

TOWARD A FISHERIES ECOSYSTEM PLAN FOR THE NORTHERN CALIFORNIA CURRENT

JOHN C. FIELD, ROBERT C. FRANCIS, AND ARE STROM

School of Aquatic and Fisheries Sciences
Box 355-020
University of Washington
Seattle, Washington 98195
jffield@u.washington.edu

We have witnessed changes in the landscape around us with the advent of technology evolved from the axe and the plow. We should expect equally profound ecological changes from modern, large-scale uses of the hook and the net. (EPAP 1999)

ABSTRACT

Recently the congressionally established Ecosystem Principles Advisory Panel issued a report on how best to amend single-species management. A major recommendation was that fisheries management councils develop a fisheries ecosystem plan (FEP) for every ecosystem under their jurisdiction. This document would be an umbrella document containing detailed information on the structure and function of the ecosystem under consideration. The U.S. portion of the northern California Current ecosystem (NCCE) may be an appropriate test case to develop some of the key elements of a draft FEP. Fishing pressure in the NCCE has been intense for decades, and the possibility of consequent large-scale ecosystem changes is large. Although fisheries science in this region has considerably advanced our understanding of the intricate linkages between fisheries production and large-scale oceanographic and atmospheric climate forcing, fisheries management efforts throughout the region may be insufficient for assessing the ecological impacts associated with fishing. We use Ecopath models to assess the state of the NCCE in the 1960s during a cool regime with low exploitation rates and high rates of zooplankton production, and also in the 1990s during a warm regime characterized by low productivity, declining stocks, and intense exploitation. We compile population parameters and diet data for 34 species/species assemblages for both time periods to generate a food web of basic trophic interactions. These models are in agreement with the general consensus that this system has been functioning at lower levels of productivity since the 1977 regime shift. More work is needed to understand the status of many NCCE populations, but stock assessments and fisheries data suggest that the observed fluctuations in many harvested populations may be rapid, highly variable, and increasingly undesirable.

INTRODUCTION

To date, most fishery management efforts in the United States continue to focus on regulatory mandates

contained in management plans based on species-specific stock assessments. The Magnuson Fishery Conservation and Management Act, which provides the legal authority for marine fisheries management, mandates that fisheries scientists and managers "prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery" (16 U.S.C. 1851). Although there is legal authority for taking into account how fishing activities affect fish habitat, this authority has generally not been used by managers, and the Magnuson Act contains no explicit direction on how managers should actively consider the indirect consequences of fishing on trophic dynamics or structure.¹

Recognizing the promise of an "ecosystem-based" approach to improving fisheries management, the U.S. Congress recently requested that the National Marine Fisheries Service (NMFS) convene a panel of experts, the Ecosystem Principles Advisory Panel (EPAP), to examine how best to build upon single-species management approaches. The EPAP's primary recommendation was that fishery management councils develop a fisheries ecosystem plan (FEP) for every ecosystem under their jurisdiction (EPAP 1999). An FEP is envisioned as an umbrella document containing detailed information on the structure and function of the ecosystem under consideration (e.g., a conceptual model of the food web and other ecosystem components, total removals from fishing, and assessments of the human elements of the ecosystem that most significantly affect fisheries). The FEPs would be intended to increase managers' and stakeholders' awareness of how their decisions affect the ecosystem. As such, FEPs would be the next major step in translating today's directed management efforts into more holistic approaches.

Our efforts have focused on using the U.S. portion of the northern California Current ecosystem (NCCE), which includes the heavily fished shelf and slope ecosys-

¹The extent to which the Magnuson Act explicitly mandates the consideration of ecosystem aspects could be arguable, as there is no mention of ecosystem considerations in the National Standards or in the FMP requirements. However, some authority is inferred in the definitions section of the act with regard to the word *optimum* with respect to yield from a fishery (Section 104-297 of 16 U.S.C. 1802), where it is suggested that optimum yield "means the amount of fish which will provide the greatest overall benefit to the Nation, particularly with respect to food production and recreational opportunities, and taking into account the protection of marine ecosystems."

tems between Cape Mendocino, California, and the northern tip of Vancouver Island, as a test case to develop what we believe to be some of the key elements of a draft FEP. Fisheries resources in the NCCE have been subjected to intensive fishing pressure for a protracted period. The abundance of coastal pelagic species such as sardine, anchovy, and herring has varied substantially over past decades, most likely in direct association with different modes of climate forcing. Precipitous declines in several stocks of Pacific rockfish (*Sebastes* spp.) and some roundfish have occurred over the last 20 years, and are evident in the corresponding declines of commercial landings (Ralston 1998). Similarly, many salmon fisheries of the NCCE, in particular ocean fisheries, have been in decline since the late 1970s. These declines are generally attributed to a combination of unfavorable ocean conditions (Hare et al. 1999), spawning and rearing habitat degradation and loss, and overfishing (NRC 1996). Juvenile salmon, a staple in the diet of many higher-trophic-level species, have been particularly affected by habitat loss and interdecadal variations in climate (Mantua et al. 1997; Hare et al. 1999); the recruitment of rockfish, the juveniles of which are also a staple in the diet of many larger predators in this system, has similarly been greatly reduced in recent decades (MacCall 2000).

The complex and fragmented design of interacting human and institutional elements hinders the transition to more holistic management efforts in this ecosystem. Under an ecosystem-based approach, management actions would be designed and monitored through an adaptive management approach (Ludwig et al. 1993), and management institutions should be designed so that resource ecology and institutional ecology overlap in a complementary manner. All of these issues of governance are particularly true in the NCCE, where numerous state, federal, and tribal institutions often seem to have different responsibilities with regard to the management of fishery resources. Of particular concern is the challenge of incorporating a longer time and broader spatial and biological view into this management arena. Thus the northern California Current may provide an opportunity to explore efforts for surmounting the impediments to sustainable and rational management of living marine resources.

WHY ECOSYSTEM-BASED MANAGEMENT?

In many fisheries it has become increasingly obvious that the ecological consequences of fishing are substantially greater and more complex than the biomass reductions of target species. These consequences may include but are not limited to mortality of nontarget species, alteration of benthic habitats and bottom topography, changes in age and size structure of fished (both target

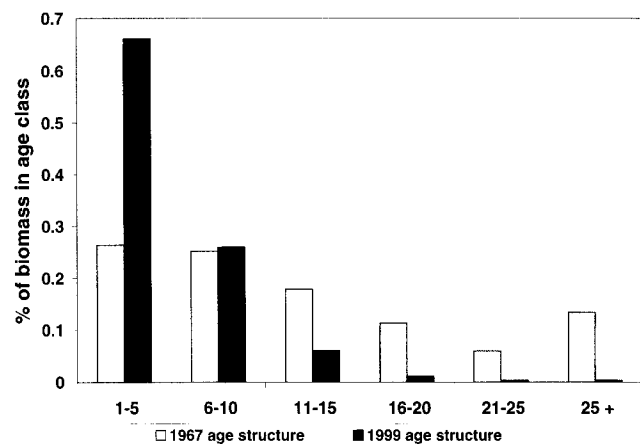


Figure 1. Changes in the age structure of the northern canary rockfish population (based on stock assessment data). Graph shows the percentage of population biomass in five-year groupings of age classes between 1967 and 1999, illustrating the shift in population biomass to younger, smaller individuals. During this same period the total population has been fished down to approximately 10% of its unfished population biomass.

and nontarget) populations, changes in sex ratios of targeted populations, and changes in the genetic structure of fished populations (Botsford et al. 1997; NRC 1999).

As one simple example, figure 1, based on the stock assessment by Crone et al. (1999), shows how the age structure of the canary rockfish population has changed over the last three decades. This figure shows an extreme case of the truncation of the age distribution of this long-lived species. Recruitment of canary rockfish has been extremely low over the last two decades, and the large proportion of young individuals does not reflect increased recruitment, but rather removals of a substantial fraction of older individuals.

In addition to population impacts, structural changes to trophic webs have been described for numerous heavily fished ecosystems (Parsons 1993; Apollonio 1994; Fogarty and Murawski 1998; Pauly, Christensen et al. 1998). Furthermore, interannual and interdecadal climate shifts affect the productivity of marine populations, with dramatic effects on fisheries (Mantua et al. 1997; Anderson and Piatt 1999; Hare and Mantua 2000). The effects on marine ecosystems as a consequence of fishing activities, notably as direct effects of fishing gear on benthic habitats, are poorly understood in most systems, but have been shown to be substantial where evaluated (Auster et al. 1996; Engel and Kvitek 1998).

Figure 2 is a simplistic representation of how traditional approaches to fisheries management, which focus primarily on interactions between commercially important populations and fishing activities, could be broadened to include basic interactions between commercial and noncommercial species, the effects of fishing activities on habitat, and the large-scale impacts of climate forcing on ecosystem productivity and structure.

