Application of Ecosystem-Based Fishery Management Approaches in the Northern California Current

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Abstract

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Ecosystem principles and approaches offer promise to improve the current fisheries management regime. However there is considerable confusion about how an ecosystem-based approach can be implemented, and how to transition to such an approach. This dissertation focuses on the development of an ecosystem perspective for managing fisheries in the Northern California Current (NCC). Focal areas include the development of word models and historical perspectives of the ecosystem, quantitative characterization of the food web and major trophic interactions, exploration of the interactions between climate and fishing on ecological structure and dynamics, the development of potential ecosystem metrics, and the exploration of means to link ecosystem information and model results to management. The results of this dissertation can improve our understanding of the benefits and potential shortcomings of holistic management approaches, and contribute to the growing field of ecosystem modeling from both a qualitative and quantitative perspective, and can be of direct use to the Pacific Fisheries Management Council (PFMC) and other stakeholders in west coast fisheries.

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Introduction

> *For scientists to continue the policy of focusing on disciplinary pieces at the expense of the whole will leave them handmaidens. This would fit Tuchmans's definition of folly, albeit scientific folly, in being "the perverse persistence in a policy demonstrably unworkable" for making the "simultaneous and complementary advances" required of science and fishery management. (Smith 1998)*

In the Northern California Current, a great many fish populations and the communities that depend upon them are in a state of crisis as a result of a combination of factors. Many long-lived and slow growing groundfish stocks have been severely depleted, and obligatory rebuilding plans suggest that some could take decades to centuries to recover. The condition of several stocks is so poor that the Pacific Fisheries Management Council (PFMC) found it necessary in 2003 to close a vast majority of the continental shelf to most fishing gears as an emergency measure; a draconian yet necessary action that has resulted in dramatic impacts to fishermen and fishing-dependent communities. Salmon crises have been ongoing in the Pacific Northwest for decades, driven by a complex combination of factors, although recent changes in ocean conditions have also boosted salmon production in some regions to record levels. Fisheries for highly variable coastal pelagic populations could be entering a critical phase as well, as some stocks may have recently entered into a period of low productivity. Yet other fisheries, such as those for high turnover invertebrates such as Dungeness crab and pandalid shrimp, have been thriving in recent years.

Status quo management efforts in each of these fisheries has generally been crisis-based rather than proactive. However there is a growing national and international recognition for the need to develop a new paradigm in fisheries and marine resource management (McEvoy 1996, Botsford et al 1997, NRC 1999a, Mangel et al. 2000, Mace 2001, Pauly et al. 2002, Gunderson and Holling 2002, Pikitch et al. 2004). There is a clearly perceived need for the development of a more proactive approach to fisheries management, with greater accounting of the significance of climate variability, ecosystem dynamics, life history characteristics and species interactions as they in turn are integrated with socio-economic dynamics into the management context. While efforts to develop an ecosystem focus in fisheries modeling and management are far from new (Laevastu and Larkins 1981, Evans et al. 1987), the desire to do so has increased as both stakeholder and public perceptions of fisheries have evolved from limitless frontiers to systems with limits and thresholds (Hanna 1997, EPAP 1999, NRC 1999a). Although the direct application of ecosystem modeling and management strategies in fisheries systems has historically been limited (Mangel et al. 2000, Goodman et al. 2002), the role of such approaches should hold promise in the future of marine resource management.

In recognition of the potential for an ecosystem-based approach to improve fisheries management, Congress in 1996 requested that the National Marine Fisheries Service (NMFS) convene a panel of experts to examine how best to amend or supplement current single species management approaches. The panel's primary recommendation was that Fishery Management Councils develop a Fisheries Ecosystem Plan (FEP) for each ecosystem under their jurisdiction (EPAP 1999). A FEP is envisioned as an "umbrella document" containing detailed information on the structure, function, and trends of the ecosystem under consideration. These plans would be intended to increase the awareness of managers and stakeholders of the consequences that fishing (and other) activities have on the ecosystem, and would be the next major step in translating today's directed management efforts into more holistic approaches. Perhaps more importantly, FEPs offer the means to actually phase ecosystem-based management approaches into the legal and institutional framework of the current management regime, supplementing the existing (generally single-species based) approach with ecosystem principles, objectives and policies.

The common threads of an ecosystem-based management approach involve taking a more holistic view of managing resources in the context of their environment. For marine fisheries this must take into greater consideration the interactions between climatic and oceanographic processes, the connections and interactions between fished and unfished populations in the ecosystem and the role of humans as both predators and competitors in such ecosystems. Recognizing that all management decisions have impacts on the ecosystem being exploited, an ecosystem-based approach to management seeks to better inform these decisions with knowledge of ecosystem structure, processes and functions. This dissertation focuses on the development of descriptive and mathematical models of the Northern California Current (NCC), a region of the larger California Current System (CCS) that includes the (formerly) heavily fished shelf and slope environment between Cape Mendocino, California and Cape Flattery, WA. These models will describe the major physical, biological and social (fishing) components of this ecosystem, detail energy pathways and major species interactions, reproduce large scale dynamics of the system over time, and suggest potential metrics and insights for assessing the impacts of fishing and climate on the ecosystem.

These objectives overlap with four of eight key elements of Fisheries Ecosystem Plans envisioned by the Ecosystem Principles Advisory Panel (EPAP 1998), which are:

- A characterization of biological dynamics of the ecosystem.
- Development of a conceptual model of the food web.
- An estimation of total removals by fishing and how those relate to standing biomass, production and trophic structure.
- Potential metrics or indices of ecosystem health.

The remaining key elements of FEPs as envisioned by the EPAP panel are certainly no less crucial. They include descriptions of the habitat requirement of different life history stages for all organisms representing the "significant food web," assessments of how uncertainty is characterized and what types of buffers are included in management actions, descriptions of long-term monitoring data and how they are used, and an assessment of the relevant ecological, human, and institutional elements of the ecosystem which are outside of the jurisdiction of either the management council or the Department of Commerce. The rationale for focusing on the first four elements lies in the conceptual design of this research approach, which emphasizes the development of models, visualizations and insights that will contribute to an improved understanding of ecosystem structure, function, and impacts from fishing. In addition to representing a meaningful contribution to the developing field of ecosystem modeling and management approaches, this product should be of direct use to the Pacific Fishery Management Council and other stakeholders.

Chapter 1 includes a descriptive word model of the Northern California Current (NCC) ecosystem, including historical and contemporary fisheries, in order to develop a conceptual basis for the quantitative modeling that lies ahead. This chapter reviews key elements about the physical environment, particularly the climate and oceanographic processes that drive the variability in production and dynamics in this ecosystem. The focus of Chapter 2 is the definition and quantification of ecosystem components, energy pathways and trophic interactions in this ecosystem, using the Ecopath modeling approach (Polovina 1984, Christensen and Pauly 1992). This chapter will draw upon extensive literature to develop the model, and will present model structure, inferences (specifically with regard to what seem to be most significant trophic interactions) and visual representations of ecosystem trophic structure. Chapter 3 focuses on the dynamic modeling of the NCC, starting with the static models presented in Chapter 2 and available fisheries statistics, survey information and climate data. Finally, Chapter 4 will take the results and insights from the first three chapters and develop proposals to integrate ecosystem-based management approaches into the current management regime in the NCC. As such, Chapter 4 embodies the overall purpose of this dissertation, which is to confront what we know about this ecosystem with descriptions and models of system behavior, and use the insights we gain in hindsight to help us understand how we might aspire to manage fisheries resources into the future.

Chapter 1

> *What a fishery is, descriptively, and what management ought to try to sustain, prescriptively, is an interaction between three variables: an ecosystem, a group of people working, and the system of social control within which the work takes place (McEvoy 1996)*

1.1 Introduction

This chapter describes the physical and biological structure of the Northern California Current (NCC) ecosystem through the development of a word model and literature review of dynamic oceanographic and ecological processes. I also discuss the history of human intervention in this ecosystem to set the context for understanding the potential role of fisheries and other activities over time. The structure of the chapter is based on McEvoy's (1996) model of fisheries systems. This model develops the idea of a fisheries system as the interactions between three key elements; ecology (the physical and biological elements of the ecosystem), economy (fisheries and communities) and governance (the management system). Without a viable ecology, the economy suffers, and without a healthy economy the likelihood that users will practice unsustainable interactions with the ecology increases. Because fisheries are so widely acknowledged to be classic commons problems, both the economy and the ecology clearly suffer without an effective system of social control.

Figure 1.1, by Femia (2003)[1] shows these key elements, each of which will be developed in greater detail in the word model that follows. The chapter will begin with

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[1] This figure is one of several developed by A. Femia, in close collaboration with V. Agostini, R. Francis, J. Little and the author, which were intended to provide clear and meaningful graphical representations of

a review of the dynamic nature of the climate and environment, and how these have shaped the biota of the ecosystem. This is followed by a review of fisheries development over the past two centuries. The governance regime is considered briefly, and will be revisited as related to both the ecology and the economy of the system in Chapter 4.

1.2 The Northern California Current (NCC) Ecosystem

The term ecosystem is generally defined as a "functional unit of the environment" within which the basic processes of energy flow and cycling are identifiable and can be (relatively) localized. In this sense, marine ecosystems are extremely difficult to identify, as most are relatively open systems, with poorly defined boundaries and strong interactions across broad spatial scales. Eastern Boundary Current upwelling ecosystems are especially problematic, as they are characterized by fluctuations in physical conditions and productivity over multiple time scales (Parrish et al. 1981, Mann and Lazier 1996). Food webs tend to be structured around coastal pelagic species that exhibit boom-bust cycles over decadal time scales (Bakun 1996, Schwartzlose et al. 1999). Similarly, the top trophic levels of such ecosystems are often dominated by highly migratory species such as salmon, albacore tuna, sooty shearwaters, fur seals and baleen whales, whose dynamics may be partially or wholly driven by processes in entirely different ecosystems, even different hemispheres. Although attempts have been made to develop criteria for defining large marine ecosystems (Sherman and Tang 1999, Longhurst 2003), any effort to set boundaries over an ecosystem is ultimately biased, since linked processes typically drive ecosystem dynamics over multiple time and space scales (Levin 1992).

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the fisheries system, particularly physical and biological interactions, in the California Current. Many of the figures that resulted from this collaboration are included in this dissertation, Others are in Femia (2003) or are forthcoming in additional manuscripts.

Faced with the challenge of defining boundaries to such ecosystems, it is useful to consider the hierarchical nature of ecosystem structure proposed by O'Neill et al. (1986). They suggest that a watershed may be an ecosystem, as well as a component of a larger ecosystem, up to the level of the global system. This conceptual framework lends some sanity to the concept of drawing boundaries across this complex, open environment. For quantitative modeling in particular, geographical boundaries must be defined, albeit with the recognition that many species cross these boundaries continuously in either anticipated seasonal migratory patterns or less predictable shifts in abundance and distribution related to variability in physical conditions.

The shelf, slope and offshore regions of the California Current System have their greatest changes in physical and biological characteristics at major promontories along the west coast. These include Point Conception, Cape Mendocino, Cape Blanco and the northern tip of Vancouver Island (U.S. GLOBEC 1994). The northern half of the CCS, the region of coastal ocean between Cape Mendocino and Vancouver Island, is often described as a zoogeographic transition between Californian and Aleutian biological provinces (Bottom et al. 1993). Although this entire area should rightly be referred to as the Northern California Current Ecosystem, the political boundary between the U.S. and Canada (which runs southwest off of Cape Flattery, WA) has been used here as a troublesome, but necessary, boundary for the purposes of these modeling efforts. This is due both to data limitations and the significance of model results and implications to regional management entities.

Thus the region explicitly modeled for this dissertation includes the entire area between the nearshore and the continental slope to a depth of approximately 1280 meters. The offshore boundary was chosen as it represents the limits of available data from continental slope surveys, and the approximate limits of historical and contemporary fishing effort for most fishing gear. Much of the vast offshore reaches of the California Current itself are beyond the boundaries described here, and there is an unavoidable bias in both data and detail towards the continental shelf and slope biota (hake, sardines, groundfish, crustaceans) in the ecosystem as opposed to many of the offshore pelagic components (albacore, coastal sharks, migratory marine mammals). Similarly, this definition is intended to exclude estuaries, littoral zones and other nearshore environments, despite the fact that many of these are important habitats for early life history stages of key components in this model (including Dungeness crab, many juvenile flatfish and some juvenile rockfish). For the purposes of this dissertation, this region will be referred to as the Northern California Current (NCC), although much of the discussion of physical forcing and influence is relevant to the entire California Current System.

1.3 The California Current System

One of the first tasks in developing an understanding of this ecosystem is to put the dynamics of the region into the context of larger physical environmental processes in the Northeast Pacific (NEP). The California Current is essentially the eastern limb of the Central Pacific Gyre, and begins where the west wind drift (or the North Pacific Current) reaches the North American Continent. This occurs in a "rather confused manner" near the northern end of Vancouver Island, between 45 and 50° north and 130 to 150° west (Ware and McFarlane 1989). Here a divergence in the prevailing wind patterns causes the west wind drift to split into two broad coastal currents, the California Current to the south and the Alaska Current to the north (Figure 1.2). As there are really several dominant currents in the region, all of which vary in geographical location, intensity and direction with the seasons, this region is generally referred to as the California Current System (Hickey 1979).

The California Current is a year-round feature consisting of a massive equatorward flow of the cool waters of the west wind drift. The current is best characterized as a shallow, wide and slow moving body of water, ranging from the shelf break to 1000 kilometers offshore, with the strongest flows at the sea surface, and in the summertime (Dodimead et al. 1963, Hickey 1979, Lynn and Simpson 1987). This surface current is matched in the summer by the California Undercurrent, which moves water poleward from the south in a deep yet narrow band of subtropical water typically found just off of the shelf break at depths of 100 to 300 meters. The undercurrent flows from Baja California to Vancouver Island, transporting warmer, saltier southern water poleward along the coast (Hickey 1979), as does the wintertime poleward offshore flow at the surface known as the Davidson Current. The Davidson Current is increasingly considered to be the winter manifestation of the California Undercurrent, and this too seems to be matched by a winter equatorward countercurrent at depth, known as the Washington Undercurrent (Hickey 1998). Figure 1.3 shows a simplified schematic of the seasonal cycle of the dominant large-scale flows in the California Current system, developed by Femia (2003) and based on Hickey (1998). On average, the California Current reaches a maximum in spring and summer, when the flow moves inshore, closer to the shelf break. The California Undercurrent develops in late spring through early summer and persists into the fall (dark blue). During late summer and fall there is considerably more mesoscale variability in flow patterns, with fields of cyclonic and anticyclonic eddies and considerable mixing of water masses between shelf and offshore waters (Brink and Cowles 1991). Beginning in the fall, and through the winter, the northward flowing Davidson Current is the dominant feature over the shelf and beyond the shelf break (Hickey 1998).

The dynamics over the shelf are generally forced by regional wind fields, which tend to be equatorward in the spring and summer, and poleward in the winter. Spring and summer equatorward winds drive offshore Ekman transport of surface waters, which is balanced by the upwelling of deeper waters that tend to be cooler and nutrient rich.[2] Although the scales of the wind fields tend to be large, there are significant spatial differences over both alongshore and cross-shore directions, often related to the geographic barriers described earlier. Between the Strait of Juan de Fuca and Cape Blanco, summer upwelling leads to the development of an equatorward upwelling jet over the continental shelf (Hickey 1998, Barth et al. 2000). The shelf narrows as it approaches Cape Blanco, intensifying the energy of the jet (Bateen 1997, Barth et al. 2000). As this jet reaches the Cape it turns sharply offshore, mixing the cool, nutrient rich waters of the jet with the warmer, less productive waters of the slow-moving California Current. These interactions lead to the development of eddy fields and mesoscale variability in primary and secondary productivity that distinguish the region south of Cape Blanco from that to the north (Strub et al. 1991). Mackas et al. (in press) have also suggested that there is a strong advective connection over the shelf between the Alaska Current and the California Current in the transition region off of British Columbia, with both seasonal and interannual variability in the direction of transport.

All these currents, countercurrents, undercurrents, jets and meanders transport water masses of different origins and characteristics, as well as the nutrients and organisms entrained within them, to the California Current System. Although a wide spectrum of water characteristics exists, these water masses (and their associated biota) can be generally broken out into four categories based on the characteristics of their source waters relative to long term mean conditions (Lynn and Simpson 1987).[3] These are:

- Subarctic Pacific waters that originate in the Gulf of Alaska, tend to be cooler, less saline and higher in oxygen and nutrients.

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[2] As a result, upwelling regions are among the world's most productive, accounting for as much as half of the world's exploitable fish production while covering only 0.1% of the ocean's surface area (Ryther 1969). They are also amongst the world's most dynamic ecosystems, as climatic processes over multiple scales impact both the local wind field and the source waters, resulting in dramatic variability in physical conditions and production from year to year, and decade to decade (Parrish et al. 1981, Bakun 1996).

[3] A fifth category that is quite minor overall but can be of major importance at times is freshwater from the terrestrial environment, in particular spring freshet events that form the Columbia river plume.

- Central North Pacific (CNP) or North Pacific Current waters tend to be warmer, more saline, and poor in both oxygen and nutrients.
- Equatorial, or "spicy" waters, delivered by the California Undercurrent (summer) and the Davidson Current (winter), tend to be warm, saline and generally nutrient poor.
- Upwelling waters, pulled to the surface by equatorward winds and Ekman transport in the spring and summer, tend to be cooler, more saline and nutrient rich, but often low in oxygen.

Interannual and interdecadal variability in physical processes often favor some source waters over others, and this in turn contributes to large-scale variability in primary and secondary production in this ecosystem.

As a result of the annual variation in flow regimes in the CCS, the seasonal dynamics of the zooplankton community structure is counterintuitive. Subtropical copepods are abundant year-round in offshore waters, and during the winter in the waters over the continental shelf due to the northward-flowing Davidson Current. By contrast, subarctic, or boreal species are generally most abundant during spring and summer months, particularly in years that the transport of subarctic waters into the coastal environment is strong. Although local wind fields and coastal upwelling ultimately drive the primary production at the base of the food web, growing evidence suggests that changes in the community composition of zooplankton is a more significant indicator of productivity, and that these in turn are related to large scale physical processes in the NEP (Peterson and Keister 2003, Peterson and Schwing 2003).

Wickett (1967) demonstrated that secondary productivity off southern California was influenced by the advection of northern water from the west wind drift, such that interannual differences in southern Ekman transport explained 50 to 60 percent of the variance in zooplankton biomass. Similarly, Chelton and Davis (1982) recognized that the California and Alaska Currents seem to fluctuate out of phase, such that "when the poleward transport of the eastern limb of the subpolar (Alaskan) gyre increases, the equatorward transport of the eastern limb of the subtropical (North Pacific) gyre decreases." Their results were based on the observation that coastal sea level typically reflects the magnitude of this transport in the California Current, such that elevated sea level nearshore indicates poleward geostrophic flow (typical of El Niño events), while depressed sea level nearshore indicates equatorward geostrophic flow (often associated with La Niña events). Chelton et al. (1982) followed up these observations by proposing that when the bulk of the divergent flow is to the south, the California Current experiences greater southward geostrophic transport, more productive source waters and higher secondary production in the region off of southern California.

Fulton and LeBrasseur (1985) further demonstrated that the zooplankton biomass, and even the mean size of copepods, was greater in the northern portion of the California Current when transport was high. They defined a transport-driven shifting subarctic domain in the northern reaches of the CCS, the margin of which was characterized by abrupt declines in zooplankton biomass south of the subarctic boundary (Figure 1.4). Although the physical dynamics are now thought to be more complex than their model, it is clear that climate driven changes in transport and ocean conditions dramatically affect both the species composition and productivity of zooplankton in the northern California Current (Mackas et al. 2001, Peterson et al. 2002, Peterson and Schwing 2003). In the late 1960s and early 1970s, the dominant copepod species in the NCC during the summer tended to be subarctic (or boreal) types such as *Pseudocalanus mimus*, *Calanus marshallae* and *Arcatioa longiremis*; species that are commonly found over shelf waters throughout the Gulf of Alaska (Peterson and Miller 1977). Data suggest that northern species became relatively less abundant, while southern species such as *Paracalanus parvus* and *Calanus pacificus* were more abundant through the 1980s and early 1990s. These southern species were almost completely dominant during the 1997-98 El Niño, at which time standing biomass was near all time lows (Peterson et al. 2002). Since 1999, northern species have again dominated numerically during spring and summer, and the standing biomass of zooplankton has been roughly double that during the warm years prior to 1999 (Peterson and Schwing 2003).

Although there are less data available for euphausiids and other large zooplankton, evidence exists for similar changes in their abundance and productivity as well. Euphausiids in the NCC are generally one of two species; *Euphausia pacifica* tends to be more abundant in offshore waters and *Thysanoessa spinifera* in inshore waters. Food web studies off of the Oregon coast summarized in Brodeur and Pearcy (1992) found that both species were considerably more abundant as prey during high upwelling conditions in 1982 and 1984 as compared with the low upwelling conditions in 1981 and during the 1983 El Niño. Tanasichuk (2002) estimated that the biomass of *T. spinifera* decreased by as much as 75% between 1991 and 1997 off of Vancouver Island, although he also cautioned that the major euphausiid species seem to respond differently to physical variability. As with copepods, abundance and productivity seem to have increased since 1999. Swartzman and Hickey (2003) describe an increase in euphausiid biomass following the 1999 shift in parts of the California Current (generally south of Cape Blanco) based on hydroacoustic data from triennial cruises. Feinberg and Peterson (2003) examine a dramatic increase in the duration and intensity of euphausiid spawning off Oregon between 1996 and 2001. All of these observations paint a picture of considerable year to year, and decade to decade, variability in the physical and biological characteristics of the water masses that regularly flow in the Northern California Current ecosystem.

1.4 Interannual and Interdecadal Climate Forcing

The El Niño/Southern Oscillation (ENSO) is widely recognized to be the dominant mode of interannual variability in the equatorial Pacific, with impacts throughout the rest of the Pacific basin and the globe (Mann and Lazier 1996). During the negative (El

Niño) phase of the ENSO cycle, jet stream winds are typically diverted northward, often resulting in increased exposure of the west coast of the U.S. to subtropical weather systems (Cayan 1989). Concurrently, coastally trapped waves propagate the equatorial ENSO signal northward along the west coast of Central and North America as far as the subarctic, resulting in increased poleward advection, warmer sea surface (and subsurface) temperatures, elevated coastal sea levels, and deepened thermoclines (Bakun 1996). The impacts of these events to the coastal ocean generally include reduced upwelling winds, deepening of the thermocline, intrusion of offshore (subtropical) waters, dramatic declines in primary and secondary production, poor recruitment, growth and survival of many resident species (particularly salmon and groundfish), and northward extensions in the range of many tropical species (Wooster and Fluharty 1985, Pearcy and Schoener 1987, McGowan et al. 1998, Pearcy 2002). Interestingly, both the frequency and magnitude of the ENSO cycle seem to have increased since the late 1970s, and some global climate models have suggested that ongoing climate change could lead to increases in the frequency and intensity of El Niño events (Timmerman et al. 1999).

A series of investigations of interdecadal variability in both ocean conditions and salmon productivity culminated in a major paper by Mantua et al. (1997) who defined what is now commonly referred to as the Pacific (*inter*)Decadal Oscillation, or PDO (Mantua and Hare 2002). The PDO is defined as the leading principal component of North Pacific (above 20°N) sea surface temperatures between 1900 and 1993, and superficially resembles ENSO over a decadal time scale. During positive regimes, coastal sea surface temperatures in both the Gulf of Alaska and the California Current tend to be higher, while those in the North Pacific Gyre tend to be lower; the converse is true in negative regimes. Evidence suggests that there have been two full PDO cycles in the 20th century. Cool (negative PDO) regimes occurred between 1890 and 1924, and from 1947 to 1976, while warm (positive PDO) regimes from 1925 to 1946 and again from 1977 to 1999. Variation in the productivity of salmon stocks throughout the Northeast Pacific seems to track these changes in ocean temperature, such that positive PDO regimes are associated with increased productivity of salmon stocks from western Alaska to northern British Columbia, and negative regimes favor stocks from California to southern British Columbia (Hare et al. 1999).

