystem context required for sustainable management of these fisheries.

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