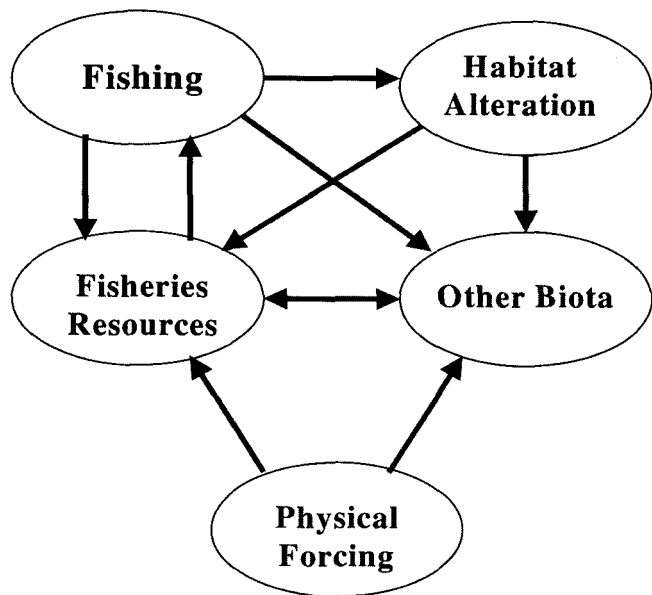


Figure 2. A conceptual outline for incorporating ecosystem considerations into fisheries management.

It is widely recognized that an ecosystem approach to fisheries management will have different meanings for different people. As with much environmental legislation, a mandated ecosystem-based approach will invite controversy about its implementation, regardless of the definitions put into the law. The discussion on what an ecosystem-based approach might mean to managers is broad and often tortuous, yet some mention of key views is worthwhile. For example, Grumbine (1994) suggests that managing for ecological integrity would mean that commodity extraction should be relegated to an ancillary goal. As the EPAP report (1999) points out, when fishing is examined from an ecosystem context the rationale for surplus production is unclear; before the advent of fisheries all production was recycled within ecosystems. Other stated consequences of fishing include inducing ecological changes among competitors, predators, and prey, and such changes could imply future levels of surplus production that approach zero for some populations well into the foreseeable future. This is in direct conflict with the assertion by some that the adoption of an ecosystem-based approach should lead to healthier and more dependable fisheries. For example, the NRC Council on Sustainable Fisheries Report (NRC 1999) suggests that the goals of an ecosystem-based approach are to “rebuild and sustain populations, species, biological communities and marine ecosystems at high levels of productivity and biological diversity, so as not to jeopardize a wide range of goods and services from marine ecosystems, while providing food, revenue and recreation for humans.”

Like so many policy and management approaches, the purported objective in the NRC report is to maximize

many variables at once, thereby implying that all of the objectives are mutually compatible. This approach, like that of traditional fisheries management, continues on the assumption that fisheries can safely remove surplus production without consequences to the ecosystem; as implied by the conclusion that although adaptation of such an approach will likely cause short-term economic losses and impacts to communities, the ultimate outcomes should not include decreased yield, since rebuilt populations should increase sustainable yield (NRC 1999).

These assumptions are difficult to justify given the current poor state of knowledge about the aforementioned ecological consequences of fishing on marine ecosystems, revelations that many long-lived species have considerably lower rates of production than previously thought and may take many decades to recover, and our inability to clearly define what might or might not constitute a “healthy” marine ecosystem. Moreover, there should be little reason to use higher potential yields as a selling point of ecosystem management, as the solution to a stock’s inability to produce some level of sustainable yield would (and under the Sustainable Fisheries Act, legally should) ostensibly be reached through the adoption of quota reductions and stock rebuilding plans under a single-species approach. In the future, as policymakers and resource managers struggle to consider what ecosystem management is, perhaps it will be worthwhile to step back and consider what it is not.

One potential outcome of implementing an ecosystem-based approach could be reduced stability or predictability in future fishery yields. A reduction in predictability does not necessarily imply that most current yields are stable, but rather that the pursuit of stability for economic and allocation purposes may be in conflict with the notion of adaptive management of ecological resources. Holling and Meffe (1996) argue that the pursuit of stability is part of the explanation for why many resource management efforts have failed, because the objectives of many such efforts have been to reduce the natural bounds of variation in ecological systems in order to make them more predictable and more reliable for extractive needs. Holling and Meffe argue that the key to natural resource management, whether it be single-species or ecosystem management, is to retain critical types and ranges of natural variation in ecosystems, and to facilitate existing processes and variabilities rather than attempting to alter or control them.

Perhaps one example of such an approach can be observed in the recently approved fishery management plan for coastal pelagic species (PFMC 1998). The plan was based on the premise that the theoretical definition of maximum sustainable yield (MSY) as a constant level of catch should not be applied in fisheries for coastal pelagic species such as sardine, anchovy, and mackerel because

of the high sensitivity of the productivity of these stocks to changes in environmental conditions. Instead, management is based on the application of a baseline “cut-off” population biomass, below which directed harvests are not allowed, and above which allowable landings are based on a fraction of the available biomass above the cutoff level. This approach allows for high harvest rates during favorable environmental conditions but forces fishing mortality to zero if the stock declines to a baseline biomass.

Apollonio (1994) suggests that in marine ecosystems, the ecological role of fishing is comparable to the role of apex predators. It follows that, analogous to the way biological feedback mechanisms underlie natural predator-prey relationships, appropriate feedback mechanisms between vessels and target species should exist to keep the system in balance. In order for fishing to be ecologically sustainable, Apollonio argues, the ecological impacts of fishing should be similar to the natural impacts of apex predators. This may imply that during unproductive years, decades, or even longer periods, the yield of many species, indeed of many ecosystems, may be unsustainable from the perspective of stock, species, or system productivity.

The Pacific Council’s Coastal Pelagic Species FMP is one step toward the application of this principle, yet in practice these balancing mechanisms are scarce because of external subsidies, which have the effect of maintaining fisheries that might be otherwise unprofitable. Instead, fleet buildups continue far beyond what might be sustainable as stocks are fished down to (and often beyond) the estimated size that produces the maximum sustainable yield. The existence of strong incentives for vessels to switch rapidly from one fishery to another when catches decline, and the ability for effort to shift massively over short time periods would suggest that the feedbacks that might exist in a more typical predator/prey system are substantially diminished.

For the northern California Current, our initial work has focused on preliminary attempts to address three of the eight key minimum actions envisioned in the EPAP report as elements of demonstration fishery ecosystem plans. These include a characterization of biological dynamics of the ecosystem, development of a conceptual model of the food web, and the estimation of total removals and how those relate to standing biomass, production, and trophic structure. A summary of our early efforts to address these elements makes up the remainder of this paper.

The remaining five key elements of FEPs as envisioned by the EPAP panel are certainly no less crucial. They include descriptions of the habitat needs of different life-history stages for all plants and animals that represent the “significant food web” and how they are

considered in conservation and management measures; an assessment of how uncertainty is characterized and what types of buffers are included in management actions; the development of indices of ecosystem health as targets for management; descriptions of long-term monitoring data and how they are used; and an assessment of the ecological, human, and institutional elements of the ecosystem that most significantly affect fisheries and are outside of Council/Department of Commerce authority (see Fluharty and Cyr, this volume, for greater detail). For all of these actions, the FEP process would provide an opportunity to refine, integrate, and further develop the substantial efforts that have already been made by government and academic workers.

THE NORTHERN CALIFORNIA CURRENT ECOSYSTEM

The continental margin of North America off the coasts of northern California, Oregon, Washington, and southern British Columbia is a productive coastal upwelling region that has long supported commercial harvest of a variety of marine resources. The entire California Current ecosystem (CCE) is an “open” system, meaning that it is a transition environment between subarctic and subtropical water masses and the freshwater systems that enter the ocean along its landward boundary (Hickey 1989).

This region is also an ecotone comprising a small number of endemic coastal species and a larger mixture of subarctic and subtropical species, many near the periphery of their distributional range (Bottom et al. 1993). The northern half of the CCE, the region of coastal ocean between Cape Mendocino, California, and the northern tip of Vancouver Island, B.C., is described as a zoogeographic transition between Californian and Aleutian biological provinces. We refer to this region as the northern California Current ecosystem, and presume that this system may be an appropriate ecological unit for regional management as the focus of this paper.

A growing body of research has shown that during the twentieth century, both El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) processes had major impacts on the organization and dynamics of marine ecosystems of the NE Pacific Ocean and, as a result, on fisheries operating within those ecosystems (e.g., Wooster and Fluharty 1985; Francis et al. 1998; McGowan et al. 1998; Anderson and Piatt 1999). Because the effects of climate are so pervasive in the NCCE, as a first step to ecosystem reconstruction it is essential to understand past patterns of climate as they may have affected the NCCE. As an example of how past climate patterns have influenced the NCCE, we will briefly examine information about the presence of Pacific sardine in the region over the last two centuries.