Although the precise mechanism for the PDO remains elusive, the pattern is clearly linked to variability in atmospheric conditions. The average wintertime Aleutian low both deepened and moved eastward in the post-1977 regime (Mantua et al. 1997), resulting in considerably stronger eastward wind stress (Parrish et al. 2000). This increase in wind stress has been tied to the observed cooling (and increased productivity) of the waters in the CNP and Alaska Gyre (Brodeur and Ware 1992, Polovina et al. 1995), and the consequent warming of coastal waters in the Gulf of Alaska and California Current (Mantua et al. 1997). Parrish et al. (2001) also demonstrated a southern displacement of the center of winter surface wind stress of about six degrees latitude, and a change in the mean direction of wind stress near the coast to a northeasterly direction (into the Gulf of Alaska) over the same period. Their observations support an oscillation of dominant modes of transport between northern and southern bifurcation of the west wind drift, and perhaps more importantly suggest that water entering both the California and Gulf of Alaska Currents has been of a more subtropical (central Pacific gyre) origin since the 1976 shift.

In a more recent effort, Hare and Mantua (2000) compiled 100 physical and biological time series throughout the Northeast Pacific, including time series of recruitment and abundance for commercially important coastal pelagics, groundfish and invertebrates. They found that the dominant principal component of these 100 time series has the same trajectory as the PDO, consistent with anecdotal accounts of covariance between the PDO and many other physical and biological indices. Growing evidence also suggests that the PDO shifted from a positive to negative regime since 1999, a period that has seen cool coastal ocean temperatures, high southward transport and tremendous salmon productivity (Peterson and Schwing 2003).

Yet considerable confusion remains regarding both the mechanisms and interactions between monotonic (global change), interdecadal (PDO) and interannual (ENSO) climate variability. For example, McGowan et al. (1998) acknowledge that interdecadal regime shifts seem to have occurred in both the California Current and Gulf of Alaska, but cite a lack of evidence for an interdecadal signal in mass transport from the north. Additionally, because the PDO is derived from detrended time series, it may not reflect large scale indices of global change. For example, Levitus et al. (2000) evaluated over five million ocean temperature profiles taken between 1948 and 1998 and estimated that mean global ocean temperature had risen by 0.31°C over that period. Schwing and Mendelssohn (1998) had found that between the 1940s and 1990 there was a general increase in upwelling winds throughout much of the CCS, a phenomena predicted by Bakun (1990). They suggested that the cooling of surface and near-surface ocean temperatures would have been anticipated with increased upwelling was masked by basin-scale and global ocean warming (Roemmich and McGowan 1995). This was confirmed by Mendelssohn et al. (2003) who found long-term warming trends in the upper 50 to 75 meters of the water column using subsurface temperature records in the California Current.

Perhaps more interesting is the recent analysis by Bond et al. (2003) who demonstrated that while the spatial patterns of warming and cooling over the last four years have been similar to those prior to 1977 for some areas (such as the CCS), they have been extremely different in others. This was particularly true for high latitude areas such as the Bering Sea and the Sea of Okhotsk. Bond et al. (2003) suggest that since the early 1990s the climate signal in sea surface temperature data has not been dominated by the PDO signal, but rather by a second mode of SST variability. This suggests that the limitations of the PDO (or other decadal-scale) paradigm into the future include poor predictability or coherence throughout the North Pacific climate system on multiple time scales. Their conclusions reinforce the message of Mantua and Mote (2002) and Mantua and Francis (in press), regarding the inherent uncertainty of any future climate under global change scenarios. They argue that the only reliable prediction may be that the climate of the future is not likely to resemble the climate of the past century. Consequently, the best prediction that climate models or modelers may be able to offer is to expect the unexpected.

1.5 Interactions between Climate and the Ecology

The effects of climate on the biota of the California Current System (CCS) have been recognized for some time. Hubbs (1948) believed so strongly in the correlation between water temperature and fish distributions that he felt “justified in drawing inferences, from the known data on fish distribution, regarding ocean temperatures of the past.” It is worth noting that Hubbs had already drawn distinctions between eras that seemed to be associated with the establishment of warm-water populations over long time periods, and the occasional warm years (generally associated with stronger El Niño events) that brought irregular tropical or subtropical fish much further north along the coast. While Hubbs’ work focused on the southern reaches of the California Current, such changes in distributions occurred in the north as well. For example, Pacific sardine (*Sardinops sagax*) were first described in the Pacific Northwest in late 1700s, yet subsequent investigations were conspicuously absent of any mention of sardines north of California for nearly 100 years. In the late 1880s, during another apparent warm period, they were again observed in large numbers in Puget Sound and into Canada (Strom 2003).

Oral accounts have also revealed that bluefin tuna (*Thunnus thynnus orientalis*) were at least sporadically abundant (and hunted) in the fiords of Vancouver Island during warm summers between 1880 and 1890, and archaeological evidence suggests that native peoples irregularly hunted bluefin off of Vancouver Island for millennia (Crockford 1994).[4] Such evidence suggests that interdecadal patterns of warming and cooling at least as far back as the 19th century were similar to those previously described for the 20th. Following a shift to cool conditions in the late 1940s and 1950s, it was clear that the range of the sardine contracted north to south, as evidenced by the sequential collapse of fisheries from British Columbia and the Pacific Northwest, past Monterey all the way to San Pedro in the Southern California Bight (Murphy 1966). Similarly, as sardines have recovered over the last two decades, they have done so from south to north (Emmett and Brodeur 2000, Conser et al. 2003), reaching even far into the Gulf of Alaska during the anomalously strong El Niño event of 1997-98 (Wing et al. 2000). This is consistent with the notion that sardines tend to expand northward in both abundance and range during warm regimes (MacCall 1990,[5] McFarlane et al. 2002), a characteristic that seems to be shared with other coastal pelagic species.

Pacific hake (*Merluccius productus*) in particular have long been known to be sensitive to climate-induced variability in both production and distribution. In the spring of each year adults migrate from their winter spawning grounds off southern California and northern Mexico to their summer feeding grounds off the Pacific Northwest coast (Bailey et al. 1982). As seasonal residents of these waters, hake are often the most abundant species in these seas, and are the target of the largest (by volume) U.S. fishery

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[4] One could imagine that the occurrence of bluefin tuna in coastal fiords may have bee in response to an abundance of sardine, as Polovina (1996) observed that bluefin seemed to alter their trans-Pacific migratory patterns in the late 1970s to take advantage of abundant sardines off of the coast of Japan.

[5] MacCall (1990) developed a basin model for such populations, in which the optimality of habitat increases towards the bottom of the topographically irregular basin, and the shape of the basin itself may change over time in accordance with fluctuating environmental conditions. Although the model was developed to capture the population dynamics of the central subpopulation of northern anchovy (*Engraulis mordax*), it is also appropriate for consideration of how the distribution and abundance of other coastal pelagics may be dictated over time by long term variability in ocean habitat.

south of the Bering Sea. Dorn (1995a) observed that a much greater proportion of the hake biomass extends north of the US/Canada border during warm years than cold years, a distributional shift that has long complicated management of this shared resource between the U.S. and Canada. Ware and McFarlane (1995) went a step further and estimated that every 1°C increase above average sea surface temperature (SST) in British Columbia resulted in an additional 170,000 metric tons of hake distributed north of the U.S./Canada maritime border. This pattern was exacerbated in the extremely warm El Niño year of 1998, when hake traveled deep into the Northwest and many of the larger, older fish were found as far north as the Gulf of Alaska. By contrast, in the cold subarctic-water year of 2001 few hake ventured beyond even the California-Oregon border (Swartzman and Hickey 2003).

The dramatic distributional shifts of adult hake seem to be matched by equally spectacular biological explosions when recruitment conditions are good. In the early 1980s, two strong recruitment events (in 1980 and 1984) caused the estimated stock biomass to nearly triple, from approximately two to six million metric tons (Figure 1.5). Consequently, hake were extremely abundant through the late 1980s, to both the benefit of their predators and the detriment of their prey.[6] Although a mechanism explaining the success of these year classes has proven elusive (Smith 2000), it is clear that such tremendous shifts in distribution and abundance have major impacts on regional ecosystem processes. Pacific hake have been implicated as potential predators of juvenile salmon (Emmett and Brodeur 2000), and are voracious predators of euphausiids, shrimp, herring and other forage fish. All of these are prey to salmon, rockfish and other groundfish that compete with hake. Shrimp and herring are

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[6] During this same period, the average weight at age of hake began to decline substantially, such that a twelve-year old fish which weighed (on average) over a kilogram in the late 1970s and early 1980s weighed barely 800 grams by the late 1980s and less than 700 grams by the early 1990s. It is unclear whether the declining size at age is related to environmental covariates, from density-dependent effects, some combination of the two, or other factors entirely.

commercially important species. The relative abundance or scarcity of hake thus has tremendous consequences to both the food web and to fisheries in the NCC.

In sharp contrast to the volatile population cycles of hake, mackerel and other migratory pelagics, many of the resident groundfish in the California Current have evolved an entirely different approach to coping with environmental variability. Prior to the development of fisheries, a majority of the biomass of sablefish (*Anoplopoma fimbria*), Dover sole (*Microstomus pacificus*) and many rockfish (*Sebastes* and *Sebastolobus*) populations were composed of individuals greater than 20 years of age, with individuals commonly reaching ages of 100 or greater (Love et al. 2002). Gunderson (1977) and Leaman and Beamish (1984) were among the first to suggest that the failure to consider the role of longevity in Northeast Pacific groundfish could lead to tremendous management failures. As Leaman and Beamish (1984) suggest, the large standing stocks of older individuals are simply maintaining themselves within the dynamic bounds of their ecosystem, bounds that are inconsistent with intensive harvest rates. Conover (2000) also suggests that truncating the age distribution of stocks with long reproductive lifespans nullifies bet-hedging as a viable life history strategy, particularly as compared with what existed prior to fishing. There is also evidence of changes in both the condition of post-parturition larvae and the timing of spawning between younger and older female rockfish; the inference being that a broad distribution of age structure benefits recruitment by both increasing the condition of larvae as well as increasing the probability that some larvae will be exposed to optimal environmental conditions (Bobko 2002, Berkeley et al. 2004).

By altering the fundamental life history characteristics of such populations, we may be engaged in what Stergiou (2002) calls the “tropicalization” of exploited species. In other words, we are imposing traits on these populations, such as faster growth rates, smaller size, and earlier maturity schedules, that are ill-suited to the environment in which they live. Longhurst (1998) delivers perhaps the most eloquent indictment of the effects of truncating age distribution, in the infamous collapse of Canadian cod fisheries, arguing that "it is surely axiomatic that the natural population age structure of any species- whether of cods or copepods- must have evolved (within the physiological capacity of each species) to optimize long-term persistence, and maximize occupation of habitat in competition with other species." In doing so he also cites the work of Lotka (1925) who argued that the variability of the age structure of natural populations is viable only within limits, and that if pushed beyond such thresholds the ability of populations to persist or recover is constrained. Longhurst refers to this as the "boundary of sustainability," and in a later paper (Longhurst 2002) argues that episodic recruitment failure is an archetypical life history characteristic of many temperate water marine fishes. Consequently, life history traits should not be forced to depart very far from the values that evolved for each stock prior to human exploitation.

Although their total abundance in the marine environment is modest in contrast to that of other stocks, Pacific salmon (*Oncorhynchus* spp.) are another important assemblage of species throughout the California Current for both economic and cultural reasons. As the bridge between freshwater, estuarine and marine environments they have evolved complex population structures and life histories to cope with the variability in each of these environments (Nickelson and Lawson 1998, Bisbal and McConnaha 1998). Hilborn et al. (2003) have suggested that this biocomplexity maintains resilience to environmental variability and change. Similarly, Mantua and Francis (in press) suggest that the physical template provided by high quality freshwater habitat is the "insurance" necessary for such population structures to persist while confronting a high degree of environmental uncertainty every year. However, this evolutionary strategy has been threatened by the combined impacts of habitat loss, hydropower, excessive harvest and hatcheries (NRC 1996a); problems that were exacerbated during generally poor environmental conditions throughout the 1980s and 1990s (Hare et al. 1999). Consequently, current salmon populations may lack the life history diversity and high quality freshwater habitat that acts as a buffer against the intrinsic variability in their ocean habitat.

Shifts in productivity and distribution are also manifest at the highest trophic levels throughout the California Current. Warm years (and regimes) have long been known to bring desirable gamefish such as tunas and billfish farther north and inshore (Pearcy and Schoener 1987, MacCall 1996, Lea and Rosenblatt 2000, Pearcy 2002). Many resident seabirds have been described as having either warm or cool water affinities, and vary their distribution, abundance, productivity and even diet accordingly (Ainley et al. 1995, Sydeman et al. 2001, Schwing et al. 2002). Migrant seabirds are also sensitive to ocean conditions. One of the most abundant migratory seabirds in the CCS, sooty shearwaters (*Puffinus griseus*), have declined by as much as 90% since the 1977 regime shift (Veit et al. 1996), although it remains unclear whether this represents an actual decline in population or a shift in distribution. The response of marine mammals to such variability is difficult to detect amidst current population increases, although high sea lion pup mortalities have clearly been associated with El Niño events (Baraff and Loughlin 2000), and there is evidence that some cetaceans undergo distributional shifts between warm and cool events (Forney 2000).

Figure 1.6 provides a conceptual image of basic physical and biological interactions in the NCC. Negative PDO conditions, or years with high southward transport in the NCC, tend to be associated with cooler SST, a shallow mixed layer, weak stratification, and higher nutrient levels. The biological response is typically a more “subarctic” food web, with a greater abundance of cool water copepods, greater productivity of forage fish, better recruitment of groundfish and survival of juvenile salmon, and relatively fewer warm water predators. Positive PDO conditions, as well as El Niño years or years with anomalous northward transport, are more often associated with a warmer, more stratified ocean, a deeper mixed layer, fewer nutrients, and lower productivity. The zooplankton community tends to be composed of subtropical species, there seem to be fewer euphausiids and forage fish, and pelagic predators such as hake and mackerel are more abundant. While this is a simplification of a range of complex physical and biological interactions, it is this general conceptual model that sets the stage for dynamically modeling physical and biological interactions in the NCC in later chapters.

We have seen tremendous gains in understanding both the nature and the response of the NCC ecosystem to variability and change, and we are increasingly aware that the consideration of these characteristics traits should be fundamental to fisheries management. Despite this, it is unlikely that we will ever fully understand the fundamental production pathways in the PNW coastal marine ecosystem from a linear causal point of view. A system as complex and variable as this one will change the magnitude and organization of ecological pathways over spatial and temporal scales that are likely to be unrealistic for data collection. Variability in physical oceanography is extremely high and the mix out there is at the mercy of the physical climate that is, for the most part, unpredictable. Pacific hake and other pelagics use space to capitalize on sporadic conditions of optimal recruitment in boom and bust cycles of abundance; longer-lived groundfish are also subject to highly variable recruitment but use time and the low metabolic requirements to outlast poor environmental conditions; and Pacific salmon have adapted a wide assortment life history types as their insurance strategy against environmental uncertainty. In contemplating the nature of the ecosystem that might be desired off of our coastline, we should consider that a resilient Northern California Current ecosystem is one that undergoes change and still retains this wide diversity of life history strategies.

1.6 Fisheries Development in the California Current

As Meine (1999) suggests, the development of a historic sensibility ought to be fundamental to conservation ecology, and we might add that context is important in understanding fisheries ecology and management as well. Providing some history of past exploitation and fisheries development in this region is key to setting the context of the present day, both for understanding the sequential nature of human-induced impacts to the biota and for relating past management practices to our contemporary understanding of the results of such actions. The marine life of the CCS has been exploited industrially for well over two centuries, and supported some of the most populous and culturally sophisticated Native American communities for countless millennia before that (McEvoy 1986, Trosper 2003). Figure 1.7 presents an accounting of the exploitation of marine resources throughout the entire California Current system over the last two centuries, illustrating both the magnitude of removals as well as the sequential nature of the development of the major fisheries in the region.[7] This figure shows that although industrial scale fishing pressure in the NCCE has been intense for only decades, substantial exploitation on various ecosystem components has been ongoing for at least two centuries.

Major impacts to the biota of the California Current began with the sequential depletion of west coast marine mammal populations in the early 19th century. The first species subject to commercial exploitation were sea otters, fur seals and elephant seals throughout the northeast Pacific. Commercial harvests of these stocks had begun following the Bering expedition in the north Pacific, and grew rapidly in the early 1800s, with tens of thousands of otter and fur seal pelts being taken each year (Scammon 1874, Ogden 1933, York 1987). Scammon (1874) suggested that hundreds

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[7] Marine mammal sources are listed in text. Landings data come from a variety of sources. Salmon landings do not reflect subsistence catches for any period. Prior to 1911, salmon landings were inferred from canned salmon production based on Cobb (1930), and from 1911 to the present from commercial landings (excluding interceptions) compiled by Hare et al. (1999) and PFMC (1999). Other catch data were taken from Sette and Fiedler (1928; no data are available prior to 1888), data from U.S. Bureau of Fisheries Statistical Digests, and CDFG records available online from the Pacific Fisheries Environmental Laboratory. Catches since 1956 were taken from stock assessments where available, supplemented with data from Lynde (1986) up until 1981, and PacFIN from 1981 to the present. Estimates do not include unreported landings or discards, and should be considered minimum estimates of total mortality. Offshore fisheries for albacore, other tunas, billfish and pelagic sharks are not included.

of thousands of elephant seals must have been taken in the early part of the century based on crude estimates of oil production during that period, and they were commercially extinct by the 1870s (Stewart et al. 1990). Approximately 9,000 to 15,000 Guatalupe fur seals, California and Steller sea lions were taken each year for both food and oil between the 1850s and the 1870s (Rowley 1929, Cass 1985). Seabirds were also exploited in the 19th century. Ainley and Lewis (1974) describe the historical use of murres and other seabirds when the Farallon Egg Company supplied bird eggs to the growing gold rush population in central California. They estimate that as many as 14 million eggs may have been taken between the mid 1800s and the turn of the century, with the result that the Farallon murre population may have declined from nearly half a million birds to less than 5000 by the 1920s.

By the turn of the century, sea otters, elephant seals and Guadalupe fur seals were on the verge of extinction (Stewart et al. 1990, Carretta et al. 2002). Mortality on what few animals remained was high; the only sea otter pelts taken in 1904 sold for $250, and specimens of the nearly extinct elephant seals were highly valued by museum collectors well into the early 20th century (Stewart et al. 1990). California and Steller sea lion populations rebounded modestly towards the end of the 19th Century, but were reduced to low levels again from the early 1900s through the 1930s by a mix of fishermen, bounty and “trimmings” hunters, and specimen collectors (Bonnot 1928, Rowley 1929, Cass 1985).[8] In the Pacific Northwest, hunting for meat, fur or bounties was widespread throughout the 1920s and 1930s (Scheffer and Slipp 1944, Fisher 1947), and continued at least into the 1960s (Newby 1973). Although interactions with commercial fisheries continue to be a source of mortality for west coast pinnipeds, most populations in the CCS have been increasing, many dramatically, since the 1960s (Baraff and Loughlin 2000, Carretta et al. 2002).

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[8] The “trimmings” were the lips (with whiskers attached), gall bladder and genitalia of breeding bulls, which were extremely popular in Chinese markets. Both species of sea lion were targeted by specimen collectors, and female California sea lions in particular were collected for zoological parks and circuses throughout this period. Sea lions were also taken for use in pet food products during the 1930s.

A shore based whaling fishery began in California in the 1840s, with smaller boats operating within ten miles of the coast taking primarily gray and humpback whales (Starks 1922).[9] By 1850 as many as a dozen whaling stations were spread out between Crescent City and San Diego, but catch records for this fishery are sparse. Coastwide catches were likely on the order of several hundred whales per year (perhaps hundreds more were harpooned and lost) when the fishery peaked in the late 1860s. By the 1870s gray whales had been hunted to near extinction in the lagoons of Baja California, and the availability of humpbacks and other whales declined substantially. By the 1880s the first coastal whaling fishery in the CCS had essentially come to an end (McEvoy 1986, Gordon 1987), however two more major pulses of coastal whaling in the CCS were forthcoming.

The second phase of whaling began with the development of modern whaling methods (steamships with bow-mounted harpoon cannons) soon after the beginning of the 20th century. A station in Bay City, Washington (in Greys Harbor) took a total of roughly 2700 whales off of the Washington and Oregon coasts between 1911 and 1925, nearly 75% of which were humpbacks (Scheffer and Slipp 1948). California shore whaling stations in Moss Landing and Trinidad also took roughly 2100 whales between 1919 and 1926, nearly 90% of which were humpbacks (Kellogg 1931, Clapham et al. 1997). For both regions, the rest of the whales taken were primarily fin, sei, sperm and blue whales. Elsewhere during this period, shoreside whaling stations and floating factories in Baja California, British Columbia and Alaska took as many 3500 more humpbacks, as well as nearly 9000 fin, sei, sperm and blue whales from along the west coast between 1919 and 1929. Logbooks show that the catches of all species diminished

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[9] Although New England whaling ships had taken whales throughout the North Pacific since the late 1700s, they initially avoided coastal waters of the California Current due to the "savage disposition" of California gray whales (Gordon 1987). However as many as 650 ships and 15,000 men were engaged in the Pacific whaling industry in the middle of the 19th century, producing over 1.3 million barrels of whale oil in 1855 (Starks 1922).

rapidly coastwide in the first five years of the 1920s (Rice 1974, Tonnessen and Johnsen 1982), indicating that California Current whale populations were substantially depleted during this period.

It is interesting to consider that these removals occurred in concert with the major expansion of the California sardine fishery. Stomach contents data for northern and central California caught whales suggested that humpback, as well as fin and sei whales, fed primarily on sardines, as well as euphausiids, anchovies, herring and other prey. With an average body weight of 30 tons (for humpback whales) and an average consumption rate of roughly 7.5 times body weight by year, just 3000 humpback whales could have eaten nearly 250,000 metric tons of sardines per year.[10] This, coincidentally, is about how much coastwide sardine landings grew between the early 1920s and the early 1930s. Fur seals and sea lions, which prey heavily on sardines, were also driven to low numbers during this period.

A third pulse of shoreside whaling in California took approximately 2000 humpback, fin, sei and sperm whales between 1956 and 1964. While significant, this number paled in comparison to the estimated half million whales taken throughout the entire north Pacific between 1950 and 1970 (Springer et al. 2003), following the decline of most southern hemisphere whale populations. Catch rates of blue, fin, sei and humpback whales from California shore stations showed very rapid and obvious signs of depletion in this third pulse. Catch per unit effort (whales per catcher boat day) of humpback

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[10] Based on a diet of 50% sardines by volume, which is the approximate average from Clapham et al. (1997) over both northern and central California stations. The percentage of sardines in the diet of more northerly whales was slightly less, that of whales taken in Monterey slightly greater. No data exist for the Bay City station, for which most records were lost in fires. Bioenergetic estimates are based on Hunt et al. (2002), in which an average (30 ton) humpback whale would require approximately 440 kg/day of food at a caloric density of 1000kcal/gram (roughly between low value euphausiids and higher value forage fish). Although a significant fraction of those catches would likely have been new production, there were other whaling operations in the California Current, such as floating factories off of California and Baja California that presumably took animals from the CCS population. See Appendix A for more details, including discussion of humpback whale stock structure.

whales in particular dropped two orders of magnitude, from 0.42 to 0.005 between 1956 and 1965 (Rice 1974).