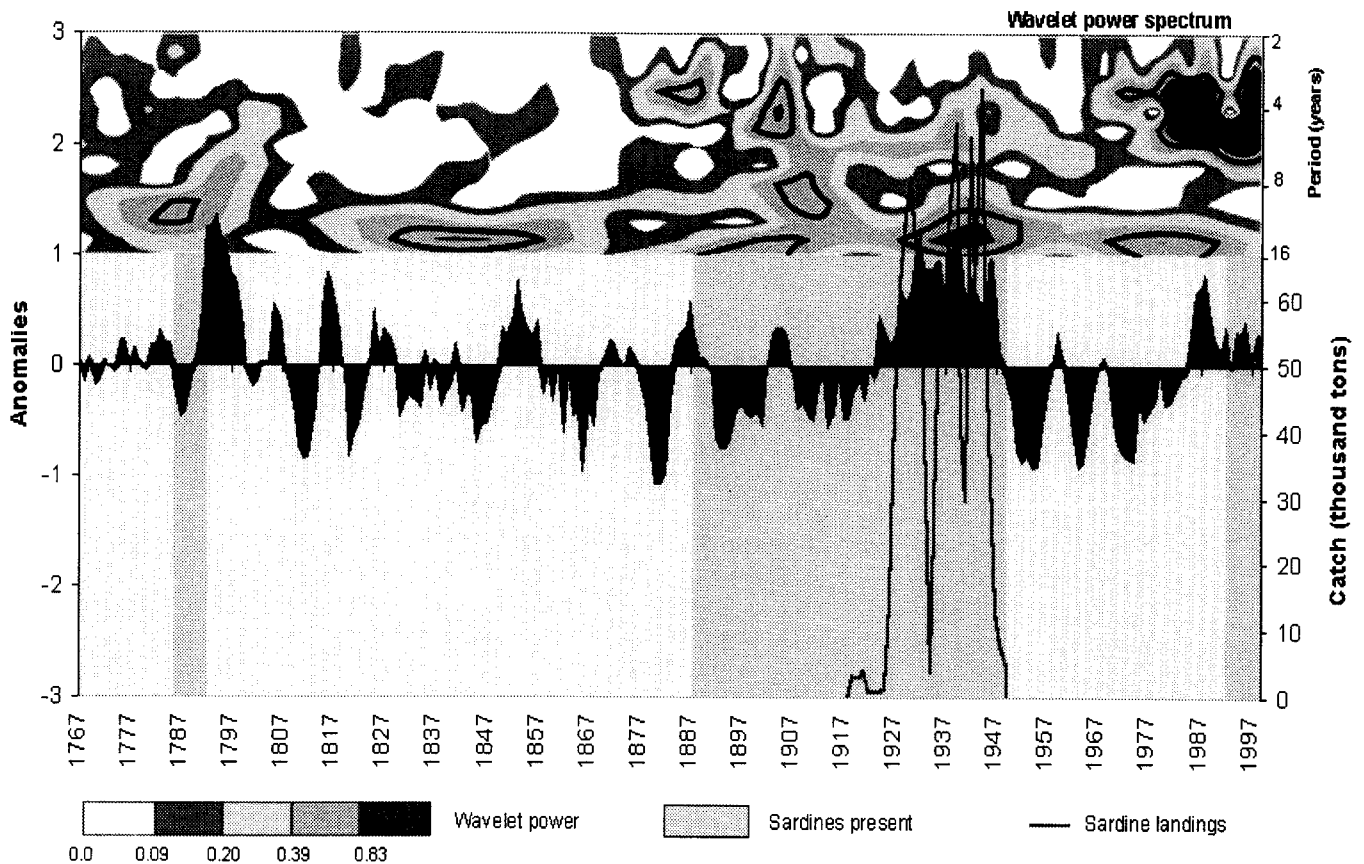


Figure 3. Pacific Northwest sardine occurrences charted against reconstructed winter PDO and ENSO wavelet power spectrum. (See footnote 1 for a summary of historical records of sardine presence/absence in the Pacific Northwest.)

Figure 3 is a composite that explores possible relationships between climatic influences and the presence and absence of sardines in the NCCE. Shaded areas indicate periods of sardine presence; solid lines indicate commercial landings in the Pacific Northwest. This information is plotted against a tree-ring reconstruction of the PDO time series (Dell’Arciprete et al. 1998) and a wavelet analysis of the ENSO cycle (top panel) as reconstructed by Mann et al. (1999). The wavelet analy-

sis provides a graphic representation of the intensity, or magnitude, of climate variability at various frequencies (see Torrence and Compo 1998). Darker shades in the upper panel indicate more intense ENSO periods.

Figure 3 suggests that each range expansion of sardines documented since the latter part of the eighteenth century occurred during periods of increased North Pacific climatic activity.² The first period of increased activity occurred in the late 1700s, when sardines were

²It appears that three major northward expansions in the range of sardines have occurred since the late 1700s. During the first two, sardines were abundant enough to support substantial fisheries that persisted for a number of years as far north as Puget Sound and Vancouver Island. Between 1786 and 1792 a number of accounts, including those of trained naturalists, described the native fisheries for sardines along the Pacific Northwest coast; John Meares (1791) described how “In the Spring, the herrings as well as the sardines frequent the coast in vast shoals.... The sardine resembles that of Portugal, and is very delicious; they are taken here by the people in prodigious quantities.” By the beginning of the 19th century, however, sardines were no longer being noted in the journals of explorers, naturalists, or traders, despite more extensive exploration in the Pacific Northwest region following the Lewis and Clark expedition.

Apparently sardines did not return to the Pacific Northwest until the late 1880s. Extensive scientific investigations of fisheries resources—including those conducted by the Wilkes expedition in 1841 (Wilkes 1884), the Pacific railroad surveys of 1853–57 (Suckley 1860), and the investigations of the U.S. Fish Commission in 1880–81 (Goode 1884)—failed to locate sardines in Pacific Northwest waters. The U.S. Fish Commission reported in 1884 that sardines ranged from Chile to Cape Mendocino, California. By 1888–89, however, this range had expanded to encompass Puget Sound. Sardines were found in Puget Sound waters during “the warmer part of the season, and are taken with herring and other species for market” (Collins 1892). Landings of fresh sardines in 1888 were reported to be 60,000 lbs. By 1895 sardines were occurring in “large numbers” in Puget Sound (Jordan 1895), and in 1902 were described as “abundant” (Kershaw 1902). The first official records of sardines captured in Canadian waters did not appear until January 1900, when two specimens were collected in the Strait of Georgia near Nanaimo (Clemens and Wilby 1961). Concurrent with the development of the California sardine fishery in the 1920s, a lucrative fishery for sardines began in British Columbia in 1917–18 and lasted until 1948–49, when stocks once again disappeared (Schweigert 1988).

Sardines were again observed in the waters north of Cape Mendocino in the 1980s (Emmett and Brodeur 2000) and returned to the Pacific Northwest and British Columbia in 1992 (Hargreaves et al. 1994), though not in sufficient quantities to warrant a resumption of large-scale commercial fisheries. The return may also have been short-lived. In 1998 and 1999 there was a series of massive die-offs of sardines along northern sections of Vancouver Island. These mass deaths coincided with the 1998–99 La Niña that caused sharp declines in coastal ocean temperatures (Drouin 1999).

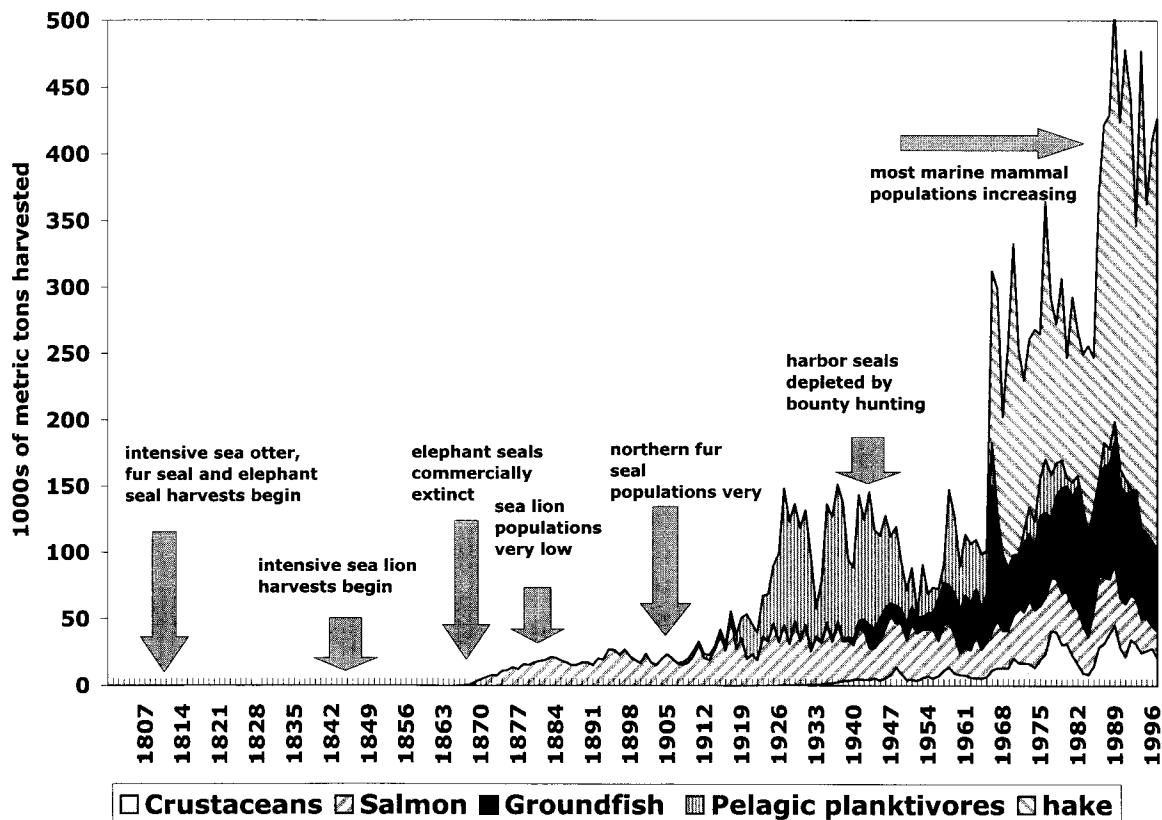


Figure 4. A summary of major removals by fisheries from the northern California Current ecosystem over the last two centuries.

apparently already in an expansion mode, the PDO was nearing a substantial peak, and ENSO activity may have been more intense and frequent than normal. It is unclear exactly when the sardines disappeared from Pacific Northwest waters during this period, but historical records suggest that they were no longer present by the early 1800s. Similarly, the expansion of the sardine population starting around 1880 coincided with increased power in both the ENSO signal and the magnitude of the PDO. Finally, the return of sardines to the British Columbia coast in the 1990s coincided with a general expansion of the coastal population, starting with the major climate shift of the late 1970s and the record El Niño activity of the 1980s and 1990s.

Sardines may epitomize the nature of change in key species in this system; their presence implies a different ecosystem state than during periods of their absence. This subsequently implies that key flows of energy and biomass in the system changed substantially prior to human intervention. Smith (1978) inferred changes of even greater magnitude in the abundance of Pacific hake in the California Current based on the scale record of Soutar and Isaacs (1974), which suggested that the abundance of hake (although these scales probably represent juvenile hake) at the turn of the twentieth century may have been as much as an order of magnitude greater than

current levels. These observations illustrate that pronounced changes of boom and bust in the natural cycles of migratory coastal pelagic species such as sardines and hake imply massive changes in primary and secondary production within the NCCE. This in turn suggests that the ecosystem was structured very differently in previous centuries than it is now.

FISHERIES DEVELOPMENT IN THE NCCE

Fishing pressure in the NCCE has been intense for decades and has effected consequent large-scale changes in the relative abundance of many key populations. Knowledge of NCCE structure and dynamics comes primarily from stock assessments, fisheries and food habits data, and oceanographic records. These sources mostly cover recent decades, and indicate high levels of physical and biological variability on broad spatial and temporal scales.

Catch statistics provide perhaps the most complete record of population trends, and indicate that rapid and possibly undesirable changes are occurring in NCCE structure. Figure 4 presents a partial accounting of catch data and major biological removals over the last two centuries, illustrating both the magnitude of removals and the sequential nature of the development of the major fisheries in the region. This figure shows that although

industrial-scale fishing pressure in the NCCE has been intense for only decades, various ecosystem components have been substantially exploited for at least two centuries.³

The first species to be the subject of major commercial exploitation were marine mammals. Fisheries for sea otters, fur seals, sea lions, and elephant seals grew to support enormous commercial harvests in the early and mid-1800s. Although few of these populations actively breed in the NCCE, all spend at least some of their time in Pacific Northwest coastal waters, and many are significant seasonal predators in the region. Estimates of actual take of most of these animals are difficult to derive: some estimates of otter and fur seal removals exist in fur trade records, but the number of elephant seals and sea lions taken for oil and meat can be only coarsely assessed.

Scammon (1874) suggested that hundreds of thousands of elephant seals must have been taken in the early part of the nineteenth century, and the species was commercially extinct by the 1870s. Specimen and museum collectors continued to take elephant seals even as the population was on the verge of extinction (Stewart et al. 1994).

Sea lions were originally taken for meat to supply the early hunters of sea otter along the California and Pacific Northwest coastline, and continued to be killed both as potential competitors for commercial fish as well as for their trimmings (the testes and penises of breeding bulls) following commercial depletion in the early twentieth century (Bonnot 1928).

Fishermen and bounty hunters along the U.S. and Canadian coastlines targeted harbor seals until the 1960s (Bonnot 1928; Newby⁴). Gray, humpback, sperm, and other whales were targeted for well over a century throughout the northeast Pacific. Such removals kept most pinniped and cetacean populations at low to moderate levels until the middle of the twentieth century, and only in the last several decades have populations of many marine mammals increased to substantial numbers.

Although many species of fish and shellfish throughout the NCCE have been harvested by native peoples

for millennia, some at rates that may have approached later commercial levels (Yoshiyama et al. 1998), large-scale commercial harvests of fish in the region generally did not begin until many marine mammal populations had been substantially depleted. The salmon fisheries were among the first to develop: the first salmon cannery was opened in 1864 along the Sacramento River, but was soon moved to the much more productive Columbia River. By 1885, salmon catches in the Columbia alone topped 40 million pounds, and salmon fisheries had expanded to nearly every major watershed in the Pacific Northwest (Cobb 1930). Salmon fisheries continued to dominate the region, even as the soon-to-be legendary California sardine fishery was initiated in the early twentieth century.

Total coastwide sardine landings would reach over 700,000 metric tons (t) per year. Although the vast majority of sardine landings were made in the southern part of their range, up to 80,000 t a year were caught in the summer fisheries of the northern California Current between the 1920s and 1940s. When this fishery began to collapse in the 1940s, it did so from north to south, and it has long been suspected that changes in marine conditions played a role in this population decline (Ueber and MacCall 1992). In British Columbia, substantial herring fisheries had developed during the period of the sardine fishery, and grew rapidly following the sardines' departure from northern waters (Waddell and Ware 1995) while anchovy and mackerel populations underwent substantial (and perhaps sequential) fluctuations in the southern part of the sardines' former range (MacCall 1996). As the sardine population has increased over the last two decades, the fishery has also undergone a resurgence, with sardines once more being fished in commercial quantities between Baja California and British Columbia.

Pacific halibut was the first of the groundfish species to be targeted by commercial fisheries, although flatfish, lingcod, rockfish, and sablefish were all supporting substantial fisheries throughout the NCCE by 1900. Total landings of all groundfish grew gradually throughout the twentieth century, approaching 20,000 t per year in the early 1960s. During the mid-1960s the Soviet Union (and several other nations) began fishing for hake and rockfish in the coastal waters of Oregon, Washington, and British Columbia, and coastwide landings quickly reached several hundred thousand metric tons per year (primarily hake). As a result of the declarations of 200-mile fishing zones by both the United States and Canada in the late 1970s, these foreign fisheries were phased out as domestic fleets developed, and overall landings continued to grow as the fleets greatly exceeded the capacity needed to harvest the resource (PFMC 1993). Following the rapid development of domestic fisheries, it was found that many of these stocks were consider-

³Data are incomplete, and from a variety of sources; salmon landings since 1911 were compiled by Hare et al. (1999), prior to 1911 are inferred from canned salmon production described by Cobb (1930). Pelagic planktivores (sardine, anchovy, herring, smelt, and shad) data were taken primarily from PFMC 1998, except for herring data taken from Waddell and Ware 1995 and very early landings from Sette and Fiedler 1928. Early groundfish and crustacean fishery data were also taken from Sette and Fiedler 1928, with later data from U.S. Bureau of Fisheries Statistical Digests. Groundfish and hake data between 1954 and 1980 were taken from Lynde 1986 and more recently from the Pacific Fishery Management Council (PFMC 1999) and Waddell and Ware 1995. Currently missing are Canadian data for groundfish landings prior to 1920 and all Canadian crustacean fisheries; errors are possible from other data sources, and not all estimates include unreported landings or estimates of discards, and thus should be considered minimum estimates of total mortality.

⁴Newby, T. C. Changes in the Washington state harbor seal population, 1942-1972. Unpubl. Rep.

ably less productive than originally thought. Subsequently, allowable landings of many groundfish species have been greatly curtailed in recent years, and recovery plans for depleted stocks are likely to limit effort for less-depleted stocks in the near future.

Crustacean fisheries also developed early in the Pacific Northwest, particularly fisheries for Dungeness crab and pandalid shrimp. For at least a century, landings of these populations appear to have fluctuated widely over relatively short periods of time. Evidence indicates that these fluctuations represent actual population swings, and recent research suggests that Dungeness crab dynamics respond to both internal population feedback, and large-scale environmental forcing (Higgins et al. 1997). It follows that such extreme population variability may be a response to a combination of anthropogenic influences (e.g., fishing, habitat degradation) and fluctuating oceanographic conditions.

Additionally, Hannah and Jones (1991) document an apparent change in the age structure of pink shrimp (*Pandalus jordani*), which they believe is at least partially attributable to fishing. The pink shrimp is a sequential hermaphrodite in which age-1 shrimp are typically male and turn female as they reach age 2 (few, if any, of this species live beyond age 3). Hannah and Jones's work documented a shift in the age structure of landed shrimp to a substantially greater percentage of age-1 shrimp and fewer age-2 and -3 shrimp. These changes were accompanied by an increased percentage of shrimp maturing directly into females at age 1.