Collectively, these removals kept most pinniped and whale populations at low to moderate levels until the middle to late 20th century. In the last several decades, populations of most marine mammals in the CCS have recovered, some have perhaps exceeded historical levels of abundance (Baraff and Loughlin 2000). Otters now number in the several thousands, elephant seals in the tens of thousands, and California sea lions in the hundreds of thousands. Grey whales staged a dramatic recovery in the 20th century, due in a large part from stringent protection in their calving grounds off of Baja, Mexico. Humpback whales are thought to number nearly 6000 animals in the North Pacific, perhaps half their abundance at the beginning of the century, but far above the estimated 1200 animals in 1966 (Carretta et al. 2002). Appreciation for the historical impacts of whaling and sealing, and the potential cascading impacts to marine ecosystems, has grown as marine mammal populations have recovered (NRC 1996a, Jackson et al. 2001, Springer et al. 2003). Consequently, understanding the timeline and magnitude of such removals is important for considering the context in which later removals of fish and invertebrates occurred, especially with regard to modeling potential interactions between contemporary commercial fisheries and growing in marine mammal populations.

Fishing, particularly for salmon, was the foundation for the livelihoods of native communities for thousands of years, as well as an enormously important industry along the west coast from the earliest days of settlement (McEvoy 1986, Lyman 1988). Commercial removals of fish did not truly begin until the development of the Sacramento river salmon fisheries in the late 1800s, and grew rapidly as tens of thousands of disappointed miners sought other livelihoods. Although the Sacramento river cannery soon failed, canning operations quickly developed on the Columbia River, where the salmon fishery grew from just 4000 cases in 1866 to over 450,000 cases (over

20 million pounds) by 1876 (Cobb 1930). By 1885, salmon catches in the Columbia alone topped 40 million pounds. Thus, salmon have continued to be among the most valued, and most vulnerable, fisheries in the NCC since the earliest days of human settlement (Nehlsen et al. 1991, NRC 1996a).

Of the major historical fisheries in the California Current, probably the most notorious is the sardine fishery, immortalized by John Steinbeck (1947) in *Cannery Row*. Although sardines had been fished since the mid 1800s, markets for canned sardines (and later highly lucrative markets for fishmeal and fertilizer) did not develop until World War I. Sardine fishing took place from British Columbia to Southern California, and landings grew from roughly 70,000 metric tons per year in 1920 to a peak of over 700,000 metric tons in 1936. The fishery began to collapse shortly after World War II, with the sardines disappearing first from the waters off Vancouver Island, then Washington, Oregon and Northern California (Murphy 1966, Radovich 1982). Debates began shortly thereafter, and continue to this day, regarding the relative contributions of fishing and environment as contributing to the decline (Clark and Marr 1955, Smith 1994). By the late 1950s a small fleet of boats remained fishing off of San Pedro in the Southern California Bight, driven by exponentially increasing prices for the striped bass bait (McEvoy 1986). By the time the fishery was finally closed in 1968, the estimated biomass of sardines was estimated to be only a few thousand metric tons, a decline of nearly three orders of magnitude from the biomass in the 1920s and 1930s. The population recovered dramatically in the 1980s and 1990s, associated with the changes in environmental conditions described earlier. Since 1999 sardines have once more been harvested in substantial volumes throughout the Pacific Northwest, albeit as much as an order of magnitude less than historical levels.

Halibut and other groundfish were among the species harvested by coastal native cultures throughout the California Current region, and soon became a staple of early explorers and traders throughout the Northeast Pacific. By 1892, coastwide catches of halibut and other flatfish, cod, rockfish and sablefish combined were over 10 million pounds per year, although the majority was taken from the coastal inland waters of San Francisco Bay, the Columbia River estuary, and Puget Sound. Through the early 20th century longline fisheries for halibut and sablefish expanded, as did paranzella (two-boat trawl) fisheries that had begun as early as 1876 in San Francisco. The introduction of otter trawls to west coast fisheries following World War I was associated with a gradual expansion of the trawl fleet northwards, and by the late 1930s the center of west coast trawling had shifted from San Francisco to Eureka (Scofield 1948). A sharp increase in effort and landings occurred during World War II, spurred on by both a need for inexpensive protein from flatfish and rockfish (much of which was ordered by the Army), and engine lubricant from the livers of dogfish, soupfin and basking sharks. Some 15 trawlers were active along the Oregon Coast prior to WW II, with an average capacity of 26 tons. This number grew to 43 by the end of the war, and 69 by 1960, with concurrent increases in capacity as well (Harry and Morgan 1961). Demand for groundfish dipped slightly after the war, but trawlers kept busy as a market for mink food[11] supplemented markets for fresh and frozen fish. The fishery grew steadily in the 1950s and 1960s following the postwar dip.

The industry diversified in the 1950s and 1960s, as fisheries for Dungeness crab, pink shrimp and albacore tuna developed and expanded alongside existing fisheries for salmon and groundfish. In the late 1960s (and through the 1980s) massive fleets of Japanese, Russian and Polish trawlers, many of them recent expatriates of declining whale fisheries, began intensively fishing the continental shelf and slope waters of the Northwest. The size and capacity of these trawlers stood in sharp contrast to the coastal fleets of trollers, draggers and crab boats, and helped fuel the desire to nationalize marine resources and develop greater domestic fishing capacity. Senator Warren

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[11] In 1956 over 14 million pounds of fish, over half of the Oregon trawl landings, were used for mink farming (Niska 1969). By 1964 both total landings and the markets for food fish had increased, and less than 15% of trawl landings went to mink farms.

Magnuson captured the mood of the day, when he advised fishermen and scientists that "You have no time to form study committees. You have no time for biologically researching the animal. Your time must be spent going out there and catching fish… Let us not study our resources to death, let's harvest them" (Magnuson 1968). As the growing conservation movement of that era drove passage of a plethora of environmental legislation in the early 1970s, environmental concerns soon matched the desire to nationalize marine resources (consistent with a global push by many other coastal states to do the same). The Fishery Conservation and Management Act of 1976 (later reauthorized as the Magnuson-Stevens Fishery Conservation and Management Act, or MSFCMA) ultimately included objectives that included both developing domestic fisheries as well as attaining sustainability as defined by the concept of maximum sustainable yield (MSY).

The greatest increases in capacity, effort and landings in the NCC took place between the early 1970s and the early 1980s, driven both by the increased availability of subsidies and loan guarantees, and declining opportunities in salmon fisheries.[12] Between 1970 and 1978 shrimp landings in the NCC grew from 7,000 to 37,000 tons, this from a modest 2000 tons in 1960. Participation in the Oregon Dungeness crab fishery grew from a few dozen vessels to over 600 between 1975 and 1981 (Anonymous 1981). The Oregon trawl fishery grew tremendously, doubling the number of vessels and quadrupling capacity between 1976 and 1982 (Smith and Hanna 1990). The nearly overnight development of a midwater trawl fishery for widow rockfish caused landings of that species alone to jump from 1100 tons in 1978 to over 28,000 tons in 1981 (Gunderson 1984).[13] By 1984 over 400 vessels were major

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[12] Some fishermen criticized loan guarantee programs as a disruptive element in west coast fisheries, a source of "ridiculous, easy money." They suggest that the rapid growth of the shrimp fishery as a result of federal loan guarantees may have prevented "a kind of natural selection that would have kept the shrimp industry at a reasonable level of effort" (Schafer 1981).

[13] Twenty years later the person attributed with developing the widow rockfish fishery would correct the early estimates of catch rates of 30 tons per hour, claiming that in the early days he often caught four times as much in less than ten minutes (B. Fisher pers. com).

participants in the west coast groundfish fishery alone, and a significantly greater number participated in crab, shrimp, salmon and albacore fisheries.[14]

Following this intensive growth came the first major signs of strain on the resources. The salmon fishery experienced declines following the 1982-83 El Niño, Dungeness crab and pink shrimp began their (apparently periodic) downturns, and there was a growing recognition that the groundfish resource had been pushed to, if not beyond, the limit. Early warning flags had been raised within the groundfish fishery as both trawl and fixed gear fleets grew out of proportion to the resource. A 1982 article in *Pacific Fishing* magazine suggested that the groundfish fleet was "already overcapitalized," and many participants already believed that limited entry or attrition was unavoidable (McNair 1982). Scientists had also begun to confront the low productivity of the resource relative to the catching power of the fishery and the vagaries of the environment (Leaman and Beamish 1984, Gunderson 1984, Francis 1986). The Groundfish Fishery Management Plan (FMP) that had been implemented by the Pacific Fishery Management Council (PFMC) in 1983 had established a regulatory regime based on individual trip quotas, which evolved into a strategy that used monthly limits on landings by vessel. This was driven by the desire of processors to maintain year-round markets, and a general reluctance by fishermen to limit access to the fishery. As allowable catches were reduced, monthly catch limits declined substantially. Fishermen quickly grew bitter about the declining opportunities to fish, and both fishermen and scientists grew concerned over the increasing levels of regulatory discards created by the trip limit regime (Pikitch 1991, Hanna and Smith 1993, Finley 1996).[15]

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[14] Hastie (pers. com) estimated the number of vessels with over $25,000 revenue (1999 dollars) from groundfish in 1984 at 423; that number peaked at just over 500 in 1992 and dropped back to 404 by 1999. Additionally, over 2500 vessels reported over $1000 of groundfish landings in 1984 (most of these were participants in the open access fishery); that number dropped to 1260 by 1999.

[15] Finley (1996) interviewed several west coast trawlers and wrote that "stringent trip limits means lots of discarded fish, and nobody is more unhappy about that than the fishermen who throw good fish overboard to comply with regulations."

Declines in catches and revenue, threats of future reductions, and fears that limited access in Alaskan fisheries could increase effort on the west coast finally led to substantive discussions on license limitation in the late 1980s. Yet it was not until 1994 that limited entry was formally established in the groundfish trawl fishery, following eight years of plan development, review, modification and legal challenges (Hanna 1995). Although some lucrative new markets developed and consequently increased the profitability of some fishing strategies (particularly sablefish and thornyheads), the 1990s brought ongoing waves of declines in trip limits (Figure 1.8), and consequently profitability. These reached crisis proportions in the late 1990s, triggered by poor recruitment levels and a series of pessimistic stock assessments (Ralston 1998) that ultimately led to a federal fishery disaster declaration in 2000.[16] Even then, it was not until 2002 that the groundfish fishery truly hit bottom. By that time nine stocks had been listed as overfished or depleted,[17] some with rebuilding plans that were anticipated to require decades, if not centuries, to meet their targets. This led to massive area closures over the continental shelf, and rockfish landings were reduced to incidental bycatch levels.[18]

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[16] The groundfish fishery was declared a commercial fisheries disaster by the Secretary of Commerce (then William Daley) in January of 2000, as a result of "undetermined, but probably natural, causes." The administrator for the NMFS Northwest Region (then Donna Darm), testified before the Senate Commerce Committee that although a combination of the climatic factors contributed to recruitment and biomass declines, "these declines were not detected for some time and harvest rate policies were based on assumptions of higher levels of productivity."

[17] Currently seven west coast *Sebastes* sp. Stocks and two other groundfish are listed by the PFMC as overfished or depleted; canary (*S. pinniger*) Pacific Ocean perch (*S. alutus*), cowcod (*S. levis*), bocaccio (*S. paucispinis*), widow (*S. entomelas*), darkblotched (*S. crameri*) and yelloweye (*S. ruberrimus*), the other groundfish are lingcod (*Ophiodon elongates*) and Pacific hake (*Merluccius productus*). The status of many stocks is unknown; of over fifty species of *Sebastes* listed in the Groundfish FMP, only 14 have had formal stock assessments as of 2003.

[18] A series of three area closures were initiated in 2003 to protect stocks of several species of *Sebastes* rockfish. These include the cowcod conservation areas (off of southern California), the yelloweye rockfish conservation area (off of northwest Washington) and the rockfish conservation areas (encompassing a broad swath of the continental shelf between the U.S./Mexico and the U.S./Canada borders between depths of 150 and 300 meters). More details regarding the specific regulations and spatial extent of the closures are available from the PFMC website or in the Code of Federal Regulations (50 CFR 660.304).

Historically, when faced with reductions in the abundance, catchability or demand for one resource, fishermen have turned to other fishing opportunities. McEvoy (1996) illustrates how over a century of climate shifts in California fisheries have been associated with large-scale movements of labor, capital and technology that subsequently spurred the development of newer, and in many cases significantly larger, fisheries. Dalton (2001) evaluates changes in effort and gear between different fisheries in Monterey Bay. He demonstrates that climate affects fisheries beyond the obvious mechanism of local abundance, through the consequent effects on prices, effort and forward-looking behavior. However it is also true that fisheries do not respond to the same feedbacks as most natural predator populations, as they can vary their maximum capacity to consume prey on nearly annual time scales, rather than time scales relative to the generation time of their prey (Rice 2001). Consequently, when mean generation times do approach scales comparable to responses by fisheries, feedback mechanisms between fishing fleets and their prey should exist to keep the ecological role of fishing comparable to the role of apex predators (Apollonio 1994).

This may, perhaps, help to explain why some of the seemingly more sustainable, albeit highly variable, fisheries in the NCC are those for shrimp, squid, and crab.[19] These species have short generation times and high production to biomass ratios, especially when contrast to longer lived rockfish, flatfish and other groundfish. Hannah (1995) has suggested that the trawl fishery for pink shrimp actually does behave similar to a top-level predator. As the fishery is regulated solely by season, with no spatial or catch limit controls, the fleet tends to fish aggressively in localized areas where high concentrations of shrimp are found. When catch rates drop, vessels distribute effort more evenly over space. Perhaps more importantly, effort may be redistributed to other fisheries, such as salmon, groundfish, and crab, until the resource is abundant again.

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[19] While Orensanz et al. (1998) among others have demonstrated that crustacean fisheries are far from immune to the threat of overexploitation, natural feedback between the resource and the fishery for some high turnover stocks may help to buffer stocks from collapse under current management regimes.

This was suggested by Hanna (1992) who found that the diversification of fishing strategies, between groundfish, shrimp, and crab, benefited fishermen in the NCC by virtue of reducing the variability of landings and earnings.

Although Pacific salmon also have short generation times, anthropogenic factors related to freshwater habitat may complicate meaningful feedback between the resource and the fishery. The greatest lack of feedback exists for groundfish fisheries. Large and vulnerable standing stocks, combined with low productivity even in the most favorable environmental conditions, leave few natural incentives for humans to be prudent predators. Control must therefore filter through regulatory regimes that seem to be equally void of feedback mechanisms (Hanna 1997). Forty to fifty years ago, the coastal fishing fleets may have been small enough to be balanced against the ups and downs of more variable resources, and harvest capacity was more balanced against the overall productive capacity of the resource. While most fishing vessels today continue to participate in multiple fisheries, limited fishing opportunities, combined with the excess capacity in most fleets, restricts the diversity in fishing strategies that might have contributed to greater sustainability for the human components of this fishery system.

1.7 Fisheries Management in the NCC

Ideally, the objectives of natural resource management are to create legislative or regulatory means to sustain resources and those dependent on them.[20] In fisheries this includes evaluating the productive capacity of the resource, regulating effort or access to the resource to levels that do not exceed that capacity, addressing jurisdictional incoherence and making decisions regarding allocation. Among the most important

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[20] Sissenwine and Mace (2003) make the point that fisheries management and governance are commonly though of as synonymous, when governance is instead more broadly defined to include formal or informal rules and norms that influence behavior.

tasks is addressing trade offs between the multiple objectives of both user and special interest groups, and legal mandates or requirements. As McEvoy (1996) and Eagle et al. (2003) suggest, fisheries management in the U.S. has instead often amounted to one special interest group having access to resources while denying it to others. The Magnuson Act may have been the clearest example of this, as a primary objective of the Act was to nationalize marine resources in the newly declared 200 mile exclusive economic zone (EEZ) and make the transition to the sustainable domestic utilization of living marine resources (Macpherson 2001). Yet according to Hanna (2000), the west coast fishing industry and management community was able to transition into the Council system without sparking major enmity between interest groups, in part due to a history of interstate cooperation and industry participation in decisionmaking.

The other primary accomplishment of the Magnuson Act was to codify the then widely accepted definition of sustainability, the concept of maximum sustainable yield (MSY). MSY is itself a theory that was painstakingly developed, intensely debated and prematurely eulogized (Larkin 1977, Smith 1994). The essence of the concept is that for any given resource there can be estimated levels of surplus production that may be safely removed from a given population, while maintaining a stock at that level in perpetuity. This surplus production has a single maximum, MSY. Yet immediately following passage of the Magnuson Act, data on abundance and productivity existed for relatively few of the commercially significant species in the NCC. Although allowable catches were rarely exceeded, these catches (in retrospect) were often significantly greater than the resource was able to support; as large standing stocks were able to maintain high catches for an extended period before such limitations were recognized. As foreign fisheries were displaced, management plans were implemented that were perceived as less unobtrusive than controls over access. For New England groundfish, mesh size regulation became the regulatory tool of choice for managers (Hanna 2000). Along the west coast, cumulative trip quotas were implemented for groundfish. Capacity soon overwhelmed the productivity of resources along both of these coastlines, and regulatory measures such as mesh sizes and trip limits became increasingly restrictive as allowable catches declined.

While subsequent reauthorizations somewhat clarified the language and intent of the Magnuson Act, major conservation reforms did not really occur until passage of the Sustainable Fisheries Act (SFA) amendments in 1996. The SFA had the multiple objectives of ending overfishing, rebuilding depleted stocks, protecting habitat, reducing bycatch, removing excess capacity, and maintaining coastal communities (among others). The first major impact of the SFA was the closure of major loopholes that had allowed overfishing to continue. MSY was redefined as a limit to be avoided, rather than a target, and the optimum yield (OY) was to be set as MSY as *reduced* by any relevant economic, social, or ecological factors. Biological reference points based on proxies of MSY had been developed earlier, largely based on simulation models (Clark 1991, Clark 1993, Thompson 1993, Mace and Sissenwine 1993), and these served as thresholds and limits for managers where maximum yields could not be reasonably estimated. As a result, the SFA has been widely credited with reducing overfishing, as the consequences of exceeding biological limits can be readily portrayed to decision makers in terms of the risk to the resource (Mace 2001). However the economic hardships associated with reduced yields, and the tough requirements of rebuilding plans in some regions, have led many fishermen and industry spokesmen to suggest that the SFA is resulting in unprecedented impacts to coastal communities.[21]

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[21] For example, Gerald Gunnari, a Coos Bay trawl fisherman, complained that “The cutbacks we are facing proportionately affects our ability to pay our bills too, destroying generations of hard work and the very infrastructure dependent upon the fishing community” (oral testimony to the Subcommittee on Fisheries Conservation, Wildlife and Oceans of the Committee on Resources, April 30, 1998). Similar sediments were expressed by Ginny Goblirsch, of Oregon Sea Grant and the Woman’s Coalition for Pacific Fisheries during a field hearing on SFA implementation held in Newport, OR in 2001, when she said that “The economic consequences of the cuts in available harvest are being felt throughout our communities- from fishing vessels, fish plants, ports, support services and charterboats to the community at large. The change and uncertainty facing the entire fishing industry now is unprecedented and will likely be even more traumatic that the salmon crisis… No amount of aid will take the place of a business, a lifestyle and a livelihood that has defined and supported our coastal communities since the coast was

Hilborn (2002) argues that the Council process often fails as a result of the complexity of the Council structure, the lack of direct authority and accountability for individual fisheries, and the absence of firm allocations or property rights for user groups. Although they have been largely successful in achieving many conservation objectives, mandates to end overfishing and rebuild stocks have resulted major impacts on coastal communities in the NCC (albeit impacts that would not have been avoided under stock collapses). The SFA further crippled the potential of industry and policy-makers to adapt to changes by removing critical management tools, such as individual transferable quotas, from the regulatory toolbox. Despite progress that had been made towards implementing ITQs for some sectors of the fishery and interest in broadening the program in others, the Pacific Council maintained a wasteful regulatory regime based on trip limits. An untimely sequence of poor environmental conditions throughout the 1990s exacerbated the already substantial conservation problems associated with resource declines, and painted perhaps as bleak a picture as could be made for the future of salmon and groundfish resources through the late 1990s.

1.8 The Future of Northern California Current Fisheries

We have seen that myriad of energetic oceanographic processes shape the physical environment and drive the production at the base of the food web. Short bursts of primary production fuel the rapid transfer of energy into zooplankton, shrimp, squid and forage fish. What is not consumed or assimilated returns to the benthos to follow alternative energy pathways through the detrital loop. These surges of energy are either accumulated slowly in vast populations of long-lived, slow growing deepwater fishes or exported out of the system in giant bursts of energy by migrant fish, birds and marine

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first settled" (written testimony to the Senate Committee on Commerce, Science and Transportation Field Hearing on the Decline of the West Coast Groundfish Fishery, January 16, 2001).

mammals. Over time, increasingly large amounts of this energy have been re-routed through human pathways, removed from the system with increasing rapidity by growing fleets of whaling ships, trollers, pot and trap fishers, seiners, long-liners and trawlers. The abundance of many top predators has varied by orders of magnitude over relatively short (decadal) time scales, the vast stores of energy which formerly existed in long-lived populations have been severely depleted, and much of the freshwater habitat that provided salmon with resilience to environmental uncertainty has been lost. Although the cyclical explosions of energy in coastal pelagic and other migratory populations continue, they appear to have been disrupted as a result of our past failure to accommodate the boom and bust cycle of these outbreaks.

Most coastal fisheries have repeatedly been managed as if the ecosystem was capable of providing a steady and predictable supply year after year. The only trick was trying to figure out what that supply was. For salmon, this meant building hatcheries to replace wild fish once produced in freshwater habitat lost due to dam construction. For groundfish it was assumed that the massive stocks of biomass sitting along the continental shelf and slope implied equally massive productivity, and coastal fleets were built under the assumption that the only significant constraints should be maintaining steady supplies to fill markets. Despite over a century of evidence to the contrary, the science underlying most fisheries management has continued to be based primarily on the idea of a static environment, linear causality and the simple equilibrium properties of populations. Over the last several decades, the institutions intended to maintain viable fisheries and healthy resources have been unable to meet the challenge. The need to move beyond traditional equilibrium-based management approaches has been well recognized for decades, yet because such movement pushes us into unfamiliar territory, there remains substantial reluctance to doing so.

A growing movement recognizes the shortcomings of traditional “command and control” types of management when faced with the importance of natural variation within systems and the complexity of human and ecosystem interactions (Holling and Meffe 1996, Gunderson et al. 1995). Levin (1998) has used the term “complex adaptive systems” to describe ecosystems in which “macroscopic system properties such as trophic structure, diversity-productivity relationships, and patterns of nutrient flux emerge from interactions among components, and may feed back to influence the subsequent development of those interactions.” Examples of such systems abound, Levin argues, including developing organisms, natural selection and evolution, maturing ecosystems, economic systems, and the global biosphere. All of these are characterized by nonlinear rules of interaction and threshold behavior as the system evolves, and all may experience change as a result of random events (mutation, environmental variation) that can lead to multiple outcomes or states depending upon accidents of history. Heterogeneity is an indispensable element of such systems. Gunderson and Holling (2002) argue that the both diversity and variability are essential for ecosystem health. Their “golden rule,” based on Holling and Meffe (1996), is that the key to maintaining resilience in natural resource management is to facilitate existing processes and variability, rather than attempt to alter and control them. Similarly, Berkes et al. (2002) argue that socio-ecological resilience is a function of the livelihood security of stakeholders (be they individuals or groups), as defined by entitlements and access to resources.