To summarize, it is clear that major shifts in the biomass, productivity, and life-history characteristics of key trophic components have occurred in response to both human activities and environmental variability. Figures 3 and 4 are intended to scale the importance of considering the long-term effects of both climate and human disturbance, in order to develop a sense of history for what little we might know about the nature of past population changes in this ecosystem. These population shifts include volatile increases and decreases (crustacean populations); predictable large-scale spatial migrations (pelagics such as hake and sardine as well as many seabird and marine mammal populations); periodic species range expansions and contractions (sardine); changes in age structure of harvested populations (groundfish and shrimp); and recent steady biomass declines (many groundfish and salmonids).

These dynamic species assemblages and interactions define the trophic structure of the northern California Current, a structure that has changed substantially over time and space. Furthermore, the large-scale physical and biological properties of the NCCE (e.g., temperature and flow patterns, primary and secondary production) also vary greatly over time and space with

atmospheric forcing. Meine (1999) suggests that the "development of an historic sensibility ought to be considered fundamental to conservation biology"; we would argue that such a sensibility should be an integral part of fisheries biology and management as well, and is relevant in the context of both climatic and anthropogenic forcing mechanisms.

Although much more could be known about the trophic structure of the NCCE, it is clear that many species assemblages (and their ensuing interactions) are complicated and highly dynamic (Brodeur and Pearcy 1992). Thus, it may be that static fisheries models are not adequate for governing dynamic trophic systems, yet tangible objectives for ecosystem-level management initiatives remain ill-defined. If ecosystem-based approaches to fishery management are to be mandated by law or otherwise implemented, a major question will be how, if at all, managers might be able to ultimately incorporate insights and results of climate, trophic, dynamic, or other ecosystem models into management or policy objectives.

ECOLOGICAL MODELING OF THE NCCE

One opportunity for evaluating both the nature and the scale of such trophic interactions is to use ecological modeling. As a starting point, our efforts have focused on quantitatively defining NCCE trophic structure, using available information to explore the productivity of key populations in this region and evaluate how historical removals relate to standing biomass, production, and trophic structure. So far, we have centered on the initiation of an Ecopath modeling project designed to amass critical data on abundance, food habits, and other trophic factors. Future objectives include using dynamic simulations to incorporate modes of environmental forcing into dynamic simulations.

The intent of the discussion here is to explore the potential applications of one type of ecological model as a tool for describing the interacting effects of climate and trophic assemblages and deriving insights which could ultimately be useful for managers. With regard to the utility and application of multispecies or ecosystem models in particular, Hollowed et al. (2000) provide a comprehensive review of the most commonly used methods and their potential utility for measuring fishing impacts on marine ecosystems.

Ecopath was originally designed by Polovina (1984) and evolved into a software application, including a dynamic version called Ecosim, by workers at the University of British Columbia (Christensen and Pauly 1992; Walters et al. 1997). Essentially, Ecopath is a steady-state model that emphasizes natural rates of growth and consumption of marine populations. Given adequate data from fish bioenergetics models or diet composition studies, it provides a framework for summarizing information over

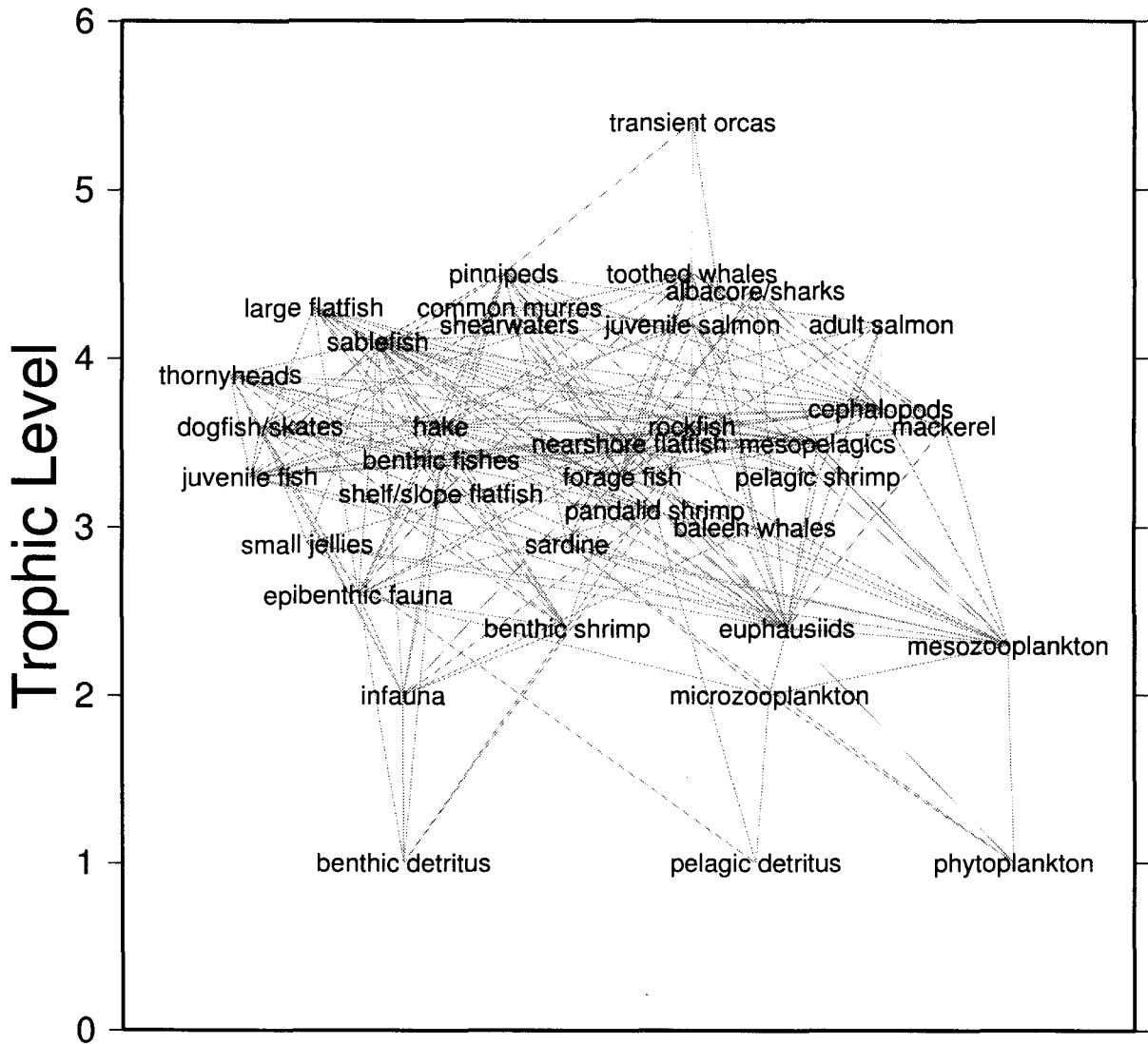


Figure 5. A model of the basic trophic components of the northern California Current food web. Despite massive aggregations of species and species assemblages, the picture illustrates the complexity of trophic interactions and the multitude of pathways for energy in this ecosystem.

trophic levels, emphasizing natural rates of growth and consumption of marine populations. This allows small-scale studies or models to be viewed in a common currency, in the context of the ecosystem as a whole. While the equilibrium assumptions of the Ecopath model do not allow for the determination of “true” biomasses or rates in a changing system, the modeler may use the software’s bookkeeping to examine the basic trophic processes; for example, to learn whether a predator or fishery may be consuming more forage than is hypothesized to be available, and thus if its existence is putting pressure on other ecosystem components. The assumption is that over an appropriate period of time (say a decade or a regime) a mass-balance model can be generated to represent the basic trophic interactions between major ecosystem components.

Although the stochastic nature of most (if not all) populations and population parameters would suggest that a range of values would better explain seasonal and interannual changes, the static approach is useful from the standpoint of generating a “snapshot” of some mean state(s) of the ecosystem under different time periods or circumstances. The quick examination of many components of the system essentially extends the concept of maximum sustainable yield to multiple interacting species, suggesting a management framework for examining the consequences of altering species abundance and species assemblages.

It must be stated at the outset that these models rely heavily on “back-of-the-envelope” calculations—stable, oversimplified trophic webs—and thus cannot reliably model sudden ecosystem shifts to new states. Yet this

generality and overstability may be their greatest recommendation. These models' potential may lie in developing metrics (e.g., the amount of primary production removed by fishing) relating measurable ecosystem quantities to levels of risk incurred by exploitation. At this time and despite great effort, measurable and meaningful metrics of ecosystem health, stability, and resilience have been elusive (Murawski 2000). Thus as a tool for developing management rules of thumb for avoiding ecological catastrophes, the comparison of simple, stable, pre- and postmanipulation equilibria or functional models with historic records of change in exploited ecosystems warrants further evaluation.

We have used preliminary Ecopath models to compare the state of the NCCE between the 1960s—a cool regime characterized by low exploitation rates and high rates of zooplankton production—and the 1990s—a warm regime characterized by low productivity, declining stocks, and intensively regulated fisheries following several decades of intensive exploitation. Population parameters and diet data for some 34 species or species assemblages were compiled or estimated for both time periods to generate a food web of basic trophic interactions (fig. 5).

The data used to estimate the parameters of this model come from a wide range of sources, including stock assessments, published literature, grey literature, and in many instances general review papers of basic population parameters. Model documentation and descriptions of data and data sources are available in Field and Francis.⁵ The challenges in compiling adequate data to parameterize the model inevitably suggest suspect results; because of the paucity of information regarding the dominant planktonic and nektonic populations in this region, some gross estimation and generalization is unavoidable. Nevertheless, we believe such models are extremely useful both for visualizing the nature of the system being managed and beginning to understand how major changes in species abundance or productivity might reverberate up or down through the food web.

Figures 6 and 7 show greatly simplified versions of trophic flow diagrams and energy pathways through the NCCE as modeled in the early 1960s and 1990s, and generated by aggregating the parameters for the 34 species and species assemblages shown in figure 5. The size of the boxes (if they were to be viewed in three dimensions) would be proportional to the log of estimates of average annual biomass (B) in the different assemblages. The average estimated production in the assemblages is given as P and consumption is given as Q. For lower trophic levels (in which annual production is the key param-

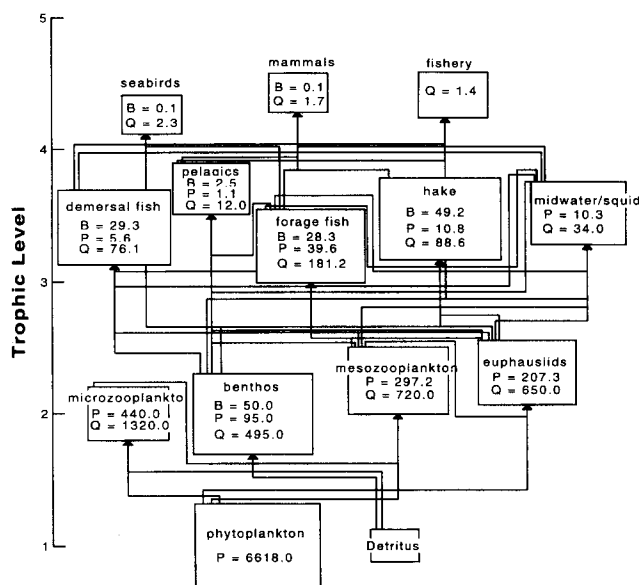


Figure 6. Simplified mass balance models of aggregated ecosystem components and major trophic flows in the northern California Current during the early 1960s. Units are wet weights of biomass (grams/square meter).

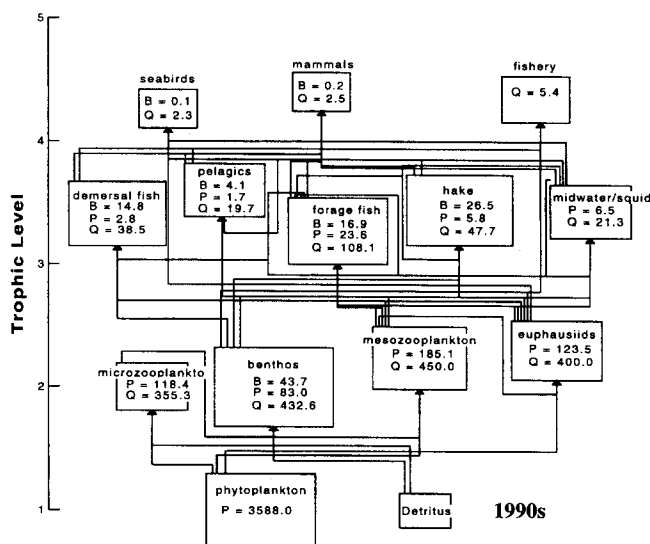


Figure 7. Simplified mass balance models of aggregated ecosystem components and major trophic flows in the northern California Current during the mid-1990s. Units are wet weights of biomass (grams/square meter).

ter) these estimates are based on a top-down estimate of consumption requirements of upper-trophic-level predators, calibrated to the extent possible by existing assessments of planktonic and nektonic standing stocks and productivity for the two time periods in question. Although the parameters and estimates need further refinement, we believe that these figures represent a reasonable assessment of the key energy flows and trophic pathways through the system. At a minimum, these comparisons provide some measure of how the massive changes in the biomass of commercially important species have

⁵Field, J. C., and R. C. Francis. MS. in prep. Static and dynamic models of the northern California Current ecosystem. Fisheries Research Institute Reports.

reduced the consumption requirements upon the lower trophic levels necessary to sustain those populations.

One interesting consequence of this change is that there does not appear to be any evidence for major shifts or increases in the abundance of other species or species assemblages to take advantage of what might be perceived as an increase in the availability of forage resulting from declines in the relative abundance of commercially important predators, as has been suggested in other systems such as the Georges Bank (Fogarty and Murawski 1998). Although data on the relative abundance of target and nontarget species are sparse, preliminary work to develop diversity indices of upper-trophic-level predators based on fisheries survey data for the early 1970s and the mid-1990s also suggests no major shift in the relative composition of groundfish assemblages in the INPFC Columbia area (S. Gaichas, pers. comm.), although Emmett and Brodeur (2000) have found substantial shifts in the relative abundance of pelagic predators.

The above situation may be in contrast with other heavily fished ecosystems, in which major shifts in species or community composition have followed major disturbances. Until recently, levels of secondary production throughout the 1990s have seemed far below long-term averages; the abundance of many key forage species has been greatly reduced (Emmett and Brodeur 2000); recruitment of rockfish and survival of salmon smolts have reached all-time lows (Hare et al. 1999); and the average weight-at-age for some species, such as hake and yellowtail rockfish, have been below the long-term means (Dorn et al. 1999; Tagart et al. 2000). Massive changes in the species composition and biomass of euphausiids, copepods, and other planktonic organisms have also been documented (McGowan et al. 1998; Mackas et al., in press). All of these factors suggest that this system has probably been functioning at lower levels of productivity over recent years, as associated with the aforementioned changes in climate forcing and physical conditions following the 1977 (and perhaps 1989) regime shift (Hare and Mantua 2000). As alluded to earlier, the evidence for a large-scale climate shift that has affected the distribution and abundance of key populations in the NCCE is widespread, and improving our knowledge of the mechanism and consequences of these shifts is the focus of major investigations by CalCOFI, GLOBEC, the JISAO Climate Impacts Group, and many other research entities.

The nature in which such a shift in productivity may be interacting with the concurrent and ongoing removal of a substantial fraction of the higher-trophic-level biomass in this ecosystem remains unclear. Our hope is that further insight into the nature and consequences of climate shifts, and into the interaction between such changes and ongoing effects associated with fisheries removals

might be uncovered through both static and dynamic modeling of this and other ecosystems. Over recent years dynamic models have been used to consider the impacts of fishing on marine ecosystem dynamics (Kitchell et al. 1999; Trites et al. 1999; Olson et al.⁶), and we expect that such modeling efforts might have much to offer in terms of insights toward considering large-scale ecological interactions in fisheries management.

As suggested earlier, another application of such models could be in deriving metrics or indices, which might be useful in assessing ecological health or stability, or comparing the nature and magnitude of human-induced disturbance between ecosystems. Jarre-Teichmann and Pauly (1998) used an index of the flow from primary production to higher trophic levels imbedded in the Ecopath software to assess the relative effect of fishing removals as a percentage of the production necessary to support fisheries on coastal pelagic species in several coastal upwelling systems. Their findings suggested that major fisheries for coastal pelagics removed between 1% and 15% of the primary production in these systems during distinct time periods. Perhaps more significantly, the magnitude of exploitation was more dependent upon the target species than on the total landings between systems; in other words, removals of species with higher trophic levels had a correspondingly greater effect on the percentage of primary production required (PPR) to sustain them. In these models, estimates of PPR are made for each trophic pathway, and energy flows are raised to primary production equivalents by means of methodology suggested by Ulanowicz (1995) and described in more detail in Christensen et al. (2000). The statistic of primary production required to support fisheries removals is thus a measure of the total amount of new production removed from exploited populations, scaled to the appropriate trophic level.

An example of how this index might be useful for comparative purposes is presented as figure 8. This figure shows total removals (landings and some measure of discards) in metric tons per square kilometer from three ecosystems in different time periods plotted with the estimated percentage of relative production necessary to support these landings (as above, the primary production raised to the equivalent trophic levels of the catches).