Although the principles seem sound, the means to operationalize such concepts are poorly defined. McEvoy (1996) advises that “the best that fisheries managers can do is to monitor and adjust the interaction between a volatile ecology, a creative economy, and society’s understanding and control as they go along.” Gunderson et al. (1995) reach a similar conclusion, observing that the heart of sustainable development is the release of human opportunity, requiring “flexible, diverse and redundant regulation, monitoring that leads to corrective responses, and experimental probing of the continually changing reality of the external world.” Levin (1998) argues that if resilience is to be a goal of management in any complex adaptive system, it is essential to understand the processes that enable the system to maintain heterogeneity in the face of both changing environmental conditions and human impacts. While this is certainly true, from a practical sense we know that even correlative studies that have convincingly linked climate with the variability of exploited resources are rare, if they exist at all.[22] Thus it may be necessary at times to implement management measures based on perceived relationships and processes even when mechanisms for the same are not fully understood.

The California sardine management model is a case in point. The current management plan for coastal pelagic species (PFMC 1998) sets harvest rates based on the three year running average of the Scripps Pier sea surface temperature and a minimum stock size threshold (MSST).[23] These in turn are based on simulation modeling of observed long-term population dynamics and environmental correlations (Jacobson and MacCall 1995). The result is a plan that allows for high harvest rates during favorable environmental conditions, and harvest rates that approach zero during periods of low productivity. Although there is no clear mechanism defining the relationship between SST and sardine productivity, the relationship is straightforward, supported by a long time series of data, and useful for implementing a control rule. As such, it is consistent with the implementation guidelines for the SFA, which include allowances for shifting

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[22] For example, Logerwell et al. (2003) developed a General Additive Models (GAMs) that seems to have some predictive power in estimating marine survival for Oregon coastal coho salmon. The model uses pre-smolt sea surface temperatures (SST), the date of the spring transition, spring sea level (representing transport) and post-smolt winter SST to explain 75% of the variation in coho survival between 1971 and 2001. However Mantua and Francis (in press) make a convincing case that few, if any, of these variables are predictable beyond real time observations in any meaningful sense of the word. Consequently the long-term forecasting ability of such models is limited, and the models are likely to be useful only in the context of short-term (year-to-year) predictions of survival or recruitment. Despite such shortcomings, these efforts represent considerable success in explaining the impacts of environmental variability on high value resources, and as such these efforts represent valuable tactical knowledge with which we might inform managers and decision-makers about the likely consequences of short-term variability.

[23] This FMP was really an amendment to the Northern Anchovy Fishery Management Plan (PFMC 1978) which was the first FMP to informally include ecosystem considerations, through recognition that 'benefit to the nation occurs by leaving fish in the ocean.' Specifically, the Northern anchovy FMP considered the role of anchovies as forage for gamefish, seabirds and marine mammals, and in doing so established a minimum biomass below which most landings were prohibited.

biological reference points where evidence exists that the productivity of stocks has changed. The sardine control rule also demonstrates that provisional linkages and correlations can be successfully applied to generate management models within the bounds of the existing legal regime for managing marine resources, and perhaps more importantly, demonstrates that management is both willing and able to implement regulatory measures that recognize both the variable nature of populations, and the needs of other elements of the ecosystem.

This suggests that future management plans, efforts and institutions should have both the regulatory flexibility and the capacity to implement a focus on resilience. This could be done by supplementing contemporary quantitative targets (catch quotas or target biomass level) with qualitative targets that are widely recognized as important to the sustainability of the resource. This is not to say that single species models and reference points should be replaced, tremendous gains have been made in the science and interpretation of single species reference points and thresholds (Mace 2001).[24] Yet these measures should be supplemented with protections for habitat and metrics of ecosystem characteristics and biocomplexity. Although habitat considerations have been promoted closer to the limelight as a result of the essential fish habitat (EFH) provisions of the SFA, there is still room to recognize other basic ecological indicators, such as the diversity of age structure in long-lived populations, or a variety of salmon life history in a watershed; targets that imply population resilience as best we are able to understand it. Uncertainty must be confronted not only with Bayesian distributions around estimates of spawning stock levels and the steepness of spawner recruit curves, but with ecological insurance in the form of marine reserves, habitat protection, environmental control rules and greater consideration of life history characteristics. While this will unavoidably involve incorporating contentious ecological concepts and

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[24] This success is significant, for although reference points do not capture all real or potential risks to exploited populations and ecosystems, even the most vocal critics of the single-species paradigm acknowledge that an ecosystem-based approach is unlikely to be an improvement in areas where single-species based management advice has not been effectively implemented (Pauly et al. 2002)

qualitative estimates of ecological health and integrity, it will also force resource users and managers to confront the impacts of their decisions on the ecosystem beyond the traditionally narrow bounds of single species management.

1.9 Summary

This chapter sets the stage for the quantitative modeling efforts to come, by providing a context for the physical, biological and human interactions in the NCC. Clearly the feedbacks, interactions and complexities of these elements of the fisheries system are far from fully understood. However this should not preclude the development of an ecosystem perspective for understanding the system and modeling system interactions and behavior. Although drastic simplification is unavoidable, models provide basic bookkeeping tools for evaluating what we believe we know about structure, function and productivity of the whole ecosystem. Just as single species models are incomplete snapshots of complex and dynamic populations, ecosystem models are incomplete simplifications of extraordinarily complex communities and environments. Nevertheless, they have an important role to play in adopting an ecosystem-based perspective to resource management.

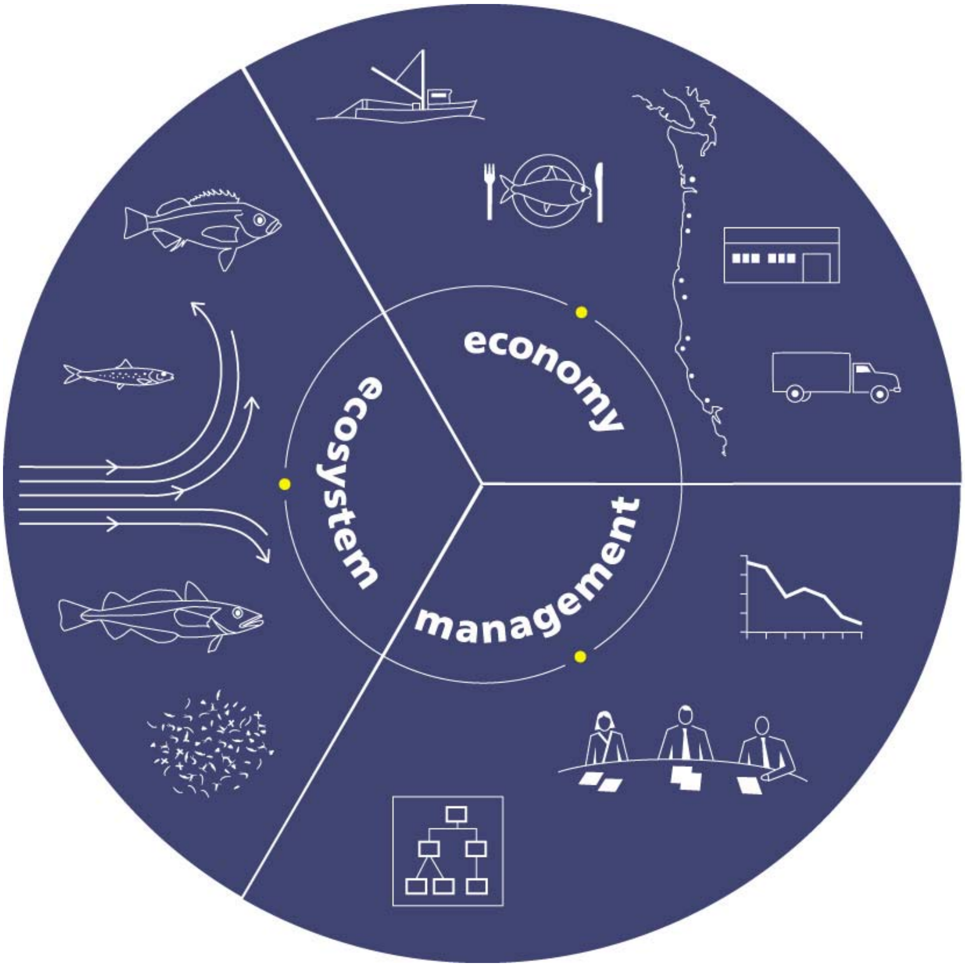

Figure 1.1: Schematic of the key elements of a fisheries system, based on McEvoy (1996); ecology (the physical and biological elements of the ecosystem), economy (fisheries and communities) and governance (the management system).

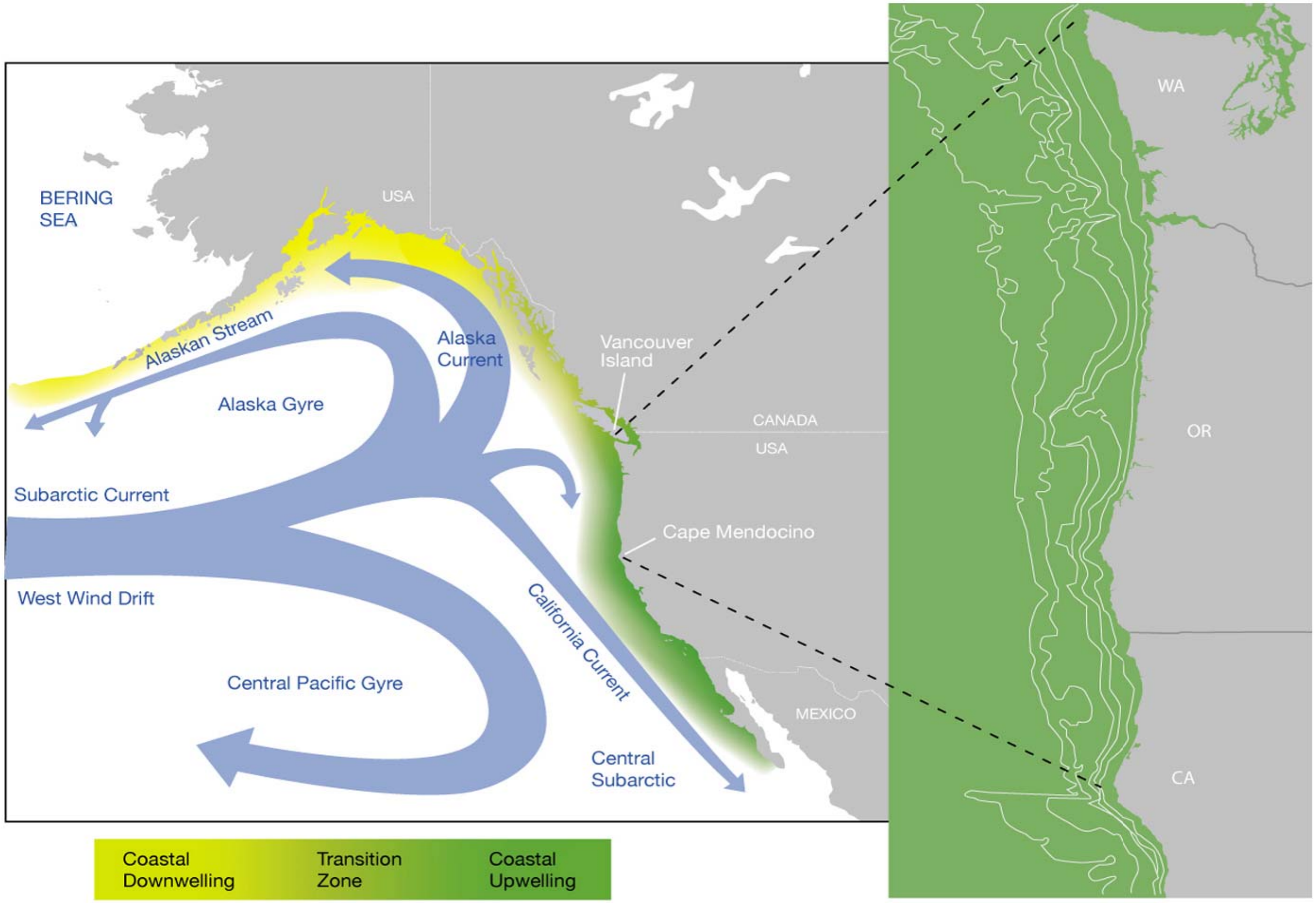

Figure 1.2: Major current patterns and ocean domains of the Northeast Pacific (after Ware and MacFarlane 1989), and bathymetry (50, 100, 200, 500, 1000 and 200 meters contours) of the shelf and slope between Cape Mendocino and Cape Flattery.

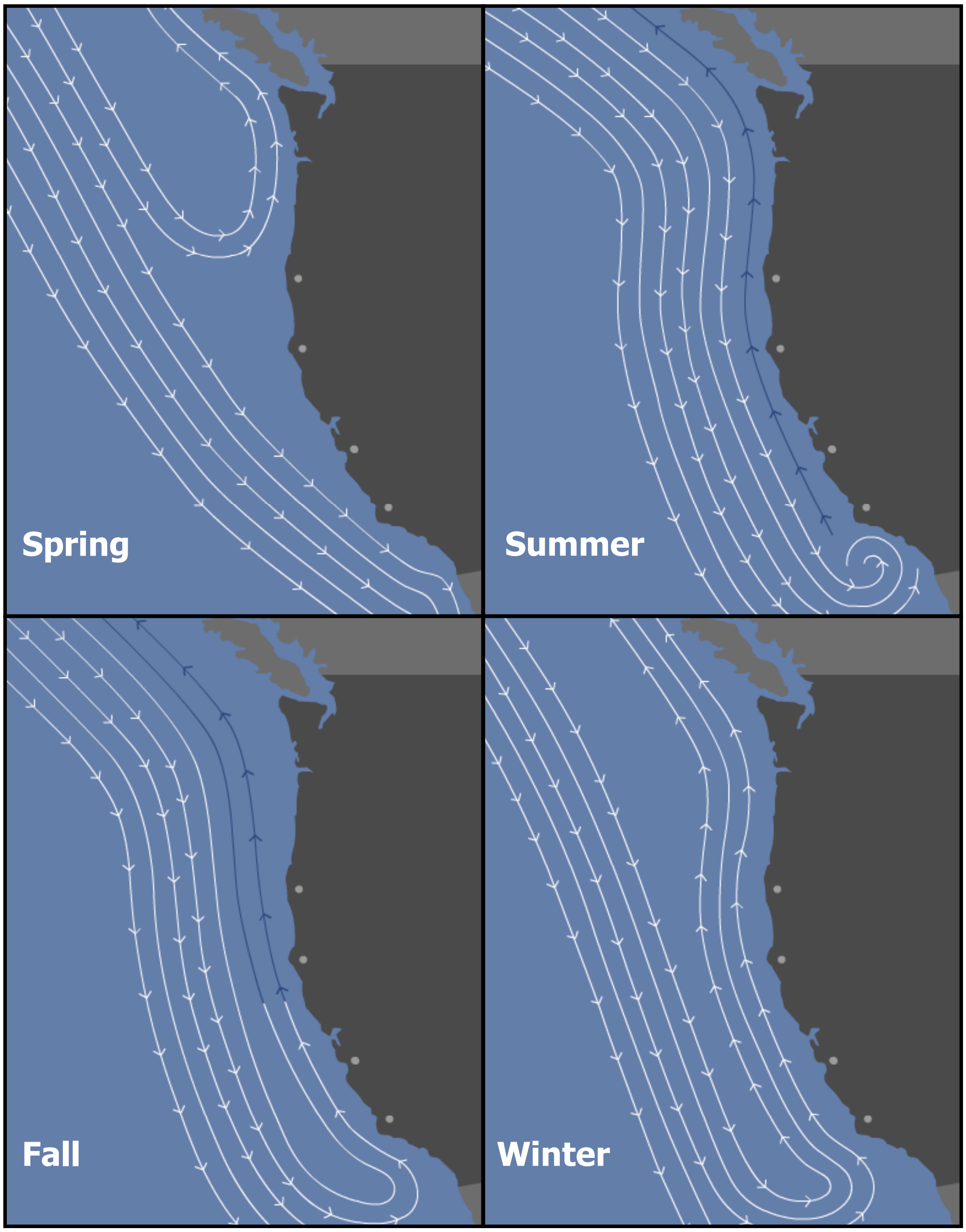

Figure 1.3: Simplistic schematic of mean seasonal variability in large-scale current patterns in the California Current, Davidson Current, and California Undercurrent. Surface currents in white, subsurface in blue (Femia 2003, based on Hickey 1998).

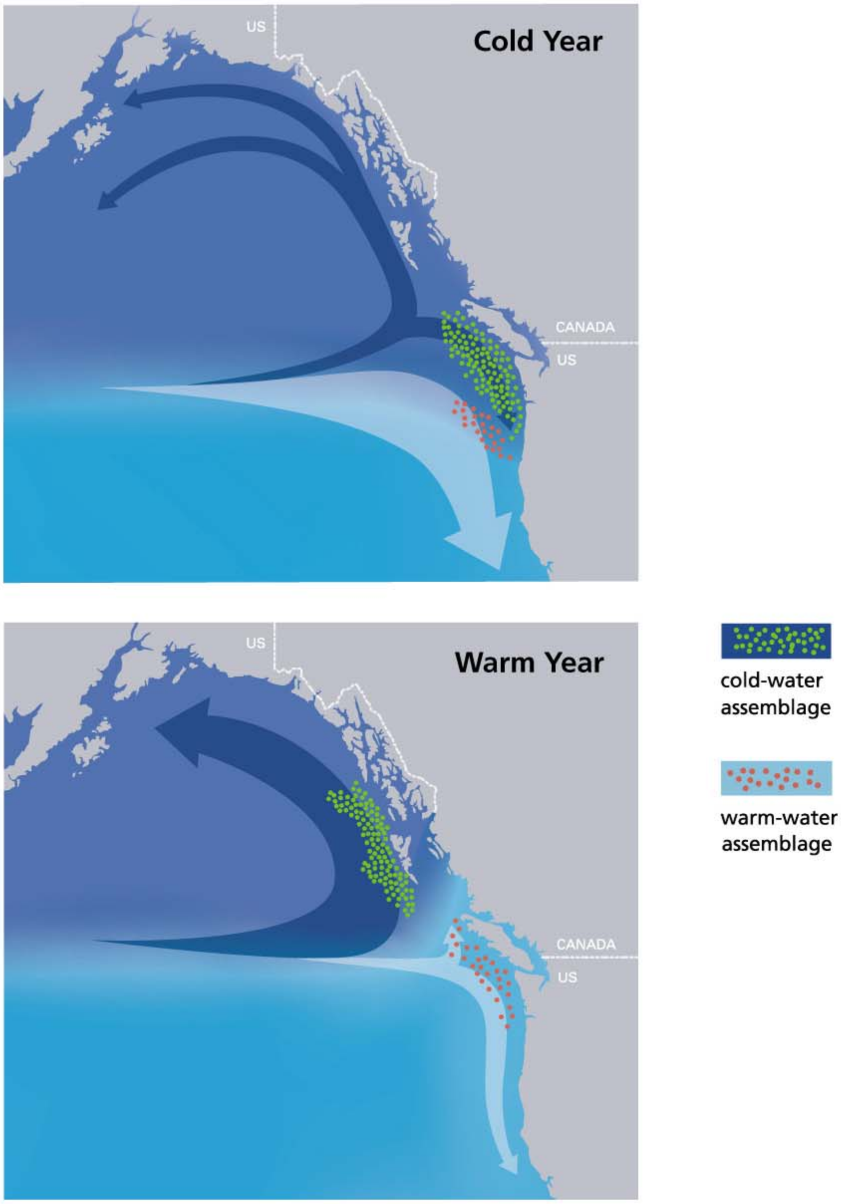

Figure 1.4: The dynamic nature of the subarctic boundary, as represented by changing patterns of zooplankton abundance (figure by A. Femia, based on Fulton and LeBrasseur 1985, Peterson and Schwing 2003).

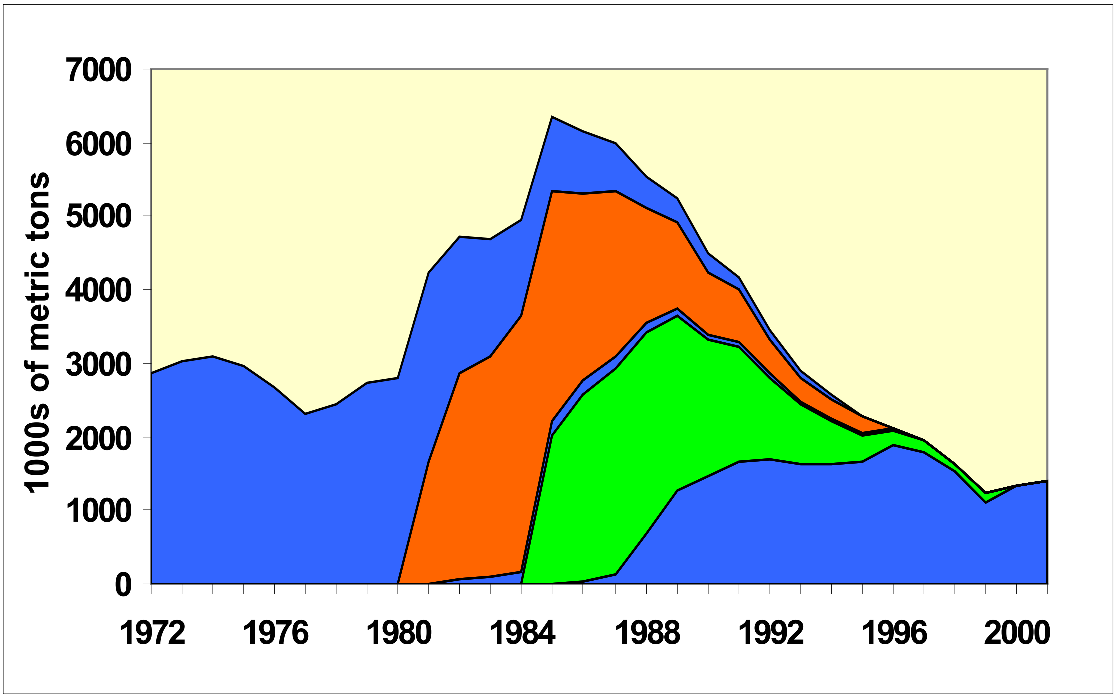

Figure 1.5: Relative contributions of the 1980 (green) and 1984 (orange) year classes to the total estimated biomass of Pacific hake population in the California Current System (Data from Helser et al. 2002). These two year classes contributed over 60%, or over two million metric tons, of coastwide hake landings between 1983 and 1997.