In the Eastern Bering Sea (EBS) models (Trites et al. 1999) there were massive harvests of long-lived, slow-growing predators, primarily baleen whales, sperm whales, walrus, and seals, with a corresponding low volume of landings in terms of tonnage but representing nearly all of the production at those trophic levels in that system. What this showed was essentially the "mining

⁶Olson, R. J., G. M. Watters, R. C. Francis, P. C. Fielder, J. J. Polovina, S. B. Reilly, K. Y. Aydin, and J. F. Kitchell. Climate forcing and ecosystem dynamics in the eastern tropical Pacific Ocean. MS. submitted to *Ecol. App.*

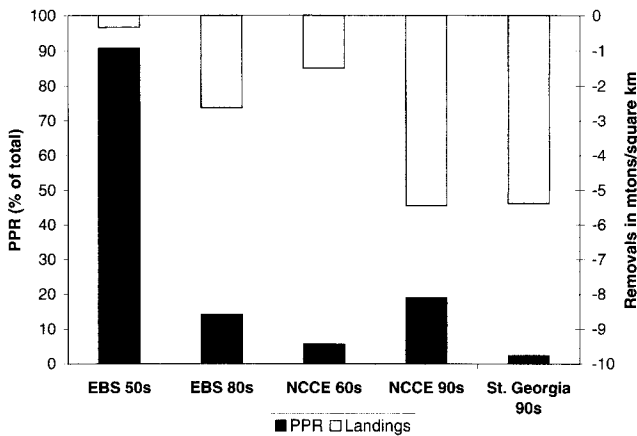


Figure 8. Fisheries removals (in metric tons/square kilometer) and percentage of primary production required (PPR) to sustain them, derived from five coastal ecosystem models. EBS = eastern Bering Sea; NCCE = northern California Current ecosystem; St. Georgia = Strait of Georgia.

out” of the biomass of higher trophic levels in the EBS during a period of intensive exploitation in the 1950s and 1960s. By contrast, in the 1980s the EBS supported the largest (by volume) fishery in the United States—the trawl fishery for walleye pollock—in addition to fisheries for Pacific cod, tanner crab, and many flatfish species. The removals (in t/km²) increased substantially; however, due to the lower trophic levels of the target species, the percentage of system production that was removed annually declined considerably.

In the northern California Current, landings were relatively low in the 1960s, less than 1.5 t/km², and the corresponding percentage of primary production required to support those landings was on the order of 6%. By the 1990s, however, the total landings had increased substantially (see fig. 4; additionally, some groundfish landings had already peaked in the 1980s and dropped by the 1990s), to an average of nearly 6 t/km²; this represented some 20% of the available production being removed by the fishery. By contrast, comparison with the (contemporary) Strait of Georgia model constructed by Pauly, Pitcher et al. (1998), removals were on the same magnitude between the NCCE and the Strait of Georgia in terms of tons per square kilometer, but because of the tremendous productivity and recycling of nutrients and energy in the Strait of Georgia, landings required a substantially greater percentage of the scaled production in the NCCE.

It is interesting to consider that the total removals per unit area, and the percentage of production accounted for in those removals, is greater in the NCCE than in the (contemporary) eastern Bering Sea. Whereas the latter is one of the most productive fishing grounds in U.S. waters, the immense area of this coastal shelf is what accounts for the tremendous volume of fisheries that it supports. While this construct of production required

to support landings may seem vague, and is certainly fraught with major uncertainties about the real nature of the food web that supports these landings, we believe that this example illustrates the means by which simple ecological models may show the nature and magnitude of human-induced disturbances, and ultimately may provide a useful index or tool for scaling the extent and magnitude of human intervention in these complex ecosystems.

CONCLUSIONS

McEvoy (1996) suggested that successful fisheries management will require that managers and policymakers “cooperate with each stock’s strategy for responding to the environment.” Clearly, this environment is modulated by variability and change in climate as well as increasing measures of anthropogenic disturbance. We believe that the development and application of static and dynamic ecosystem models will ultimately reveal useful insights about how both climate and fishing affect NCCE structure and dynamics, and will provide valuable insight into system definition and behavior. Additionally, we hope to illuminate gaps in research or knowledge that create potential management limitations and increase uncertainty. Finally, we believe that the development of such models will lead to both static and dynamic visualizations that readily convey to managers and stakeholders the dynamics of this ecosystem and potential or probable effects of alternative management approaches. Ultimately, such efforts should lead to the development of more refined models to quantify the nature of ecological change in this system as a result of both climate effects and fishing, and will be useful as a framework for incorporating ecological considerations into fisheries management practices.

It is fair, however, to suggest that such insights are unlikely to lead to any meaningful short-term solutions to current crises in the management of northern California Current fisheries. The salmon crisis or the massive problems associated with effectively managing the groundfish fishery and the recovery of depleted populations can be addressed only by a massive change in the way in which large-scale system variability and human-induced impacts (both fishery and nonfishery related) are mitigated and managed in the future. The adoption of an “ecosystem-based approach” will result neither in obvious solutions to current crises nor in a substitute for more traditional means of assessing and managing fisheries. As McEvoy (1996) suggests, “If scientific fishery management could not predict or maintain the production of individual species, it seems a bit presumptuous to expect that we could now anticipate and direct the interacting components of an entire ecosystem.”

Clearly, the adoption of a broader view of the inter-

actions between fisheries (both their biological and human components) and marine ecosystems is necessary, and we must accept the dynamic and inherently unpredictable nature of entire systems and learn to operate within the bounds of uncertainty to ensure future sustainability. The nature of the coastal pelagics FMP is a step in such a direction, as is the movement toward using marine reserves to provide refugia for species as well as opportunities to assess how disturbed and undisturbed systems may differ in form and function. Equally necessary are basic reforms in the current approach to fisheries management away from traditional focused command-and-control practices. These changes are not mutually exclusive; both can and must occur if the resources and the communities which depend upon them are to persist in the future.

ACKNOWLEDGMENTS

We thank Kerim Ayden, Troy Buckley, Lorenzo Ciannelli, Elizabeth Loggerwell, and Julia Parrish for their discussions and assistance with the models; Anna Zagorska for proofreading early drafts; and Alec MacCall and one other reviewer for their attempt to force the authors to address critical shortcomings in this paper. This work was supported by Washington Sea Grant (SG 617296).

LITERATURE CITED

- Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* 89:117–123.
- Apollonio, S. 1994. The use of ecosystem characteristics in fisheries management. *Rev. Fish. Sci.* 2(2):157–180.
- Auster, P. J., R. J. Malatesta, R. W. Langton, L. Watling, P. C. Valentine, C. L. S. Donaldson, E. W. Langton, A. N. Shepard, and I. G. Babb. 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (northwest Atlantic): implications for conservation of fish populations. *Rev. Fish. Sci.* 4:185–202.
- Bonnot, P. 1928. Report on the seals and sea lions of California. *Calif. Fish. Game. Bull.* 14:1–62.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277:509–515.
- Bottom, D. L., K. K. Jones, J. D. Rodgers, and R. F. Brown. 1993. Research and management in the northern California Current Ecosystem. *In* Large marine ecosystems: stress, mitigation and sustainability, K. Sherman, L. M. Alexander, and B. D. Gold, eds. Washington DC: AAAS Press. Pp. 259–271.
- Brodeur, R. D., and W. G. Pearcy. 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling system. *Mar. Ecol. Prog. Ser.* 84:101–119.
- Christensen, V., and D. Pauly. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Model.* 61:169–185.
- Christensen, V., C. J. Walters, and D. Pauly. 2000. *Ecopath with Ecosim: a users guide*. Fisheries Centre, University of British Columbia, Vancouver, Canada, and ICLARM, Penang, Malaysia. 130 pp.
- Clemens, W. A., and G. V. Wilby. 1961. Fishes of the Pacific coast of Canada. *Fish. Res. Can. Bull.* 68. 443 pp.
- Cobb, J. N. 1930. Pacific salmon fisheries. Appendix XIII to the report of the commissioner of fisheries for 1930. Bureau of Fisheries document no. 1092.
- Collins, J. W. 1892. Report on the fisheries of the Pacific Coast of the United States. U.S. Comm. Fish and Fisheries, Rep. to Comm. 1888. Part XVI:3–269.
- Crone, P. R., K. R. Piner, R. D. Methot, R. J. Conser, and T. L. Builder. 1999. Status of the canary rockfish off Oregon and Washington in 1999. *In* Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Portland, Ore.: Pacific Fishery Management Council.
- Dell'Arciprete, P., D. L. Peterson, R. C. Francis, and N. Mantua. 1998. Climate reconstruction through tree growth indices. *In* JISAO/SMA Climate Impacts Group year 3 progress report.
- Dom, M. W., M. W. Saunders, C. D. Wilson, M. A. Guttormsen, K. Cooke, R. Kieser, and M. E. Wilkins. 1999. Status of the coastal Pacific hake/whiting stock in United States and Canada in 1998. *In* Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Portland, Ore.: Pacific Fishery Management Council.
- Drouin, M. 1999. Pilchard die-off stirs debate. *Pacific Fishing March* 1999.
- Emmett, R. L., and R. D. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. *N. Pac. Anadr. Fish. Comm. Bull.* 2:11–20.
- Engel, J., and R. Kvitek. 1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conserv. Biol.* 12(6):1204–1214.
- EPAP. Ecosystem Principles Advisory Panel. 1999. Ecosystem-based fisheries management: a report to Congress by the Ecosystem Principles Advisory Panel. Silver Spring, Md.: National Marine Fisheries Service, NOAA.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol. App.* 8(1(supp.)):6–22.
- Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the Northeast Pacific Ocean. *Fish. Ocean.* 7(1):1–21.
- Goode, G. B., ed. 1884. Natural history of useful aquatic animals. *In* The fisheries and fishery industries of the United States. Sect. 1. U.S. Comm. Fish. Fisheries, Washington, D.C.: Government Printing Office.
- Grumbine, R. E. 1994. What is ecosystem management? *Conserv. Biol.* 8(1):27–38.
- Hannah, R. W., and S. A. Jones. 1991. Fishery-induced changes in the population structure of pink shrimp *Paridalus jordani*. *Fish. Bull.* 89:41–51.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47(2):103–145.
- Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. *Fisheries* 24(4):6–14.
- Hargreaves, N. B., D. M. Ware, and G. A. McFarlane. 1994. Return of the Pacific sardine (*Sardinops sagax*) to the British Columbia coast in 1992. *Can. J. Fish. Aquat. Sci.* 51:460–463.
- Hickey, B. M. 1989. Patterns and processes of circulation over the shelf and slope. *In* Coastal oceanography of Washington and Oregon, M. R. Landry and B. M. Hickey, eds. Amsterdam: Elsevier Science Publishing, pp. 41–116.
- Higgins, K., A. Hastings, J. N. Sarvela, and L. W. Botsford. 1997. Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. *Science* 276:1431–1435.
- Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. *Conserv. Biol.* 10(2):328–337.
- Hollowed, A. B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope, and J. C. Rice. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J. Mar. Sci.* 57:707–719.
- Jarre-Teichmann, A., and D. Pauly. 1998. Comparative analyses of trophic flows in upwelling systems: global vs. local changes. *In* Local vs. global changes in upwelling ecosystems. Proceedings of the First Climate and Eastern Ocean Systems Symposium, 2–4 September 1994, Monterey, California, P. Cury, R. Mendelsohn, C. Roy, M. H. Durand, A. Bakun, and D. Pauly, eds., pp. 423–443.
- Jordan, D. S., and E. C. Starks. 1895. The fishes of Puget Sound. *Proc. Calif. Acad. Sci.* 2(5):785–855.
- Kershaw, T. R. 1902. Annual report of the state fish commissioner to the governor of the State of Washington. Thirteenth Annual Report. Seattle: The Metropolitan Press Inc.

- Kitchell, J. F., C. H. Boggs, X. He, and C. J. Walters. 1999. Keystone predators in the central Pacific in ecosystem approaches for fisheries management. Anchorage: Univ. Alaska, Alaska Sea Grant Pub. AK-SG-99-01, pp. 665–683.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation and conservation: lessons from history. *Science* 260(5104):17, 36.
- Lynde, M. V. H. 1986. The historical annotated landings (HAL) database: documentation of annual harvest of groundfish from the northeast Pacific and eastern Bering Sea from 1956 to 1980. NOAA Tech. Memo. NMFS F/NWC-103.
- MacCall, A. 1996. Patterns of low-frequency variability in fish populations of the California Current. *Calif. Coop. Oceanic Fish Invest. Rep.* 37:100–110.
- . 2000. Summary of known-biomass production model fits to West Coast groundfish stocks. Third Groundfish Productivity Workshop, Seattle, Wash., March 20–24, 2000.
- MacKas, D. L., R. E. Thompson, and M. Galbraith. In press. Changes in the zooplankton community of the British Columbia continental margin, and covariation with oceanographic conditions, 1985–1998. *Can. J. Fish. Aquat. Sci.* GLOBEC Canada special issue.
- Mann, M. S., R. S. Bradley, and M. K. Hughes. 1999. Long-term variability in the ENSO and associated teleconnections. In *El Niño and the Southern Oscillation*, H. F. Diaz and V. Margraf, eds. Cambridge: Cambridge Univ. Press.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78(6):1069–1079.
- McEvoy, A. F. 1996. Historical interdependence between ecology, production, and management in California fisheries. In *Sustainability issues for resource managers*, D. Bottom, G. Reeves, and M. Brookes, eds. USDA Forest Service Tech. Rep. PNW-GTR-370.
- McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the northeast Pacific. *Science* 281(5374):210–217.
- Meares, J. 1791. *Voyages made in the years 1788 and 1789, from China to the N.W. coast of America*. London: Logographic Press.
- Meine, C. 1999. It's about time: conservation biology and history. *Conserv. Biol.* 13(1):1–3.
- Murawski, S. A. 2000. Definitions of overfishing from an ecosystem perspective. *ICES J. Mar. Sci.* 57:649–658.
- NRC. National Research Council. 1996. *Upstream: salmon and society in the Pacific Northwest*. Washington, D.C.: National Academy Press.
- . 1999. *Sustaining marine fisheries*. Washington, D.C.: National Academy Press.
- Parsons, T. R. 1993. The removal of marine predators by fisheries and the impact of trophic structure. *Mar. Pollut. Bull.* 26(6):51–53.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. *Science* 279(5352):60–63.
- Pauly, D., T. Pitcher, and D. Preikshot. 1998. Back to the future: reconstructing the Strait of Georgia ecosystem. *Fish. Centre Res. Rep.* 6(5), 99 pp.
- PFMC. Pacific Fishery Management Council. 1993. *Fishery management plan for the California, Oregon and Washington groundfish fishery as amended through amendment 7*. Pacific Fishery Management Council, Portland, Ore.
- . 1998. *The coastal pelagic species fishery management plan*. Portland, Ore.: Pacific Fishery Management Council.
- . 1999. *Status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000*. Portland, Ore.: Pacific Fishery Management Council.
- Polovina, J. J. 1984. Model of a coral reef ecosystem I. The Ecopath model and its application to French Frigate Shoals. *Coral Reefs* 3:1–10.
- Ralston, S. 1998. The status of federally managed rockfish on the U.S. West Coast. In *Marine harvest refugia for West Coast rockfish: a workshop*. M. Yoklavich, ed. NOAA Tech. Memo. NMFS-SWFSC-255, pp. 6–16.
- Scammon, C. M. 1874. *The marine mammals of the northwestern coast of North America*. John H. Carrmany and Co. (Reprinted by Manessier Publishing Co. 1969).
- Schweigert, J. F. 1988. Status of the Pacific sardine, *Sardinops sagax*, in Canada. *Can. Field Nat.* 102(2):296–303.
- Sette, O. E., and R. H. Fiedler. 1928. Fishery industries of the United States, 1927. In *Report of the United States Commissioner of Fisheries for the fiscal year 1928*. U.S. Dep. Commer.
- Smith, P. E. 1978. Biological effects of ocean variability: time and space scales of biological response. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 173:117–127.
- Soutar, A., and J. D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fish. Bull.* 72:257–273.
- Stewart, B. S., P. K. Yochem, H. R. Huber, R. L. DeLong, R. J. Jameson, W. J. Sydeman, S. G. Allen, and B. J. LeBoeuf. 1994. History and present status of the northern elephant seal population. In *Elephant seals: population ecology, behavior and physiology*, B. J. LeBoeuf and R. M. Laws, eds. Berkeley: Univ. Calif. Press.
- Suckley, G. 1860. Report upon the fishes collected on the survey. In *The natural history of Washington territory and Oregon: with much relating to Minnesota, Nebraska, Kansas, Utah, and California between the thirty-sixth and forty-ninth parallels of latitude: being those parts of the final reports on the survey of the Northern Pacific Railroad route, relating to the natural history of the regions explored, with full catalogues and descriptions of the plants and animals collected from 1853 to 1860*. New York: Bailliere Brothers.
- Tagart, J. V., F. R. Wallace, and J. N. Ianelli. 2000. Status of the yellowtail rockfish resource in 2000. In *Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation*. Portland, Ore.: Pacific Fishery Management Council.
- Torrence, C., and G. P. Campo. 1998. A practical guide to wavelet analysis. *Bull. Am. Meteorol. Soc.* 79:61–78.
- Trites, A. W., P. Livingston, M. C. Vasconcellos, S. Mackinson, A. M. Springer, and D. Pauly. 1999. Ecosystem change and the decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. *Fish. Centre Res. Rep.* 7(1), 106 pp.
- Ueber, E., and A. MacCall. 1992. The rise and fall of the California sardine empire. In *Climate variability, climate change and fisheries*, M. Glantz, ed. Cambridge: Cambridge Univ. Press.
- Ulanowicz, R. E. 1995. The part-whole relation in ecosystems. In *Complex ecology*, B. C. Patten and S. E. Jorgensen, eds. Englewood Cliffs, N.J.: Prentice-Hall.
- Waddell, B. J., and D. M. Ware. 1995. Historic domestic and foreign fish catch statistics for British Columbia: 1920–1991. *Can. Tech. Rep. Fish. Aquat. Sci.* 2030.
- Walters, C., V. Christensen, and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7:1–34.
- Wilkes, C. 1984. *Narrative of the United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842*. Philadelphia: Lea and Blanchard.
- Wooster, W. S., and D. L. Fluharty, eds. 1985. *El Niño north: Niño effects in the eastern subarctic Pacific Ocean*. Seattle: Washington Sea Grant.
- Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle. 1998. Historical abundance and decline of chinook salmon in the central valley region of California. *N. Am. J. Fish. Manage.* 18:487–521.