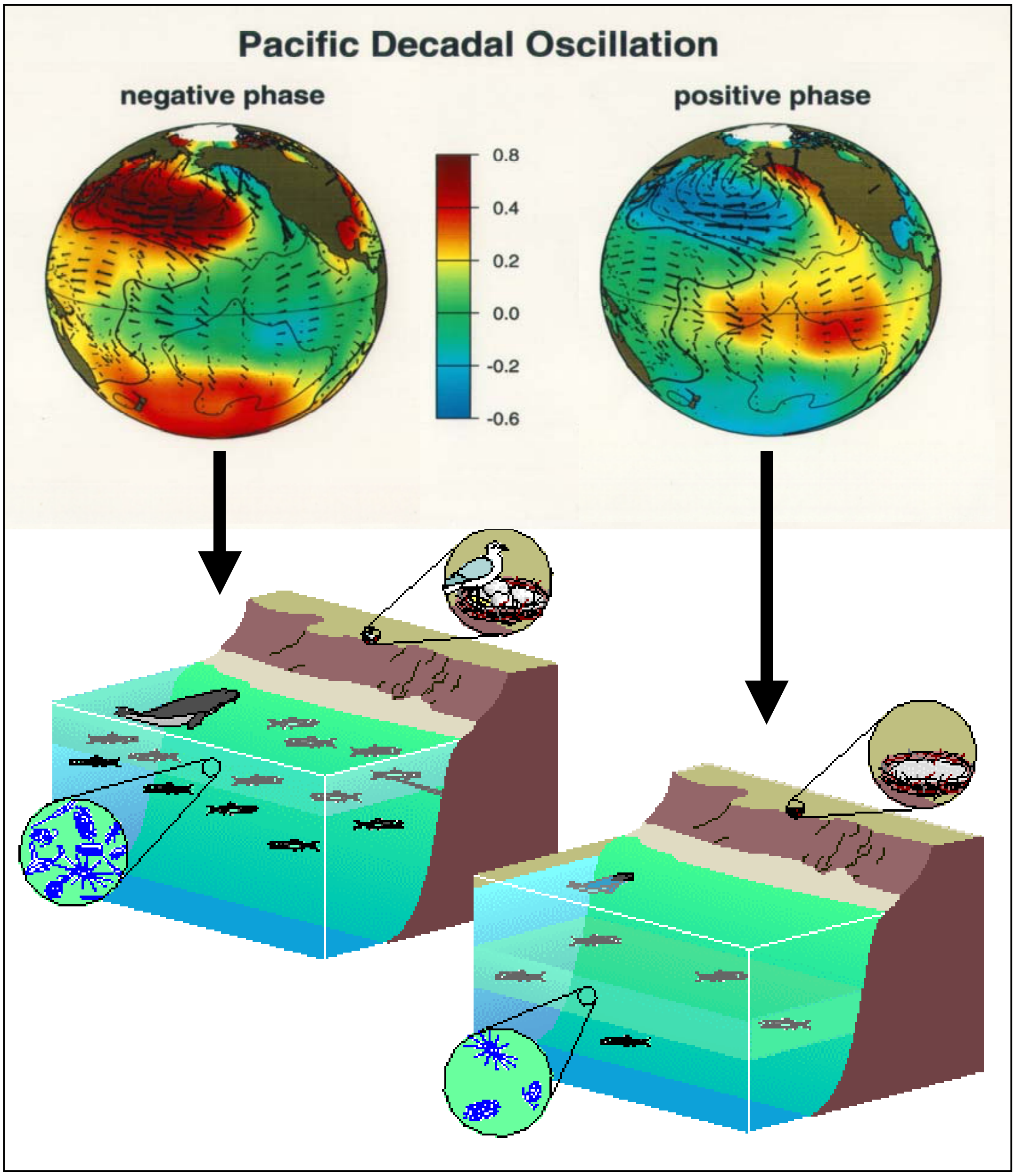

Figure 1.6: Composite from Mantua et al. (1997) and NOAA Office of Global Programs. Negative PDO conditions in the NCC tend to be associated with a cooler ocean with weak stratification, a deeper thermocline, and high nutrients; positive PDO conditions favor a warmer and more stratified ocean, fewer nutrients, and shallow thermocline.

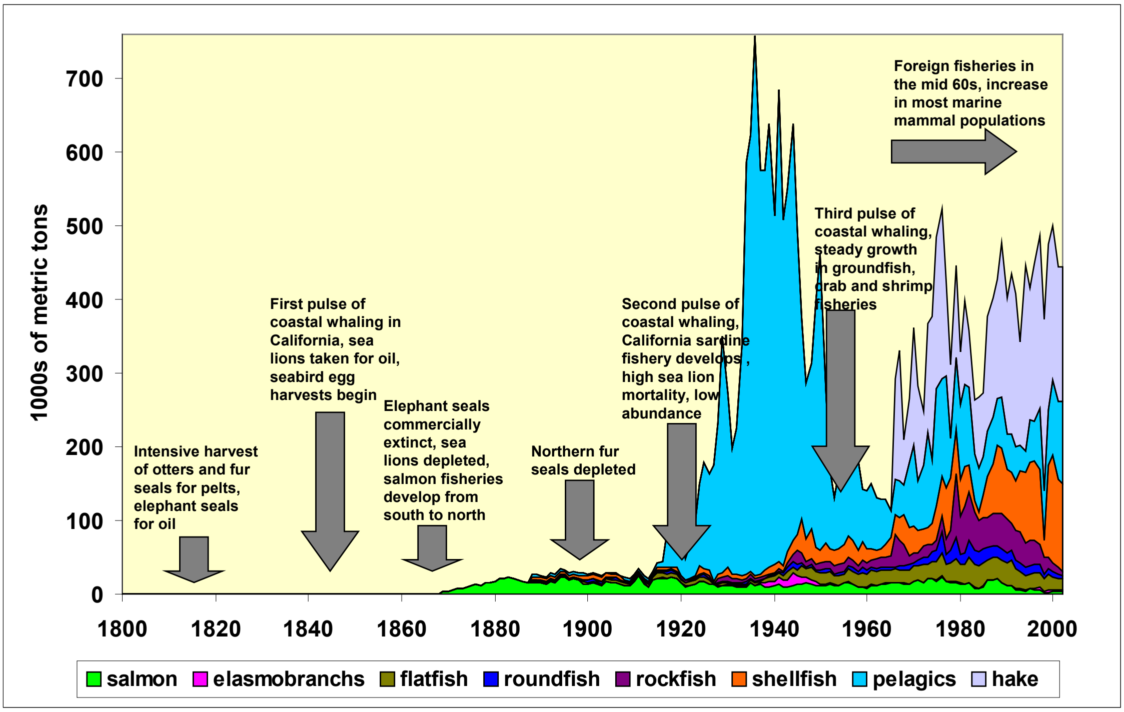

Figure 1.7: Major removals, developments and fisheries landings throughout the entire California Current System over the past two centuries (includes landings in U.S. waters only, see text for sources).

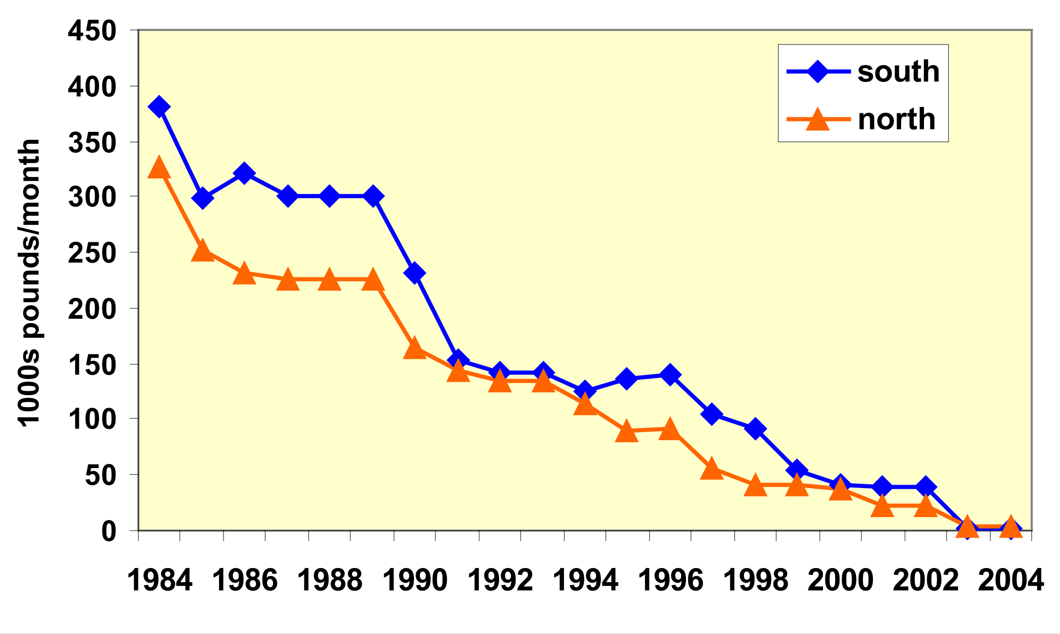

Figure 1.8: Starting yearly trip limits for rockfish in the west coast limited entry trawl fishery (including midwater gear). Boundaries defining “north” and “south” have changed considerably, and recent years have greater seasonal and species-specific complexity. Based on Hastie (pers. com.) as updated with PFMC (2003).

Chapter 2

Mathematics is a millstone that grinds whatever we put underneath it
(Krylov 1956, as cited in Longhurst 1998)

2.1 Introduction

The focus of this chapter is the quantification of ecosystem components, energy pathways and trophic interactions in the Northern California Current (NCC), using a mass balance modeling approach. In this chapter, and the accompanying Appendix, I will present the data and methods used to build the model, detail the model structure, discuss balancing issues and model inferences (specifically with regard to what seem to be most significant trophic interactions), and present visual representations of ecosystem trophic structure. The chapter concludes with the development of static model outputs as metrics of ecosystem properties, including a comparative assessment of metrics from the NCC with those generated from similar models for the Eastern Bering Sea and the Gulf of Alaska, and discussion of the potential role of such models in fisheries management. This chapter is limited to the presentation and interpretation of results from the static model. Dynamic applications are explored in Chapter 3, and additional discussion of potential model utility, interpretation and application will be a key component of the final chapter of this dissertation.

To date, most fishery management efforts in the U.S. continue, by law, to be composed of focused 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 fisheries scientists and managers to "prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery" (16 U.S.C. 1851). Although legal authority exists to take into account the direct impacts of fishing on other elements of the ecosystem, there is little explicit guidance or direction for managers to actively consider the indirect consequences of fishing on trophic dynamics or ecosystem structure. As discussed in the introduction, the Ecosystem Principles Advisory Panel recommended that Fishery Management Councils develop Fisheries Ecosystem Plans (FEPs) for every ecosystem under their jurisdiction (EPAP 1999). For the Northern California Current, ecosystem models can make meaningful contributions to at least four of the eight key minimum actions envisioned as elements of Fishery Ecosystem Plans, including:

- Characterization of biological dynamics of the ecosystem.
- Development of a conceptual model of the food web.
- Estimation of total removals by fishing and how those relate to standing biomass, production and trophic structure.
- Potential metrics or indices of ecosystem health.

Mathematical modeling has long been an essential tool in fishery management, and ecosystem based models can serve an important role in carrying out ecological mandates by providing insight into fundamental ecosystem questions.

2.2 Modeling Approach

The static ecosystem models for this chapter were built using a mass balance approach to modeling ecosystems based on Polovina (1984). Christensen and Pauly (1992) further developed this approach, dubbed Ecopath, which is currently available as part of a modeling package that includes a dynamic model, Ecosim, and a spatially-explicit dynamic model called Ecospace (Christensen et al. 2000, Christensen and Walters 2004). A comparable software package, entitled ElViz (Ecosystem Life-history Visualization) created by K. Aydin (AFSC, pers. com)was used for some estimations, simulations and sensitivity tests (particularly in Chapter 3).

In general, Ecopath is a steady-state model that integrates information from fisheries statistics, biomass surveys, stock assessments, food habits studies and bioenergetic models into a static mass balance model of ecosystem trophic structure. The origins of the modeling approach can be traced back to Steele (1974), Laevastu and Favorite (1978), and deeper into the development of theory on thermodynamics, ecosystem structure and marine ecology (Margalef 1963, Ryther 1969, Odum 1969). Polovina (1984) consolidated the theory into a simple, workable model with fisheries applications, Ecopath, which he used in an assessment of potential yield for poorly quantified components of a coral reef ecosystem. His improvements were focused on means to estimate total production, which he developed based on an observation by Allen (1971). Allen demonstrated that for populations with certain types of growth and mortality functions, in particular von Bertalannfy growth (1938) and exponential mortality, the production to biomass ratio (P/B) for a population of fish in an equilibrium condition is equal to the total mortality (Z).

Polovina's approach was further developed, and ultimately made into a widely available software application, by workers at the University of British Columbia (Christensen and Pauly 1992; Walters et al. 1997, Christensen et al. 2000). Although the current software packages include a growing array of results, statistics, and even "automatic model balancing" functions, the basic assumptions and equations are unchanged from those of Polovina (1984), which in turn are little changed from the thermodynamic assumptions that drove earlier approaches by Steele and others. The resurgence in the popularity of these (and similar) modeling approaches is not necessarily explained in terms of advances in modeling assumptions, nor an increased foundation of knowledge and data to parameterize such models, but rather to the present political resurgence of interest in developing ecosystem-based fisheries management tools and insights.

The framework of this model provides investigators with basic bookkeeping tools in order to evaluate how well conventional wisdom about a system of interest adds up, to pool together available single species data resources into a coherent food web, and consequently evaluate trophic interactions and perform exploratory analysis on ecosystems using a common framework. Although these models are often extremely data limited, and valid questions regarding many of the principal assumptions of the model framework exist, these are shortcomings shared with most ecological models, including traditional single species assessment models. Roy and Schwing[1] make this point eloquently, when they suggest that:

> A model's results do not represent any new factual knowledge generated internally to the model itself, but can only direct the knowledge, insights and assumptions that went into the model's formulation. This is a fact that must be emphasized in fisheries science, where model outputs representing the results of fairly arbitrary assumptions have come to be viewed, in a situation where real objective reality has been hard to come by, as acceptable substitutes for actual reality.

Most critical reviews of multispecies modeling approaches, including Ecopath, agree that despite conceptual shortcomings and data limitations, ecosystem models can augment contemporary single species models by confronting an array of interactions and dynamics that single-species models are less capable of addressing, including competition, predation and environmental variability (Hollowed et al. 2000, Fulton et al. 2003, Plagányi and Butterworth in press). Yet in doing so, it is as important to confront the limitations and constraints of this modeling approach as it is to understand the model structure and results. Even the most complex models are unable to incorporate all that is known about a system, and the structure of any model will inevitably reflect massive assumptions regarding both what is known, and what is important.

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[1] In Bakun and Broad (2002), discussion on the role of modeling in marine resource management in which C. Roy and F. Schwing were listed as the principle contributors.

In terms of model complexity, the Ecopath modeling approach is not comparable to biophysical process models often used in physical and biological oceanography. Instead, the appropriate comparison is with contemporary fish population dynamics models (such as surplus production models, coupled differential equation models, multi-species VPA models) more frequently used for fisheries applications (Aydin and Friday 2001). The approach used by Ecopath and Ecosim is but one of several potential modeling frameworks for investigating food webs and trophic interactions in large marine ecosystems. Several reviews of the advantages and drawbacks of various approaches, such as multi-species biomass dynamics models, multi-species VPA, individual-based models, and others, have been published elsewhere (Hollowed et al. 2000, Robinson and Frid 2002, Fulton et al. 2003). A common factor in all such approaches remains the difficult question of how model results can be applied in a useful and informative fashion. In some sense, all have the potential to allow stakeholders, managers and scientists alike to consider the potential consequences of fishing or other activities on the overall ecosystem from a more holistic perspective, a valuable result in its own right. Yet when managers require meaningful quantitative advice regarding short term consequences of harvest strategies or rates, or accurate estimates of biomass levels for data-rich species, the appropriate tools are not likely to be models such as these. The role of ecosystem models into the near future is widely recognized as one that will supplement single species models, not to replace them (EPAP 1999, Hollowed et al. 2000, Goodman et al. 2002, Christensen and Walters 2004).

Essentially, Ecopath is a steady-state model that emphasizes rates of production and consumption of marine populations. The model provides a template for integrating a wide range of biological and fisheries information from stock assessments, survey data, bioenergetics information (and models), diet composition studies, and fishing mortality. In essence, it allows smaller-scale research or model results to be viewed in the context of the ecosystem as a whole. While the lack of adequate data and model assumptions may not necessarily allow for the determination of accurate biomass levels or predation rates in dynamic systems, there is insight to be gained in evaluating relative rates of production, abundance and predation mortality among various components of an ecosystem, as well as between similarly modeled systems. The energetic accounting of the model also forces a critical evaluation of the basic interspecific interactions, which in turn allows an evaluation of whether what we believe is “known” about a system (from survey, stock assessment or other sources) “adds up” in a thermodynamic sense. To paraphrase Hilborn and Mangel (1997), the approach requires confronting models with data; with the caveat that the “data” are most often the results of models (assessment or otherwise) themselves. The resulting model provides insight about the productivity of unexploited components of the food web, improves estimates and trends in natural mortality resulting from fishing or other ecosystem changes, and allows for a more detailed evaluation of strongly interacting components within a food web.

The necessary assumption is that over an appropriate period of time (months, years or possibly regimes) a mass-balance model can be generated to represent the basic trophic interactions between major ecosystem components. It is important to note that this need not constrain the model to equilibrium, but rather only to a thermodynamically consistent state. If clear trends in the abundance of model components are known, population trajectories can be built into the static snapshot of the model (and ultimately transferred into model dynamics) to account for changing biomass levels. The equations are thermodynamically based, such that consumption of prey by predators is partitioned into respiration, new production and egestion; and new production of any component is partitioned between consumption by predators, export from the system, yield to fisheries, and biomass accumulation or decline. The key factors are shown graphically in Figure 2.1, and the main equation for the entire model is:

Equation 2.1: $$B_i\left(\frac{P}{B}\right)_i EE_i + IM_i + BA_i = \sum_j \left(B_j \frac{Q}{B} DC_{ij}\right)_j + EM_i + C_i$$

Where B is the standing biomass of a given group, i, and j represents all predators on *i*, P/B is the production to biomass ratio (typically in units of 1/year, and based on bioenergetic models, mortality rates or literature values), EE represents the ecotrophic efficiency of a component (essentially the fraction of new production that is passed up through the food web), IM and EM represent immigration and emigration used to account for model inbalances related to migration, BA is a biomass accumulation term used to reflect observed trends, Q/B is a consumption to biomass ratio (also in units of 1/year), DC is the proportional diet composition of predators *j* on prey *I*, and C is the catch by fisheries. Because the model is essentially a series of linear equations, matrix methods can be used to estimate one unknown for each component of the model. Typically the unknown to be "solved" is the *EE*, or Ecotrophic Efficiency. When biomass or P/B ratios are unavailable, this value can be specified at a predetermined level and the model can be balanced to estimate either the average biomass (B_i), the production to biomass ratio (*P/B*), or the consumption to biomass ratio (*Q/B*) (see Christensen et al. 2000 for alternative cases regarding unknown parameters). The assumptions of constant transfer rates (essentially the production of prey multiplied by the growth efficiency of its predator) are in all likelihood rarely met, and could magnify errors in a given model leading to erroneous conclusions regarding the abundance and productivity of prey species. Nevertheless, this approach is useful in assessing feasible levels of production of forage groups, such as euphausiids or forage fishes, for which adequate data on abundance or productivity seldom exists.

This illustrates to some extent how one of the greatest flaws in the model is also one of the greatest benefits. Modeling an ecosystem forces the modeler to confront data limited situations with what is known about system productivity and consumption by higher trophic levels, and arrive at plausible (depending upon the quality of the data for higher trophic levels) estimates of abundance and production for poorly understood sections of the food web. Doing so helps to highlight some of the most significant gaps in knowledge and data for a given system as well. Although the stochastic nature of population and biological rates 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 provides a framework for examining the consequences of altering species abundance and species assemblages. Yet it is worth confronting the limitations of this modeling approach from the beginning, such that all results, inferences and discussions can be made in the context of model assumptions and shortcomings.

2.3 Model Assumptions

The most pervasive shortcoming is the lack of adequate data; there generally is not enough known about most ecosystems to parameterize these models accurately. Marine ecosystems are extremely complex and many ecological processes are poorly known, particularly with regard to understanding the microbial loop, recycling, and the dynamics of lower trophic levels. Data for most lower trophic level forage species, such as benthic fauna, euphausiids, cephalopods and forage fishes, are generally sparse, as these organisms are extremely difficult to sample, although there are often plausible estimates of production, mortality and consumption rates for many species. Many higher trophic level species of fishes, seabirds and marine mammals are migrants, moving in and out of various ecosystems at differing times and rates under different environmental conditions. Frequently the best data is available for commercially exploited fish and invertebrates, but even then there tends to be a lack of information for larval and juvenile stages.

Although microzooplankton is included as a (poorly defined) component of this model, the microbial loop is not. As Rice (2001) illustrates, primary production often makes several transfers in microbial loops before being transferred to higher trophic levels, each with major potential losses of energy and biomass. However a lack of data on such processes makes incorporating the potential consequences of changes in microbial loops and recycling impossible. Instead, recycling is represented as predation on the detrital pool, and microbial processes are not explicitly considered in either model accounting or in the assignment of trophic levels. This is done to be consistent with the approach of Aydin et al. (2002) and others, as well as reflecting the lack of accurate knowledge regarding the relative role of recycling in this ecosystem.

Three detritus pools were included in the NCC models, a benthic detrital pool, a pelagic detrital pool (both represent only particulate organic matter, or POM), and a fisheries discards pool. The latter was included due to the high proportion of fisheries offal or discards in the diet of some fish stocks in the NCC, particularly sablefish and shortspine thornyheads. The benthic pool is quite obviously the fuel for the benthic food web, and is consumed by most infauna, some epibenthic fauna (including shrimps), and consumption of carrion. The pelagic pool representing both detritus that may be consumed by salps, larvaceans or other mucus web feeders, and detritus that may be recycled (for example, by bacteria that are then consumed by microzooplankton). Future versions of this model would benefit greatly by an increased focus on recycling processes.

As lower trophic levels are typically grouped together in functional groups such as “phytoplankton” and “zooplankton,” the necessary assumption is often one of functional redundancy for lower trophic levels. Functional redundancy is the general assumption that many species perform similar roles in a community, and therefore may be lost or substituted with little impact on ecosystem function or productivity as compensatory increases by similar species are expected (Walker 1992). Although

Naeem and Li (1997) have suggested that biodiversity provides ecosystem insurance and redundancy, functional redundancy is generally considered to be a reasonable assumption for lower trophic levels of marine ecosystems. Isaacs (1973), Valiela (1995) and others have pointed out that because predators in pelagic ecosystems tend to consume nearly any organism within a suitable size range, such food webs tend to be "unstructured," and the assumption of functional redundancy is generally shared with nutrient-phytoplankton-zooplankton (NPZ) models commonly used by biological oceanographers.

Whether benthic food webs may be similarly unstructured is less clear, although the assumptions of functional redundancy are equally necessary given data limitations on the species composition and productivity of benthic habitats. It is not difficult to imagine, however, that habitat structure associated with the species composition of the benthos may be an important variable with regard to both productivity and the potential recruitment success of juveniles of various species who may benefit by highly structured substrates. Although this could be incorporated into either a static or dynamic model with adequate information regarding the nature of such relationships and the impacts of fishing or other activities on such structure (for example, by having structure-providing epifauna function to decrease the vulnerability of juveniles to prey), there is no reasonable way to account for such impacts in the model without reliable *a priori* information. Functional redundancy is thus a necessary assumption in most cases, even if it is an unfair one, and it is clear that independent evaluations of the role of habitat (particularly structure forming organisms), species composition and biodiversity are equally necessary to the development of an ecosystem approach.

In considering snapshots of different climate states, or driving the model dynamically with both (or either) bottom-up or top-down climate forcing, the challenge arises that most climate impacts on production are both poorly understood and thought to be non-linear (Cury et al. 1994, Gargett et al. 1997, Loggerwell et al. 2003). Consequently, any attempt to represent climatically divergent “snapshots” of systems, or to drive the models dynamically with physical change, must confront severe shortcomings in our understanding of primary and secondary production regimes that are highly dynamic over space and time. Given poor knowledge of lower trophic level productivity and dynamics, there is an intrinsic danger in constructing models for different time periods and concluding that differences in model structure or inferred productivity are evidence of regime shifts or fisheries impacts, as opposed to simply measurement error, prey switching, continuous patterns of change, or other effects related to model uncertainty. Similarly, there is a great risk of making incorrect inferences when diet data from one period are used to parameterize a model from a different period if the abundance of either the prey or the predators has changed. The two models built for this dissertation are intended to function primarily as alternative snapshots in time, the 1960s and the 1990s model, as well as to offer different starting points for dynamic simulations. Few inferences are, or should be, drawn out of differences between the two models, aside from the very dramatic and obvious changes in the impact of fishing “down” higher (and better monitored) trophic levels inferred primarily from stock assessments. In particular, no attempt is made to “validate” shifts in climate or ecosystem state using the results. As climate variability and forcing becomes a more important factor in developing dynamic simulations, the means by which climate forcing might be used to drive ecosystem dynamics is developed in more detail in Chapter 3.

As a result of drawing in and integrating information from a wide variety of sources, the units used in such sources can pose significant challenges. Energy flow and transfer can in theory be modeled in many ways, yet often available data are reported in units difficult to convert. For example, biological oceanographers typically report estimates of primary production and phytoplankton standing stock in units of chlorophyll A, carbon, or (less frequently) dry weight per square meter of ocean surface. Secondary production is often reported in volume (ml), numbers of individual organisms, carbon, dry weight or (less frequently) wet weight, often in units per cubic meter over a section of water column.[2] Most NPZ models use either carbon or nitrogen as the currency of choice, and concurrently report on field estimates of standing biomass or production in those units (Evans and Parslow 1985, Robinson et al. 1993). Few Ecopath models use such units, although Bradford-Grieve et al. (2002) developed a carbon-based Ecopath model of the New Zealand Southern Plateau that was atypical in having greater resolution at lower trophic levels than for higher trophic levels.

Studies of benthic infauna typically report in either carbon or ash-free dry weight, as do most studies of epifauna (although fisheries surveys, which are assumed to severely undersample benthic epifauna, generally report in wet weight and numbers of whole organisms). Stock assessments of commercially important species are also in wet weight units, although they usually exclude the biomass below a given age, typically the juveniles that tend to be more important as prey for other species. Marine mammal and seabird abundance estimates are typically reported in individual sightings per unit area (over time and season). Diet studies for higher trophic levels report a wide range of units; including numbers of prey items, frequency of occurrence, volume, weight of prey items or indices derived from a range of these values. Bioenergetics models typically use carbon, joules or calories as energetic units to estimate rates of consumption, respiration and egestion, values that are generally available for many organisms from the literature, but that may vary regionally, seasonally and between individuals. Fisheries landings are typically, but not exclusively, available in units of wet weight biomass.[3]

Although the purpose of these models is generally to evaluate interactions between the physical and biological environment over all trophic levels, there is a particular focus on

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[2] Consequently, much published data are of less use to a model without knowing the average size of a copepod (or different copepods by species), the depth of a sampling instrument, data on the number of individuals per cubic meter, and other basic information.

[3] Problematic exceptions include some salmon catch records (typically reported in numbers of fish) and some early statistics for dogfish and soupfin sharks in which only the weight of landed livers, or oil produced, is reported. Data on bycatch and discards, or other sources of mortality not directly accounted for in fisheries landings, are inevitably problematic as well.

the interactions between commercially exploited species and their biotic interactions. Thus wet weight, in metric tons per square kilometer (tons/km^2, equivalent to grams per square meter) will be the units of choice for this model. Those data that exist in other forms have been converted into biomass units using the best conversion rates available.

Similar to the problems of units are the tremendous differences in energetic content between types of prey organisms. Pacific hake, for example, are highly opportunistic predators and consume a wide range of prey items, although euphausiids, forage fish and decapod shrimp represent the bulk of their diet. These organisms vary tremendously in caloric value and thus energy content; estimates of caloric value for two of the most commonly occurring vertebrate prey, northern anchovy and Pacific herring, range from 1500 to 2000 calories/gram based on time of year and condition (Boggs 1991, Anthony et al. 2000), while estimates for euphausiids and decapod shrimp are typically on the order of half of that value; ranging from 750 to 1000 calories/gram for euphausiids and 1100 to 1400 calories/gram for decapods (Davis 1993).[4] In general this might suggest that a food habits studies showing a volumetric diet composition of 35% forage fish and 65% euphausiids implies that the caloric value of these two prey was approximately equal. Yet further complicating any effort to correct for the relative value of prey in predator diets are potential differences in the energetic cost of foraging for each of the two prey items, differences in the metabolic cost of digesting each of the two prey (specific dynamic action, or SDA, although this is likely to be minor) and biases that could be related to differences in digestion rates.

Tanasichuk (1999), for example, estimated that Pacific hake digest euphausiids at significantly greater rates than herring or other forage fishes, which (all else equal) could tilt the bias of the above example into overemphasizing the importance of herring

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[4] All of these estimates represent a range of values, which can be expected to vary tremendously between individuals, seasons, years, and geographic locales. For example Willason et al. (1986) found considerable patchiness in lipid and water density, and thus energetic value, between samples of the most abundant euphausiids and copepods in the CalCOFI surveys, with more energy rich organisms located near spatially variable eddy regions and upwelling centers.

as prey even without accounting for changes in caloric value. An even more dramatic difference was uncovered by Aria et al. (2003) who found that gelatinous zooplankton such as ctenophores had digestion rates as short as an hour. Gelatinous zooplankton tended to have lower caloric values and higher water and salt content relative to other prey, the authors reported caloric values ranging between 90 to 200 calories/gram for typical coelenterates. However, the observation that they digest up to twenty times as fast as shrimp or other, denser prey would suggest that food habits studies are far more likely to underestimate, rather than overestimate, the relative importance of such prey with regard to overall caloric value.[5] The general approach here was to avoid attempts to scale stomach contents data to address potential caloric biases, particularly when such biases were likely to be in opposite directions.

Many fishes in the NCC (as elsewhere) show clear ontogenetic shifts in prey preferences over time, generally moving from lower to higher trophic levels (and smaller to larger prey sizes). Although diet data are available with size information for a few of the better sampled species (for which stage-based models could be more appropriate means of addressing such issues), it is difficult to formally confront any bias introduced by virtue of differences between the size structure of the sampled population relative to the entire population. Similarly, early modeling attempts included efforts to parameterize “summer” and “winter” seasonal models, in a large part to address the extremely important issue of seasonal variations in the productivity and distribution of migrants such as hake. However the differences and lags in the timing of various important events, such as the spring transition, zooplankton blooms and the timing of migrations from both the south and the north, pooled with suspected but unquantified seasonal changes in both consumption rates and prey availability, makes such detail overly challenging. Consequently, the final product is averaged over a full “annual”

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[5] This may be especially true for many food habits studies from trawl surveys, as standard protocol is generally for stomach samples to be processed as a low priority, usually one to two hours after the catch has been landed on the vessel. Additionally, sablefish have been observed both to regurgitate large amounts of gelatinous zooplankton (typically hydromedusae), and stomachs with large volumes of gelatinous material often burst in the process of sampling.

cycle, with biomass scaled to represent the integration of events over a year that clearly have a seasonal pattern of change.[6]

Given these challenges and shortcomings, the key to understanding the utility of these models is simply to acknowledge that such models will not fully describe these systems correctly, and to accept the possibility that many presumed interactions may not represent reality. Consequently, their utility for providing predictions or projections for biomass, productivity or sustainable yield of commercially/ecologically important stocks and assemblages under different climate and fishing regimes is limited. It must be recognized however that one could (and should) say the same for most single species models, which are ultimately built upon very similar equilibrium-based and compensatory biological functions. Single species models serve as snapshots of stock status, generally based on as much information as is possible to integrate into a model; ecosystem models can fill a similar role when supported by reasonable quantities of data and knowledge.

2.4 Northern California Current Model Structure

The Northern California Current is clearly an extremely "open" system, really a subsection of the California Current System (CCS). The entire region is extremely dynamic on multiple time scales, responding to varying modes of physical and biological variability throughout the Pacific Basin. In addition to these dynamics, there are extreme gradients in physical conditions and biological communities between the highly energetic waters of the nearshore and continental shelf, and the cold, low oxygen waters of the continental slope. As described in Chapter 1, the region modeled in Chapters 2 and 3 includes the entire area between the nearshore and the continental

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[6] In other words, if a migratory stock or species spends roughly half of its time in the NCC, the estimated biomass during that period is reduced by one-half, while consumption and production rates remain set.

slope to a depth of approximately 1280 meters (typically 20 to 80 kilometers offshore), as this represents the limits of available data from continental slope surveys and the approximate limits of most historical and contemporary fishing effort for trawl and fixed gear. Unfortunately, most surveys in the NCC have only covered waters deeper than 55 meters, and very limited data exists for waters closer to shore. These boundaries are also consistent with current and historical reporting areas for both surveys and fisheries statistics, such as the International North Pacific Fisheries Commission (INPFC) statistical areas, for which this region represents the Eureka, Columbia, and U.S. Vancouver areas.

Figure 1.2 from Chapter 1 showed the general bathymetry of the area of the NCC modeled in this exercise, Table 2.1 shows the corresponding area of different depth strata in the Northern California Current by INPFC area (data from Zimmerman et al. 1994 and Lauth et al. 1997), which sums to a total area of approximately 70,000 square kilometers. Although the true extent of the California Current itself is far seaward of these boundaries, and many important migrant fishes such as albacore, pelagic sharks, saury and jack mackerel occur largely outside this area, this region does represent most or all of the approximate known offshore and/or depth ranges for most resident and migratory groundfish species (sablefish, flatfish and rockfish), and much of the range of hake, salmon, sardine, mackerel and other migrants. This coastal margin also includes the regions of greatest biological production at lower trophic levels (over the continental shelf and along the shelf break) and the greatest densities of migratory seabirds and marine mammals (which tend to aggregate along the shelf break). Although future efforts will undoubtedly benefit greatly through the explicit inclusion of spatial distributions and habitat definitions, relative abundance in the static model is partitioned “equally” throughout the model by reducing the relative biomass to metric tons per square kilometer. Only diet preferences distinguish organisms that occupy different habitats and niches in the static version of the model.

Two mass balance models of the NCC were developed; one representing the period prior to the most intensive levels of exploitation for most NCC fisheries (the 1960s), the second representing an era following substantial growth in fisheries effort and landings, as well as tremendous environmental changes (the 1990s). Although most stock assessments provide some information on the abundance and productivity of commercially important stocks as far back as the 1960s, other parameter values are considerably less reliable than the later (1990s) version. The final model includes 63 components; 21 of which were commercially significant species or stocks of fish or shellfish, 8 of which were aggregations (at the genus or family level) of commercially significant groups (e.g., salmon, skates), 4 of which were aggregated juvenile groups (of commercially significant fishes), 11 of which were top predators (seabirds and marine mammals), 4 of which were either producers (phytoplankton) or detritus (benthic, pelagic, fisheries offal), with the remaining 15 representing broad aggregates of zooplankton, benthic fauna, and non-commercial fishes. Along with these groups, seven fisheries were included, ranging from species-specific fisheries such as salmon and Dungeness crab, to fisheries that target a wide range of habitats, species and assemblages such as shrimp and groundfish trawl.[7] As such, the model overemphasizes detail for mid-trophic level predators, in particular commercially important groundfish, for which considerably more data (and interest) tend to be focused. Other specific weaknesses in the model include the amalgamated functional groups of forage fish, mesopelagic fish, benthic fish, and cephalopods, for which species richness and diversity is very high and basic population rate or food habits data are rare.

There have been several efforts to generate both quantitative and qualitative food web and ecosystem models for Pacific Northwest marine ecosystems. Laevastu and Favorite (1977) developed a mass balance model of the California Current Ecosystem, however

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[7] There is an interest in modeling different components of the groundfish fishery in greater detail, to capture the differing species compositions of target assemblages such as the nearshore flatfish, shelf rockfish, midwater rockfish, and the deepwater complex groups described by Pikitch et al. (1988). However this level of detail was not feasible for this dissertation.

their documentation was sporadic and incomplete. Brodeur and Pearcy (1992) constructed a food web for the coastal Oregon ecosystem, based on intensive food habits and abundance studies done in the early 1980s, with a focus on the role of salmon in coastal ecosystems (Brodeur et al. 1987, Brodeur and Pearcy 1992). Robinson et al. (1993) dynamically modeled physically-forced nutrient-phytoplankton-zooplanton dynamics in the La Perouse Bank region at the entrance to the Strait of Juan de Fuca. Later models (Robinson and Ware 1999) included several key fish predators as well, and will resurface in the dynamic modeling chapter of this dissertation. Additional work off of British Columbia includes an early model of the Vancouver Island shelf (Pauly and Christensen 1996), and a similar shelf model that focused on interactions between hake, cod and pandalid shrimp (Martell 2002). Finally, Jarre-Teichmann (1996) references a model of the California Current System that was built in conjunction with models of similar upwelling systems, although the focus in this effort was on the southern California Current, and coastal pelagic species. While all of these efforts provide some guidance and information, this work represents a new effort to model the entire NCC food web.

2.5 Model Data and Parameters

The derivation of model parameters through the acquisition and evaluation of literature, grey literature and unpublished data represents the bulk of the work in assembling a mass balance model. Rarely are parameters of key importance known with confidence, and for many there may be virtually no information available. Published and grey literature sources provide glimpses of data for a wide range of time periods, seasons and regions, but rarely are methods consistent between studies. This section presents the general approach, including key sources of data and methods for deriving parameters (such as production and consumption rates), and the following section presents model results, balancing issues and model inferences. More extensive reviews characterizing the details, derivations, and literature sources for parameter values and food habits data for all model components and parameters are included as Appendix A.

Consistent long term monitoring of lower trophic levels has been rare in this ecosystem (as opposed to the relatively data rich region off of Southern California, sampled by the CalCOFI program since 1951), yet several early and contemporary studies have proven to be extremely useful sources of early data. These include:

- Survey estimates and species lists of groundfish, select pelagic nekton, zooplankton and benthic invertebrates in the 1960s Columbia River Estuary and Adjacent waters research program funded by the U.S. Atomic Energy Agency (Pruter and Alverson 1972).
- An extensive compilation of physical and biological oceanographic data from multiple research efforts off of the Washington and Oregon coasts published in Landry and Hickey (1989).
- Results from monitoring and modeling of both lower trophic levels and diet composition of higher trophic levels in the La Perouse Bank region off of the Southwest Coast of Vancouver Island since the mid-1980s (Tanasichuk 1991, Robinson and Ware 1999, Mackas et al. 2001).
- Sampling programs for zooplankton, forage fish, juvenile salmon and predators from the mid-1970s and early 1980s (Peterson and Miller 1977, Brodeur and Pearcy 1992). Many of these have been reestablished since the late 1990s (Peterson and Keister 2002, Brodeur et al. 2003).
- The U.S. GLOBEC (Global Ocean Ecosystem Dynamics) Northeast Pacific research program, undertaken since the late 1990s, with a focus on understanding the impacts of climate variability and change on physical and biological processes (U.S. GLOBEC 1994, Peterson and Schwing 2003).

The GLOBEC efforts in particular include a wide range of process-oriented research efforts, although most of the results remain forthcoming (Batchelder et al. 2002).

For higher trophic levels, especially commercially exploited species, stock assessments based on both survey and commercial fisheries data are the most reliable sources of information regarding abundance (and often productivity) when and where available. With the exclusion of some important (and abundant) invertebrate species, most commercially important fish in the Northern California Current have been rigorously assessed with growing sophistication by some of the best scientists and stock assessment methods in the discipline. Stock assessments exist for over 20 species found in the NCC, including coastal pelagics (sardine, Pacific mackerel, hake), flatfish (Dover sole, petrale sole, English sole, arrowtooth flounder and Pacific halibut), roundfish (sablefish, lingcod) and rockfish (Pacific ocean perch, yellowtail rockfish, widow rockfish, canary rockfish, black rockfish, shortspine thornyhead, longspine thornyhead, and several other minor species not explicitly included in the model that occupy part or much of the NCC).

Where stock assessments did not model population abundance as far back as the early 1960s, estimates of catches and the results of assessments were used to fit known biomass surplus production models (MacCall 2002b) to arrive at reasonable estimates for the 1960s model. For several other components, including rex sole and functional groups such as shelf and slope rockfish, survey results were used with estimates of catchability (q) borrowed from the same or similar species in other ecosystems (such as the Gulf of Alaska for rex sole) and then fit to surplus production models to estimate plausible 1960s abundance. Obviously such results are given a lower rating with regard to parameter confidence. Catch and landings data are taken first from stock assessments (where available), from the Pacfin database to 1981 other species, and from the report compiled by Lynde (1986) back to 1956. Estimates of bycatch rates were obtained from stock assessments where available, or inferred from the raw data collected during the Pikitch study of the mid-1980s (Pikitch et al. 1988, data provided by J. Wallace, NWFSC).

Survey data, while rare prior to the initiation of regular surveys, exist as far back as 1950s and 1960s, when exploratory surveys by Bureau of Commercial Fisheries did extensive trawling off the Oregon, Washington and Alaska coastlines (Alverson et al. 1964). The continental shelves of Oregon and Washington were also surveyed by state agencies in the early 1970s (Demory et al. 1976, Barss 1976), and from 1977 onward were assessed triennially, usually between 55 and 366 meters, by (summer) trawl surveys run by the National Marine Fisheries Service Alaska Fishery Science Center (NMFS AFSC).[8] Beginning in the late 1980s a series of continental slope trawl surveys between 190 and 1280 meters depth were conducted irregularly along varying sections of coastline as well (Lauth et al. 1997). Both published and unpublished data on catch rates and biomass estimates for all species caught during all shelf and slope surveys between 1977-2001 were provided by M. Wilkins (AFSC, pers. com.) and R. Lauth (AFSC, pers. com.), and were used in estimating biomass levels of many (albeit not all) of the unassessed species of rockfish, roundfish, flatfish, elasmobranchs and other components of this model. For future efforts, the increasing use of remotely operated vehicles (ROVs) and camera sleds to assess groundfish and invertebrate densities in untrawlable habitats (e.g., Wakefield 1990, Jagielo et al. 2003) will ultimately lead to improved information regarding the density and abundance of many species.

Abundance data for top-level predators, particularly seabirds and marine mammals, were obtained primarily from NMFS Marine Mammal Stock Assessments (Barlow et. al. 1997, Carretta et al. 2002), a comprehensive seabird and mammal assessment off Oregon and Washington done in the early 1990s (Green et al. 1992), and literature sources on colony and rookery densities. For many of these assessments, assumptions regarding the relative abundance within the NCC (as opposed to south or offshore of the NCC) had to be made qualitatively based on the distribution of sightings presented in the assessments, despite the fact that distributional shifts between warm and cool years have been documented for many species (Forney 2000). In other cases, particularly for migrant marine mammal species with basin-wide distributions (such as fur seals and sperm whales), available distribution (and migration timing) data were used to estimate relative densities throughout major NE Pacific provinces, and these data were used to estimate relative numbers (scaled to annual animal-years) to attempt to ensure that

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[8] See Zimmerman et al. (1994) for methods and results of a typical survey, and Zimmerman et al. (2001) for a discussion and summary of corrections made to early survey results, where problems with gear performance resulted in many hauls that had “suspiciously” low catches.

models from the GOA, EBS and elsewhere would not collectively over- or undercount total impacts from populations.

For birds, a combination of basin-wide population estimates, site-specific colony data, and at sea sightings reports (Green et al. 1992) were used to estimate abundance levels. Birds were grouped into similar guilds rather than modeled on a species-specific basis. The groups were described as the gulls (including California, herring, western and several other gull species, as well as kittiwakes, black-footed albatross and northern fulmars), murres (in which auklets, puffins and other alcids were included), and shearwaters (sooty and pink footed being the most common, but including petrels and phalaropes). Nearshore birds and pelagic birds with limited abundance (such as shorebirds, scoters, loons and others "minor" species) were not explicitly included in the model, nor were infrequent or regular predators on nearshore colonies (bald eagles, peregrine falcons and other raptors). For both birds and mammals, estimated numbers of individuals from surveys were converted to biomass using the average body weights reported in Hunt et al. (2000), which was also a primary source for energetic requirements.

The population rate parameters necessary to build the model include production to biomass (*P/B*), consumption to biomass (*Q/B*) and Egestion (*E*, generally assumed to be 0.2 in the absence of better information). Growth efficiency (GE) is essentially an "output" of the model (equal to P/B over Q/B) although GE must be included as a "known" parameter when solving for P/B or Q/B as one of the unknowns. While standing biomass is a relatively straightforward concept, both P/B and Q/B are more complex quantities, essentially condensing the whole of a species life history (growth, mortality and bioenergetics), time scale (longevity and population turnover), interspecific interactions and even recruitment dynamics into just a few simple numbers. Thus much of the life history characteristics that make a species (or assemblage) unique are lost in translation, and the model structure and dynamics are unavoidably sensitive to the assumptions made in setting the parameters that have replaced these features.

A body of literature summarizes published and inferred P/B ratios from a range of sources, including several that derive regression equations for predicting plausible values. For example, Banse and Mosher (1980) investigated P/B ratios from published studies of numerous vertebrate and invertebrate populations, and suggested that for temperate invertebrates living in aquatic environments between 5 and 20ºC, body mass (in units of kcals) at maturity was a useful predictor of P/B. Similarly, McLusky and McIntyre (1988) reviewed estimates of P/B from published studies of some 50 benthic invertebrate species of mollusks, echinoderms, annelids and crustaceans to arrive at a regression. They developed a relationship between potential lifespan (t_{max}) and P/B ratios for benthic animals in which log P/B= 0.66-0.726 (log(t_{max}). An evaluation with ocean shrimp (*Pandalus jordanii*) suggests that this is a plausible estimator. Ocean shrimp are sequential hermaphrodites that are male at age 1, typically turn female at age 2, and rarely live beyond age 3 (Hannah and Jones 1990). If we apply the McLusky and McIntyre model to a maximum age of 3, we estimate a P/B of 2.05, which compares favorably with estimated mortality rates for shrimp between 0.97 and 2.5, with a midpoint at 1.8. Additional summaries and methods for deriving P/B are found in Dickie et al. (1987), Boudreau and Dickie (1992), Pauly and Christensen (1993), Siegel (2000), Cartes et al. (2002) and references therein. Together, these provide general guidance for point estimates and ranges of plausible values for lower trophic levels.

Much preferred to literature values or estimations based on regression equations are methods for assessing P/B ratios directly through field studies. Parsons et al. (1984) suggest that if cohorts can actually be enumerated, and average weights of different life stages estimated, the simplest way to estimate production is:

Equation 2.2:
$$P_t = \frac{N - N_t * (W_{ave} + W_{tave})}{2} + B_t - B$$

Where P is the total production of a given cohort over a or unit of time, N and N_t are the number of animals alive at the beginning and at time t, W_{ave} and W_{tave} are the respective mean weights of the animals, and B and B_t are the respective biomasses at the beginning and end of time t. Total production of the population is simply integrated over each of the different life history stages of the organism. Tanasichuk (1998) used this approach for the euphausiid *Thysanoessa spinifera* in Barkley Sound based on intensive sampling done over much of the early 1990s. His results suggested that the population *P/B* ranged from 14 to 45 in any given year, with most of the variation accounted for by the proportion of larvae versus adults in the standing biomass; the lowest estimates occurred when larvae accounted for ~5% of the mean annual biomass and the highest estimates occurred when larvae were ~80% of the mean biomass. He also noted that these rates were the highest reported rates for any euphausiid species to date (he found substantially lower rates for *Euphausia pacifica*), a conclusion echoed by Siegel (2000). Interestingly Tanasichuk also noted that most of the regression methods cited earlier would have never estimated such high production rates for a (relatively) large zooplankton, for example the Banse and Mosher method would estimate an annual P/B of 1 for this species.

Another fairly reasonable mean to estimate plausible annual P/B values (and ranges) is to use NPZ model results. For example, the earlier NPZ model by Robinson et al. (1993) estimated a total annual production of copepods on the order of 287 grams m^2, and total annual production of euphausiids on the order of 96 grams m^2. The model was fit to observed estimates of standing stocks, which obviously varied substantially by season, but averages were on the order of 20 grams m^2 for copepods and 9 grams m^2 for euphausiids. This would suggest annual P/B ratios of 14 and 11 for copepods and euphausiids respectively. Generally, parameters are based on a patchwork of data, model outputs, meta-analysis, and plausibility given generally agreed upon productivity and transfer efficiencies, often with the final value (typically biomass) determined by the consumption requirements of predators.

For estimating P/B ratios for most finfish populations, Allen (1971) demonstrated that for a steady-state population with an equilibrium age structure and von-Bertalanffy growth, P/B is equal to Z (for somatic growth only). However, the primary assumptions of this estimation, a population in steady state and a stable age structure, are clearly not met for most of the important commercial species in this model. As discussed in Chapter 1, many groundfish have experienced tremendous population declines, associated with a severe truncation of age distribution. Consequently, to use Z as an estimate of P/B for canary rockfish in the 1990s, when Z may have range from 0.2 to 0.3, would greatly overestimate the actual productive ability of the stock. Instead, for assessed species with age specific abundance and weight data, estimating new production from stock assessment results directly (increase in size at age against numbers at age, accounting for mid-year mortality) is relatively straightforward based on the approach of Parsons et al. (1984) presented above and using numbers age and weight at age (by sex) from stock assessments. Estimating the production rates of unassessed species is obviously considerably more difficult, and is done using a variety of indirect methods, including literature estimates of P/B, M or Z for similar species when available, and top-down balances for those species (or juveniles of assessed species) for which predation is a major source of mortality.

Consumption rates are considerably more difficult to derive; bioenergetics models are clearly the optimum choice where possible, but the data requirements necessary to build and validate such models are tremendous. Other means, such as the stomach fullness indices (Elliot and Persson 1978), regression models (Palomares and Pauly 1988), tail aspect ratios (Pauly 1989) and simply assuming plausible growth efficiencies when P/B ratios are known are only moderate improvements to sheer guesswork, but are often unavoidable in models such as these. A better method is that of Essington et al. (2001), who traced the development and derivation of the von Bertalanffy (1938) growth equation to its origins. They found that the “usual” descriptive form of the von Bertalanffy length at age equation has at its origins a model of fish growth rates based on a bioenergetic mass balance equation, similar to those underlying contemporary bioenergetics models (Winberg 1956). Citing Pauly (1981) they derive the “generalized” von Bertalanffy model as a weight at age model in which:

Equation 2.3: $$W_t = W_\infty(1-\exp(-k(1-d)(t-t_0)))^{\frac{1}{1-d}}$$

Where W_t is weight at age, W_∞ is the asymptotic weight, k is an energy loss constant and d represents the allometric slope of consumption.[9] When fit to raw weight at age data (the authors strongly caution against trying to derive these parameters from the “specialized” length-based parameters commonly included in population biology papers and stock assessments) one can estimate the consumption rate of a population as:

Equation 2.4: $$C_{pop} = R_0 \int_{tr}^{t\max} \exp(-Z_t)H'W_t^d\,dt$$

where C_{pop} is the total consumption of the population, integrated across ages, R_0 is the recruitment rate, Z_t is the instantaneous natural mortality rate by age and H' is a consumption constant derived from the fitted von Bertalanffy parameters and the allometric slope of consumption. When possible, weight and length at age data were taken solely from the triennial survey to avoid fishery-selective bias in size at age, although the use of some fishery data was necessary for several flatfish species (data for these species were taken directly from the Pacfin biological database). Additionally, by

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[9] The parameter *d* is a unitless constant that represents the allometric slope of consumption and must be defined by the user, as must another constant, *A*, the assimilation efficiency of consumed prey. To apply these methods consistently, K. Aydin, S. Gaichas and J. Field parameterized the Essington et al. (2001) model for nearly thirty species of groundfish using raw length, weight and age data from the U.S. West Coast, the Gulf of Alaska and the Eastern Bering Sea (in addition to consulting previously published literature values) to arrive at a consistent methodology and parameter estimates. Consequently, for all of these models, *d* was set at 0.8 and A at 0.6. The resulting models also allowed a comparison of “active” and “passive” metabolisms, estimates of growth efficiency, and estimates of juvenile consumption rates.

estimating the consumption rates of individuals at age, and using stock assessment estimates of specific numbers at age, one could track expected changes in consumption rates and population growth efficiencies based on changes in the size and age distribution of the population. Combined with estimates of P/B discussed above, this approach was used to estimate the consumption rates (as well as growth efficiencies) associated with different time periods directly from stock assessment data when available, to better represent changes in population parameters associated with different time periods and fishing histories. In general, the results of this approach were generally consistent with other available and/or anecdotal information regarding most of the species for which it was used. More importantly, this approach provided a consistent template upon which to base bioenergetic parameters for a suite of important groundfish species, such that any bias inherent in this method should be constant between species, as well as between other ecosystem models constructed based on similar assumptions.

Estimation of population parameters for seabirds and marine mammals is far from easy, but relative to many lower trophic level ecosystem components, considerably more published bioenergetics information exists. In general, consumption rate estimates for marine mammals and seabirds were derived from weights at age, energetic requirements, and (generalized) prey preferences reviewed by Hunt et al. (2000) and Trites and Pauly (1998). Fewer data are available on P/B rates for either seabirds or marine mammals, and as most marine mammals are currently unexploited (with the exception of incidental bycatch in some fisheries), mortality rates were used as proxies for P/B for most species. Where mortality rates themselves could not be found, methods derived by Barlow and Boveng (1991) based on the life history tables derived by Siler (1979) and longevity (defined as the 99th percentile of the age distribution) were used to derive P/B estimates. For migrant species, the trophic impact was adjusted using biomass, rather than consumption or production rates, to scale for the fraction of time animals spent inside the NCC as opposed to elsewhere.

Interpretation of food-habits studies (where they exist), particularly for the purposes of parameterizing the Ecopath diet matrix, is also notoriously problematic. A multitude of factors will influence the food habits of fish. The most obvious is simply the availability of a given prey, and prey preferences, ontogenetic changes in prey selectivity, differences in sex, spatial factors (latitude and depth), and temporal factors (daily, seasonal and interannual variability) can all bias food habits studies. Most such studies are limited in space and time, and the results of studies separated by space and time often differ significantly. Figure 2.2 shows the temporal scale (by year, excluding seasonal variations) of available food habits data for the more commercially significant species in the NCC model, together with color coded indicators of the number of individuals sampled. Many groups have very few samples, often from only a single year and/or season, and generally from a limited local. However nearly all commercially significant species are represented, with over 32,000 samples (found) in total, although more than half of these are for Pacific hake alone.

Brodeur and Pearcy (1992), Buckley et al. (1999) and Lee (2002) are among the authors who have conducted and summarized a wide range of food habits studies and discussed potential sources of bias. In addition to seasonal and long-term changes in prey preferences and availability, bias can be introduced by such means as net feeding, changes in the digestibility of prey (Tanasichuk 1999, Arai et al. 2003), sampling individuals only from trawlable areas or at given times of the year, and simple random variability. Pooling forage species into aggregate boxes can also be misleading when evaluating relationships and competitive interactions between species, as species may feed on different life stages of prey. For example, adult hake feed largely on adult (> 17mm) euphausiids, while Pacific herring and other forage fish prey upon nauplii and smaller life stages. By contrast, scyphozoan jellyfish feed almost exclusively on euphausiid eggs. Although all are essentially competing for the same resource in this model, such competition is not necessarily direct.

As Lee (2002) points out, many food habits studies focus on aggregating individual diet information across population levels to arrive at mean values, rather than the variability in prey and prey preferences over time. The results of Brodeur and Pearcy (1992) and Lee (2002) demonstrate how dramatically food preferences can change from year to year under varying environmental conditions. This can be especially problematic where diet studies are available only for given time periods, or even when more abundant data are available for a more recent time period that are not necessarily consistent with earlier (albeit more limited) studies of a very different period. For example, Lee (2002) found that widow and yellowtail rockfish consumed as much as 75% gelatinous zooplankton by volume (principally salps, but including heteropods, ctenophores and cnidarians) during both the warm 1998 El Niño and the cool 1999 La Niña that followed. Adams (1987) had earlier found that widow rockfish consumed moderate amounts of gelatinous zooplankton (roughly 20% by volume), although yellowtail had not been previously described as predating heavily on gelatinous prey. As Plagányi and Butterworth (in press) point out, a key challenge of Ecopath is a reasonable way to adjust diet data from time periods that differ from those for which the model is ostensibly constructed to account for known or likely differences in the relative abundance of prey species.

A similar example warrants closer scrutiny. Cannibalism has been described as an important factor in the population dynamics of Pacific hake (Buckley et al. 1999). Interestingly, cannibalism is not confined to the largest individuals (although it was more prevalent in larger hake), as hake ranging in size between 20 and 70 cm will consistently consume hake of roughly half of their own size. Levels of cannibalism seem to have been low or nonexistent between the late 1960s and the early 1980s (Gotshall 1969, Livingston 1983, Rexstad and Pikitch 1986, Brodeur et al. 1987). It seems to have become more of a factor in the late 1980s and through the 1990s, as Pacific hake as prey represented more than 30% of the diet (by volume) of Pacific hake as predators over the 1990s (Buckley 1999, unpublished AFSC food habits data). This suggests that there may be density dependent processes that play a role in hake population dynamics, perhaps more so under the poor environmental conditions observed through the 1990s than during other periods. Alternatively, this could reflect density-dependent processes associated with the volatile population behavior of hake in the 1980s, when two large year classes caused a threefold increase in the biomass of hake over a period of less than five years. Many possible explanations may exist. Regardless, these observations are problematic in determining values for the diet matrix in the model, especially as more diet data for Pacific hake exists during the climatologically anomalous 1990s.

Clearly the translation of raw food habits studies into static diet matrices requires gross simplification of complex information, and although modest efforts to address these biases may be undertaken, there are rarely sufficient data to address these problems adequately. For many marine mammals in particular, most available information is from the 1960s, as traditional lethal sampling methods are rarely used in the present day. Despite these shortcomings, the food habits studies summarized here represent the best available information for trophic interactions in this ecosystem. Furthermore, for many of the most abundant and well-sampled species, the general results and prey preferences do appear to be relatively consistent between different studies over both space and time. Tables 2.2 and 2.3 present the model parameters for the 1960s and 1990s model, and Tables 2.4a, b, and c present the diet matrix used for both models.

2.6 Select Results of the Static Models

Compiling parameters is but one of several stages in building an ecosystem model, and one of the most challenging and informative actions is balancing it. In compiling biomass estimates, parameter estimates and diet data from a tremendously wide range of sources of varying reliability, it is inevitable that “thermodynamically inconsistent” results will occur. What is learned from resolving inconsistencies amongst data from a range of disparate sources can be one of the most rewarding results from such efforts. For lower trophic levels, the typical result is that estimates of standing biomass and productivity are insufficient to account for the known consumption of these organisms as prey in the diets of (generally) well accepted stocks of commercially or ecologically important predators.

The general approach, which was taken in this model, is to “set” the ecotrophic efficiency (EE) at a constant (generally 0.8) and allow the model to estimate either the biomass or P/B ratios of most important forage species (copepods, euphausiids, forage fish, benthic epifauna, pandalid shrimp) when available estimates of biomass or productivity were insufficient to balance the model.[10] As one example, there is a reasonable degree of certainty regarding the estimated abundance of Pacific hake, groundfish and other key predators generated from stock assessments. Presuming one finds the estimates (or a range of estimates) for consumption rates by hake plausible, one can accept that the estimated biomass and productivity of euphausiids and forage fish generated by the model are, at a minimum, plausible representations of lower trophic level production. It is worth noting however, that the bias here is for the estimates of lower trophic level productivity being low, rather than the (model) estimates of predator abundance and consumption rates being too high.

Table 2.5 and Figures 2.3 and 2.4 present aggregated summaries of estimated annual consumption of key forage assemblages by key predator groups. Although there is considerable uncertainty around these results, they do provide reasonable estimates of the major trophic interactions, especially relative to each other, between key predators in the NCC. For example, Figure 2.3 shows that Pacific hake are clearly the dominant

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[10] In instances where neither of these two parameters is known with any reliability, the only important “result” is the estimated total production, as biomass and P/B estimates are confounded.

predators of forage fish and euphausiids in this ecosystem, accounting for over half of the total mortality of each, as well as disproportionately high fractions of mortality for many other minor components of hake diets (pandalid shrimp, small flatfish). Bax (1991), Mangel and Nicol (2000) and others suggest that such modeling tends to lead to significantly greater estimates of abundance and production of forage species (such as euphausiids and forage fish) than estimates taken from biological or acoustic surveys. At a minimum they provide plausible representations of the relative consumption of key forage groups by alternate groups of predators (including humans). Similarly, Figure 2.4 shows that humans are the key predators of hake and groundfish in this system, catching on the order of 200,000 and 70,000 tons of each respectively, in contrast to roughly 75,000 tons of each consumed by other groundfish, and 30,000 tons of each consumed by seabirds and marine mammals.

Evaluating the relative sources of mortality for commercially exploited species is a central objective of ecosystem modeling, and one of the results for which such tools are most suited. For example, NMFS (1997) suggests that pinnipeds alone consume upwards of 200,000 tons of commercially valuable fisheries resources in the California Current. However, the vast majority of this consumption would seem to occur in the southern California Current, where the number of marine mammals (particularly California sea lions, but also many toothed and baleen whales) is both greater and experiencing greater rates of increase. The total estimated consumption of commercially important species by marine mammals for this model (in the 1990s) is on the order of 66,000 tons per year, nearly half of which is estimated to represent the consumption of Pacific hake. While this excludes some important predation of salmon in estuarine areas, particularly by harbor seals (see Appendix A for details), this also suggests that the role of marine mammals as competitors with marine fisheries is relatively minor in this region, even as some marine mammal populations continue to recover. Most of the predation pressure by marine mammals is on forage fishes and cephalopods, for which marine mammals also compete with commercially important piscivores (such as salmon, sablefish and hake). It should be noted that these estimates represent "snapshot" values, and are not intended to imply either causation or substitutability, as many of the species represented here as prey are (or were in the 1990s) currently experiencing significant downward (hake, rockfish, roundfish) or upward (small flatfish, pelagics) trajectories. Furthermore, the diet studies of marine mammals in particular upon which these general estimates are based were rarely contemporary to the 1990s.

Figure 2.5 takes a slightly finer scale look at the apportionment of total mortality (Z) for the principal guilds of the most commonly fished commercial species for both the 1960s and the 1990s. Although this figure does not reflect changes in total mortality between these two periods (which will be discussed more in Chapter 3), it does suggest a shift in major sources of predation from piscivorous fishes in the 1960s to fisheries (and moderate increases in marine mammal predation) in the 1990s. Fowler (1999) has suggested that one approach to seeking sustainable fisheries is to use other species as "empirical examples of sustainability," and to maintain fishing mortality rates within the frequency distributions of predation rates by other species. Although the resolution here is not to species, the figure clearly suggests that the fishing mortality rates of the 1960s more closely approximated natural mortality (predation) rates by major predators in the 1990s. As such, these estimates give at least a plausible graphic accounting of the relative impact of fishing in contrast to other sources of mortality.

Perhaps more interesting is the insight that might be gained when interspecific interactions at higher trophic levels are incompatible with biomass or food habits data for commercially exploited species. Early attempts to balance this model revealed that the estimated productivity of short and longspine thornyhead (*Sebastolubus alascanus* and *S. altivelis*) was far lower than that necessary to balance the consumption of thornyheads as sablefish prey. Several independent food habits studies performed at different time periods within the NCC suggested that thornyheads made up as much as

35 to 40% by volume of sablefish prey (Laidig et al. 1997, Buckley et al. 1999). The raw data from both studies were subsequently made available from the primary authors, and in it was discovered that a disproportionate fraction of thornyheads (relative to other sablefish prey) had digestion codes that rated the prey as "recently ingested." As both studies were based on samples collected from groundfish trawls, the data suggest that net feeding by sablefish within the codend of the trawl inflated the volume of thornyheads as prey in sablefish stomachs (more details are provided in Appendix A). Yet, even when accounting for this bias, it was equally clear (from well digested specimens) that thornyheads contribute substantially to sablefish diets. Sablefish predation is clearly a major source of mortality for *Sebastolobus* juveniles and adults, however their estimated contribution to the overall diet of sablefish (by volume) is likely to be well below 10%.

Interestingly, this was one of relatively few conflicting issues between estimates of biomass and productivity at higher trophic levels (other balancing issues, considerations and resolutions are discussed in more detail in Appendix A). By contrast parameterization and balancing of other models has proven more difficult as a result of such interspecific interactions in commercially important (and assessed) species. In the Gulf of Alaska, one of the most notable interactions includes arrowtooth flounder (*Atheresthes stomias*) predation on walleye pollock (*Theragra chalcogramma*). In trying to balance this model, Gaichas (pers. com.) found that the stock assessment results for these species were incompatible. The abundance of arrowtooth had nearly tripled between the 1970s and the 1990s, when the abundance of pollock had declined substantially over the same period. Consequently, there simply was not enough gross production of pollock to feed the estimated biomass of arrowtooth flounder, given the diet proportions estimated from extensive (and contemporary) food habits data.

This observation has led to interesting questions regarding the extent to which single species stock assessments may or may not always work together at system level, as well as what it might mean when they do not. Currently, this potential for increased predation on juvenile pollock has become a factor in providing harvest recommendations. Dorn et al. (2003) suggest that the "potential increase in juvenile pollock mortality adds additional uncertainty to the assessment." The result of this uncertainty was a downscaling of what was formerly predicted to be a strong year-class for Gulf of Alaska pollock. This example demonstrates how confronting inconsistencies in disparate sources of data, and consequently evaluating such interactions in greater detail, can lead to useful inferences regarding changes in both mortality and production for these species. The Gulf of Alaska example is a particularly strong one, given the richness of the data that led to the inconsistencies between assessment models.

One of the products of an Ecopath model is quite obviously a visual image of the significant food web, and conveying the relative importance of food web interactions is a critical element in conveying trophic structure and interactions (Pauly and Christensen 1993). Figure 2.6 represents an effort to find the appropriate balance between scale, clarity and detail in generalizing trophic flow and interactions; here the size of the boxes is scaled to the log of the standing biomass (within maximum and minimum levels), the estimated trophic level is along the y axis, the major energy flows are shown in blue and the minor (less than 5% of cumulative flows from a given box) in green.[11] In Figure 2.7, colors representing the alternative energy pathways such that pelagic (primary production) flux are shown in blue and the benthic (detrital loop) energy is shaded in red. Thus the varying amounts of blue or red in the boxes represent the proportion of energy from these two major pathways, and the height of the individual boxes represents the log of the mean annual standing biomass scaled relative to a maximum and minimum font size. Similarly, the width of the bars connecting the various boxes represents the biomass flux of prey to predators. Depending on the purpose and

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[11] These figures were generated with the Ecosystem-Life history Visualization (ELVIZ) modeling and visualization software developed by, and available from, K. Aydin (pers. com) at the NMFS Alaska Fisheries Science Center.

audience, some images may be deemed simply too complex for some (or all?) audiences, yet by simply integrating diets and parameter values amongst different components of the model, considerably "simpler" visual representations can be generated. In Figure 2.8 the degree of model complexity is substantially reduced, such that model detail is collapsed into generalized guilds (such as all rockfish, flatfish, roundfish, marine mammals, seabirds and fisheries). Additionally, minor flows (less than 5% of total consumption) are excluded. The result is an image in which the level of detail and complexity is considerably lower.

Another useful application of the visualization is focusing on specific elements of the food web relative to the entire (modeled) system. The software allows considerable flexibility in including or excluding various components of the model, choosing a range of color or color schemes, setting maximum and minimum box and flux sizes, and evaluating the flux of key prey items relative to others through the use of color. The scale and the pathways in this model generally revolve around the traditional, single species view for commercially important species and top-level predators, as the model is structured around integrating the results of stock assessments and surveys into an interconnected food web. Figure 2.9 is an example, illustrating the importance of euphausiids as one of the most important vehicles for the movement of energy (as represented by biomass) through this ecosystem. Here, energy derived from euphausiids is colored in red while energy from other sources (benthic production, copepods and other zooplankton) is colored in blue. The amount of red in the boxes of higher trophic levels indicates the percentage of energy originating (directly or indirectly) from euphausiids as opposed to other intermediate sources. This clearly illustrates the key role that euphausiids play in the NCC, particularly to commercially important species in this ecosystem. Similarly, Figure 2.10 shows the important interactions between Pacific hake and the ecosystem, in which only flows to and from hake are highlighted.

One of the features built into the Ecopath software is the evaluation of mixed trophic impact, which allows the user to evaluate the potential top-down and bottom-up control between species and assemblages (Christensen et al. 2000). The principles are derived from those of Leontief (1951) who developed simple matrix methods to derive direct and indirect interactions in the U.S. economy by evaluating the impacts of small changes (increase or decrease) in the demand for some sectors of the economy onto others. Ecopath uses a modification of Leontief's methods developed by Ulanowicz and Puccia (1990) in which the mixed trophic impact (MTI) of group i on group j is equal to the proportion (unitless) j contributes to the diet of i (DC_{ij}) and the proportion of predation on j that is due to i as a predator (FC_{ji}), such that

Equation 2.5: $$MTI_{ij} = DC_{ij} - FC_{ji}$$

Figure 2.11 presents the results of this matrix for the (simplified) NCC model in a format similar to Aydin et al. (2002). The results for each pairwise interaction are shown on a grid with the effect of the impacting species or group (left-hand column) on the impacted species or group (top) as circles, in which the area of the circle corresponds to the magnitude of the impact (black positive, white negative) on the impacted group. The diagonal running from the upper left-hand corner to the lower right-hand corner represents the density-dependent impact of an increase in biomass of a group on itself. The circles above this diagonal tend to represent the relationship between lower trophic levels on higher trophic levels, such that increases in lower trophic levels tend to be beneficial to higher trophic levels (bottom-up effects), the circles below the diagonal tend to represent the converse (top-down effects). The bars along the left and top of the figure are the sums of the absolute values of each impact value in the respective row or column, and represent a unitless measure of the overall impact (positive or negative) that a given group either has (left) or is subject to (top) by all other species or groups in the system.

Thus we see that increasing the biomass of phytoplankton or detritus (top two rows) has positive impacts on nearly all groups in the system, while increasing marine mammals or fishing (bottom rows) tends to have negative impacts on higher trophic level fishes (salmon, groundfish). In terms of overall roles, the higher trophic level groups producing the most impact (left hand bars) include forage fish, hake, toothed whales and fishing. The substantial effect of toothed whales on pinnipeds and baleen whales reflects the fact that orcas have been included in this group and prey upon pinnipeds and baleen whales (as well as smaller toothed whales). Interestingly, we can also see that Pacific hake seem to have negative impacts on all groups modeled here (with the exception of fisheries), through their role as either a predator or competitor with nearly every element of the food web. This may be a reasonable interpretation of the role of hake in this system, which are predators of nearly every group below them, and are the major competitors with nearly all higher trophic level predators for euphausiids, forage fish and other prey. One can also envision cascading impacts in some scenarios, for example the positive impacts of fishing on some lower trophic level groups (forage fish, cephalopods, small flatfish) and consequently the (unfished) competitors of fished species for such forage groups (seabirds), although few examples of such cascades seem to be present here.

2.7 Potential Metrics of Ecosystem Health

In discussing the problems of defining overfishing from an ecosystem perspective, Murawski (2000) makes reference to former U.S. Supreme Court Justice Potter Stewart’s classic writing of “obscenity”, in which Stewart suggests that while difficult to define, “I know it when I see it.” The analogy is appropriate, as Murawski suggests, for despite increasing calls to derive indices or metrics of “ecosystem health” for management (NRC 1999a, EPAP 1999), identifying “unambiguous, quantifiable and predictive measures of ecosystem state and flux” has proven extremely difficult. That such a challenge continues to exist is not for lack of trying, as there has been a long history in the measure and development of either “healthy” or “unhealthy” ecosystem states, and their potential role as targets, limits, indicators or simply descriptive metrics of ecosystem characteristics. Yet most attempts have focused on reductionist quantitative measures of often overwhelming complexity, and as such may fail to pack the visual punch that Stewart found necessary to make such a determination. One of the most oft-cited requirements of ecosystem metrics is that they characterize the effects of fishing relative to standing biomass and productivity (EPAP 1999, Murawski 2000), qualities that are (in theory) both unambiguous and quantifiable although in practice extremely difficult to assess with meaningful reliability. Ecosystem models may provide the best available information regarding these qualities from a perspective broader than a single species. Moreover, a comparative evaluation of similar qualities across ecosystems may be revealing in the context of patterns of productivity and standing stocks across a range of different systems.

This is by no means meant to infer that ecosystem models are the only potential source of meaningful environmental or ecosystem metrics. In fact they represent a primary source for one of several likely “families” of ecological metrics or indicators (Rice 2000). One way to “group” different ecosystem metrics into a hierarchy of metric types, would be to consider the following general classes of metrics. The most often used metrics are single species metrics such as standing and spawning biomass (usually relative to unfished or reference era conditions), recruitment indices, run size forecasts, landings, bycatch rates and fishing mortality rates. These statistics are the bread and butter of contemporary fisheries management, where the general philosophy is to protect the “key players” (and the most economically significant elements) in an ecosystem. Another class of metrics might characterize the “ecological resilience” view of ecosystems. These might include the status of top-predator or indicator species, indices of biological or genetic diversity, indices of habitat quality, or levels of toxins in the abiotic and biotic environment. Such indicators are intended to represent ecological integrity and diversity, although consensus remains to be found when attempting to quantify values, limits, thresholds and levels of biodiversity or community structure that might be desirable.[12] A third class of indicators might be physical indicators of environmental conditions; an example might be the moving average of sea surface temperature incorporated directly into harvest rules for management for Pacific sardine.

A fourth class of metrics is those that are produced or inferred by ecosystem models, and will be discussed here. These include metrics and indicators that quantify energy pathways, flows and productivity scaled to both the overall productivity of the ecosystem and the relative impacts of fishing on various functional components of the food web.[13] One of the simplest energy-based metrics is the average trophic level of the catch, as a potential indicator of shifts in community and ecosystem structure. Pauly et al. (1998) evaluated this particular theme on a global scale by demonstrating that changes in community composition and trophic webs, as indicated by global fisheries landings data and simplified ecosystem models, may be resulting in a phenomena they called fishing down marine food webs. They documented an apparent decline in the average trophic level of catches of about 0.1 per decade, with little concurrent increase in total landings. North Atlantic fisheries appeared to show the most consistent downward trend, while Southern Atlantic and most Pacific fisheries showed a range of trends, from highly variable to relatively stable to increasing. Tropical pelagic and upwelling systems tended to be the most variable. May et al. (1979) had much earlier observed that such trends may be undesirable for a variety of both ecological and

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[12] For example, Bianchi et al. (2000) evaluated demersal fish community properties in several large marine ecosystems, and showed that the size structure of such communities is significantly affected by fishing, but they were unable to suggest what an “optimum” size distribution might be or precisely how to integrate such information into management goals and objectives.

[13] A fifth class of metrics might also be considered, one in which multivariate techniques are used to integrate a wide range of empirical indicators representing all of the above families (single-species, economic, diversity, physical, and biomass or energy based) to assess dominant trajectories and trends across a range of ecosystem characteristics (Link et al. 2002).

economic reasons, particularly as “relatively large yields of stocks low on the trophic ladder usually require that their predators be driven to low levels.”[14]

The mean trophic levels of catch in the Eastern Bering Sea, Aleutian Islands and Gulf of Alaska fisheries have for several years been regularly reported in the North Pacific Fishery Management Council’s Ecosystem Considerations Chapter (NPFMC 2002), as part of the annual stock assessment and fisheries evaluation report. The trophic level of the catch is generally thought to have been relatively constant over the last several decades in these regions, however this should not be meant as a lack of evidence in community composition. For example, in west coast rockfish communities, MacCall (2002a) cites evidence that as a result of selectively fishing larger, often piscivorous species such as bocaccio and yelloweye rockfish, many intensively fished regions have become substantially more populated by smaller, and less marketable, *Sebastes* species such as Puget sound, pygmy and squarespot rockfish.

Figure 2.12 shows the estimated mean trophic level of landings in the NCC over the last 46 years, both including and excluding landings of hake, which dominate the catch. Although there is a slight decline, particularly when the hake fishery began in the mid-1960s, the overall change is relatively small (from a mean of 3.58 between 1958 and 1962, to a mean of 3.49 between 1998 and 2002). There is a slightly greater dip in very recent years, as associated with declines in groundfish landings and the resurgence of a fishery for Pacific sardine off of Oregon. Given the historical importance of sardine in the region, this is difficult to fully construe as a negative indicator. In fact, if one were to look at the trophic level of the catch through the 20th century, one would probably observe an overall increase, associated with the collapse of the sardine fishery in the 1930s and 1940s and consequent development of trawl fisheries for (higher trophic level) groundfish and hake.

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[14] May et al. also concluded that while MSY was a useful concept for considering plausible species or stock behavior at higher trophic levels, it was considerably less appropriate for species or stocks that tended to have high predation rates or other strong interspecific interactions.

As mentioned earlier, there is a potential bias involved with estimating the mean trophic level of the catch over time using the snapshot approach, as a result of potential prey switching and changes in prey availability, as well as possible changes in trophic interactions resulting from the removal of older, larger individuals by fisheries. To evaluate the former requires frequent and abundant monitoring both of forage species and of predator habits, and such monitoring is not currently afforded in the NCC. However, we can at least consider the potential impacts of the latter for species in which clear ontogenetic shifts in food habits exist, and stock assessments provide us with estimates of numbers and size at age. Figure 2.13 shows the estimated trophic level by size class of five groundfish species (Pacific hake, shortspine thornyhead, sablefish, yellowtail rockfish and dover sole) for which stomach content data over a broad size range are reasonably abundant. These suggest clear shifts in trophic level with size, ranging over nearly a full trophic level from juveniles to larger, older adults for four of the five species evaluated. Dover sole, which feed primarily on benthic invertebrates showed no significant change, possibly a slight decline. Although studies have demonstrated that larger Dover sole feed on increasingly larger organisms as they grow, it is not clear whether larger prey items represent higher trophic levels in the benthos.

Figure 2.14 takes this concept to the next logical step, estimating the consequent impact of truncating size and age distributions on the trophic level of the stocks themselves. These estimates are extrapolated by stock assessment estimates of numbers at age and mean length at age for two stocks that have shown significant (>50%) declines in total biomass over the last 40 years. Here, the decline in the trophic levels of the stocks is moderate for shortspine thornyheads (approximately 0.08 TL over 40 years) and essentially without a trend (although variable) for sablefish. This simple analysis includes several unrealistic assumptions (such as constant prey availability, constant size at age over time, and constant consumption rates over a range of size classes), and as such would benefit from a more thorough bioenergetic examination. While these results generally support the notion that fisheries are altering the trophic position of some of the top-level predators in the ecosystem, the overall impact would appear to be modest. Moreover, in considering the trophic level results of this model, there is little evidence that the fisheries of the NCC are "fishing down the food web."

Trophic level is far from the only metric of interest in considering energy-based metrics of ecosystem condition. Odum (1969) presented landmark work on energy-based metrics, including a suite of 24 energy and life-history based ecosystem metrics that characterized the nature of ecosystem development and succession. Although Christensen (1995) used these metrics in an attempt to rank marine ecosystems with regard to their relative state of maturity, the vast majority of these metrics are heavily weighted towards characterizing the efficiency and function of lower trophic levels, which are typically those components of the model for which the least information exists. As a result, the values for many of these statistics change very little even in the face of extreme perturbation, and changes that do become apparent can rarely be attributed to ecological differences that might be supported by actual field estimates of abundance or productivity (as opposed to top-down model balances).[15] These observations lead one to generalize that such metrics, while ecologically meaningful and insightful under data or knowledge-rich conditions, are currently inadequate to produce "unambiguous and quantifiable" ecosystem properties. The data simply do not exist for most marine ecosystems to make such determinations.

Meaningful insights can be gained by evaluating simple statistics related to standing biomass and productivity of the middle and top of most food webs, particularly with regard to species of commercial interest. As an example, estimates of biomass, productivity and catches were compiled for ten important "guilds" of fishes from three

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[15] By starting with existing ecosystems, running them forward in the face of very little environmental change but high top-down (fishery-induced) mortality, and comparing these qualities between the two periods, there is often very little change between many of the estimated values. By contrast, in constructing ecosystems for different time periods, or including process error (or climate "noise" of either a red or a white variety) such statistics can change substantially over even short time periods.

large ecosystem models (the NCC, the Gulf of Alaska (GOA) and the Eastern Bering Sea (EBS)[16]) in order to scale the impact of fishing on biomass and productivity. The guilds are generally defined by taxonomy (although groups such as "benthic fishes" will aggregate production from a wide range of poorly defined or quantified taxa). For all three models, standing biomass is typically derived from stock assessment (where available), survey information (where stock assessments are not available) or top-down balances for high turnover species of commercial interest such as crustaceans (note that only crustaceans of significant commercial value were included here, principally pandalid shrimps and *Chionoecetes*, *Paralithodes* and *Cancer* sp. crabs). The results are shown as Figure 2.15, in which several patterns are immediately obvious. The first is that in all three of these systems, gadids are among the most important guilds in terms of standing biomass, and to a greater extent total production (pollock and cod in the EBS and GOA, hake in the NCC), followed by small flatfish and crustaceans. Most other guilds have moderate levels of abundance and productivity relative to these groups.

The second observation, somewhat related to the first, is that the general levels of productivity throughout most of these guilds is similar in all three of these systems. This is especially interesting given the very different physical habitats and climate forcing mechanisms that determine the nature, timing and variability in productivity in these diverse regions. Although all are located on the continental margins of the Northeast Pacific, each is very different with regard to physical characteristics and the nature and dynamics of physical forcing that drive primary and secondary production. The Eastern Bering Sea (EBS) is a broad, highly productive shallow-water shelf ecosystem, where physical processes are dominated by tidal mixing and (in winter) the growth and retreat of ice edge habitat. The Gulf of Alaska (GOA) is a region with a

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[16] Values for the EBS model were provided by K. Aydin based on a slightly revised version of the model documented in Aydin et al. (2002) and for the GOA from S. Gaichas (in press). Guilds were constructed and defined in conjunction with Aydin and Gaichas, and all estimates exclude biomass and production of juveniles in split pool groups.

narrow continental shelf peppered with gullies, canyons and other small-scale physical structures that lead to complex local physics; through all of this a strong, seasonal buoyancy-driven current drives coastal downwelling in most regions, interspersed with patchy areas of upwelling. Finally, the Northern California Current is a continental shelf and slope ecosystem where the narrow continental shelf is dominated by highly seasonal wind-driven upwelling system (and coastal jet) while the shelf break and slope physical conditions are driven principally by large-scale remote forcing vis-à-vis dynamics of the California Current.

The third observation is related to the differences that are immediately apparent after making the second observation. This is that the diversity of biomass and productivity, at least amongst these definitions of guilds, seems to be the greatest in the Gulf of Alaska, and the most concentrated in the Eastern Bering Sea. Although clearly not a measure of "biological diversity" in the true sense of the word, it does seem to suggest that the community structure and interactions between organisms in the Gulf of Alaska could be more complex than those in the Eastern Bering Sea or the Northern California Current. However, it must also be recognized that all of these results were generated for the 1990s time period. The abundance of roundfish, rockfish and large flatfish would have been significantly greater in all of these systems prior to the initiation of major fisheries, perhaps nowhere more so that the California Current where declines in groundfish have been the most extreme. Although it is extremely difficult to demonstrate, it is not difficult to imagine that a more evenly distributed community structure, even at this coarse level, might more adequately represent an unfished functional state of nature.

Given these results, it is relatively easy to take the next step and evaluate the amount of either standing biomass or new production removed by fisheries in these time periods. Figure 2.16 shows these estimates, in the same units and for the same guilds that were presented in Figure 2.15. Figure 2.17 shows the same estimates as a percentage of annual production and of standing stock. Note that these are comparative measures, and standing stock represents averages over several years as balanced by production and removals. Again, several patterns are immediately obvious. The first is the tremendous discrepancy between guilds regarding the percentage of standing stock removed versus the percentage of new productivity removed. Clearly, the species with low turnover rates tend to have greater proportions of new production removed by fisheries; even while acknowledging that these functional groups are aggregations of a wide range of life history types, it is clear that some functional groups are impacted considerably more than others. The second observation is the tremendous discrepancy between systems, where clearly fisheries in the Northern California Current were removing a disproportionately greater percentage of new production for most of the guilds shown here than either the Eastern Bering Sea or the Gulf of Alaska. As a simple rule of thumb, a fishing mortality rate of F=M would generally result in fisheries removing precisely half of a stock's new production at equilibrium, and a fishery at F_{msy} would generally remove slightly more than that for most life history types. However, despite there being (as of yet) no clear means with which to define what percentage of new production removed might be appropriate beyond familiar single-species reference points, the visual image that results from comparing the impact of fishing on these three ecosystems should suggest to most that the fisheries in the NCC are the least likely to be sustainable.

These simple comparisons provide an opportunity to evaluate the productivity of intensively versus lightly fished species and guilds, as well as compare the impacts of fishing between different ecosystems. However they do not necessarily address the overall scale of fisheries relative to the productivity of the entire ecosystem. In terrestrial systems, Vitousek (1986) showed that about 40% of potential net primary production is diverted into human uses such as food, agriculture, and industrial uses. Pauly and Christensen (1995) included in the output of Ecopath models a similar estimate of "primary production required" (PPR) to derive a similar index for marine ecosystems. The PPR concept is tied directly to the idea of "emergy," or "embodied energy," which was first described by Odum (1988) and expanded upon by Christensen (1995). It can be generalized by the principle that more production is necessary to support a unit of a predator (such as a sablefish or a marine mammal) than a planktivore (such as herring) due to the number of trophic pathways required to sustain each. Consequently, removals of the former have a greater energetic cost to the system in units of embodied energy. These differences can be accounted for in a routine derived by Ulanowitz (1995), in which the consumption by a species or group (or landings by a fishery) are multiplied by a transforming factor such that all flows (at all trophic levels) are expressed in a common currency scaled to the absolute level of production at the base of the food web.

Using these routines, existing (representative) models for various types of marine ecosystem and FAO data on global fisheries landings, Pauly et al. (1998) estimated that approximately 8% of the ocean's primary production was required to sustain global marine fisheries in the early 1990s. This value was significantly lower in open ocean gyres (~2%) and much higher for temperate water continental shelf ecosystems (ranging from 24 to 35%), an observation that raised questions in the authors' minds about the carrying capacity of coastal ecosystems relative to pelagic. Figure 2.18 presents estimates of PPR, in conjunction with estimates of total catches (landings and estimated discards) in metric tons per square kilometer from the EBS, GOA and NCC in the 1990s, and the NCC in the 1960s. Again, several features of interest are apparent. First, the figure suggests that total removals per unit area, and the percentage of production accounted for in those removals, is greater in the 1990s model of the NCC than in either the EBS or the GOA, where the latter systems are both considered among the most productive fishing grounds in U.S. waters. This suggests that it is in a large part the immense area of the Eastern Bering Sea coastal shelf that accounts for the tremendous productivity of its fisheries. More significantly, it also suggests that the relative impact of fisheries in the NCC ecosystem was on the order of twice that in either the EBS or the GOA.

The objectives of an ecosystem-based approach to fisheries management, and the utility of any metrics of ecosystem qualities that might be relevant to such an approach, is largely in allowing scientists, stakeholders, decision-makers and managers to recognize and acknowledge how marine systems are structured and how fisheries activities scale to the productivity of marine ecosystems. Certainly the quality of information used to parameterize these models varies considerably from species to species, and from system to system. Yet when constructed carefully, such models represent the best available scientific information regarding major trophic interactions and energy flows. As such, they should be valuable additions to the (often overwhelming) suite of information presented and available to those making management decisions. While these simple estimates have not yet attained a sophistication for which targets or thresholds could be defined, quantified and measured, they may serve a greater purpose by simply presenting graphic statements that a suite of reference points pooled together from many single assessments can less adequately relay.

2.8 Chapter Summary

This chapter, and the documentation included in Appendix A, records and discusses the quantification of ecosystem components, energy pathways and trophic interactions in the Northern California Current (NCC), using a mass balance modeling approach and the best available data on abundance, productivity and food habits for major ecosystem components. In balancing the model, insights were gained concerning the tremendous significance of hake as both a predator and competitor to other elements of the ecosystem, to potential bias in food habits sampling that overemphasizes the tight coupling of sablefish to longspine thornyheads, and to the relative roles of fisheries and top-predators as sources of mortality for long-lived and slow-growing groundfish. Particular emphasis was made on presenting insightful visual representations of ecosystem trophic structure and energy flow, and on using comparative evaluations of model outputs to scale the impacts of fishing on ecosystem structure and productivity.

The comparison of flows among various components of the ecosystem, and a concurrent analysis of the ecological "system-wide" cost of fishing are important visual and quantitative tools that allow managers and stakeholders to increasingly envision the role of fisheries in altering energy flow through marine ecosystems. Certainly the quality of information used to parameterize these models varies considerably from species to species, and from system to system. Yet when constructed carefully, such models represent the best available scientific information regarding major trophic interactions and energy flows. As such, they should be valuable additions to the (often overwhelming) suite of information presented and available those making management decisions. Although many metrics would suggests that NCC groundfish harvests during the 1980s and 1990s were substantially greater than the productivity of the resources, one could consider whether these model results and statistics might have made a difference to managers, had they been available to complement single-species information in 1990. Would managers and stakeholders have found themselves compelled to grasp the disconnect between harvests and productivity when faced with system-wide indices and images that integrated information across a wide range of stocks? Given an opportunity to visualize the relative impact of fishing on the Northern California Current ecosystem, especially when contrasted against the impacts of fisheries of ostensibly a similar magnitude in more northern waters, would the Pacific Council have recognized ecosystem overfishing when they saw it?

Table 2.1: Total area of the Northern California Current (in square kilometers) by depth strata (in meters) and INPFC area.

	all depths	0-55	55-183	184-366	367-1280
US Vancouver	9490	2054	3518	1181	2737
Columbia	39408	6260	15642	4025	13481
Eureka	20279	7269	4091	1076	7843
All Areas	69176	15582	23251	6282	24061

Table 2.2: Parameter values for the 1960s NCC Ecopath model.

Group name	Trophic level	Biomass (t/km^2)	Production/ Biomass	Consumption/ Biomass	Ecotrophic efficiency	Production/ consumption	Total catches	Accumulation (t/km^2/year)
phytoplankton	1.0	55.150	120.00	-	0.43	-	0.000	0.000
infauna	2.0	35.700	2.50	12.00	0.89	0.21	0.000	0.000
amphipods	2.0	4.380	3.50	22.00	0.80	0.16	0.000	0.000
epibenthic	2.5	12.564	2.00	10.00	0.80	0.20	0.012	0.000
micro-zoop	2.0	3.947	100.00	300.00	0.80	0.33	0.000	0.000
copepods	2.2	16.609	14.00	70.00	0.80	0.20	0.034	0.000
euphausiids	2.1	27.037	8.00	40.00	0.80	0.20	0.000	0.000
carniv-zoops	3.1	7.731	2.00	10.00	0.80	0.20	0.158	0.000
small jellies	2.3	1.342	9.00	30.00	0.80	0.30	0.000	0.000
large jellies	3.2	1.168	3.00	12.00	0.80	0.25	0.000	0.000
pandalid shp	2.8	1.518	2.00	10.00	0.80	0.20	0.000	0.000
benthic shp	3.0	1.608	2.50	12.00	0.80	0.21	0.000	0.000
dungeness	3.5	0.843	0.75	3.80	0.71	0.20	0.000	0.000
tanner crb	3.0	0.975	0.30	1.50	0.80	0.20	0.000	0.000
cephalopods	3.6	2.059	2.00	6.00	0.80	0.33	0.000	0.000
forage fish	3.2	27.101	1.50	6.00	0.80	0.25	0.004	0.000
mesopelagics	3.2	7.575	0.60	3.00	0.80	0.20	0.000	0.000
benthic fish	3.3	4.110	0.50	2.50	0.80	0.20	0.100	0.000
macrourids	3.7	0.468	0.20	1.00	0.38	0.20	0.000	0.000
sardine	2.8	0.663	0.50	5.00	0.80	0.10	0.000	0.000
mackerel	3.5	0.286	0.35	6.00	0.71	0.06	0.001	0.000
salmon	4.1	0.367	0.93	5.82	0.83	0.16	0.014	0.000
hake	3.6	25.990	0.23	2.50	0.58	0.09	0.141	0.000
skates	4.0	0.421	0.20	2.00	0.51	0.10	0.046	0.000
dogfish	4.1	1.000	0.20	2.50	0.17	0.08	0.028	0.000
sablefish	4.1	2.756	0.06	1.95	0.44	0.03	0.011	-0.008
juv rock	3.3	0.704	1.50	6.00	0.80	0.25	0.029	0.000
POP	3.3	1.217	0.07	2.00	0.77	0.04	0.000	-0.010
canary	3.2	0.757	0.10	1.60	0.43	0.06	0.045	-0.006
widow	3.5	2.828	0.14	2.10	0.46	0.07	0.008	0.023
yellowtail	3.6	1.966	0.11	1.60	0.65	0.07	0.027	0.000
black	4.0	0.407	0.09	1.95	0.77	0.05	0.020	0.000
shelf rock	3.7	1.179	0.10	1.90	0.64	0.05	0.006	0.000
slope rock	3.3	0.864	0.06	1.45	0.86	0.04	0.025	0.000
ssthorny	4.0	0.751	0.07	0.45	0.74	0.14	0.017	0.000
lsthorny	3.7	1.800	0.05	0.35	0.89	0.14	0.003	0.000
juv thorny	3.4	0.714	0.50	2.50	0.80	0.20	0.009	0.000
juv round	3.2	0.247	1.50	5.13	0.80	0.29	0.000	0.000
lingcod	4.3	0.522	0.24	2.20	0.13	0.11	0.012	-0.007
juv flat	3.1	0.959	1.00	4.00	0.80	0.25	0.000	0.000
english	3.2	0.600	0.35	2.12	0.89	0.17	0.057	-0.019
petrale	4.1	0.326	0.28	2.00	0.52	0.14	0.032	-0.015
small flat	3.4	3.684	0.50	2.50	0.80	0.20	0.026	0.000
rex	3.1	0.400	0.50	2.12	0.84	0.24	0.020	-0.005
dover	3.1	3.861	0.08	1.10	0.42	0.07	0.093	-0.040
arrowtooth	4.3	0.321	0.34	2.12	0.47	0.16	0.027	0.000
halibut	4.3	0.089	0.34	2.12	0.51	0.16	0.003	-0.002
albacore	4.3	0.014	0.36	7.30	0.64	0.05	0.000	0.000
coastal sharks	4.4	0.050	0.18	2.80	0.47	0.06	0.000	0.000
shearwaters	4.2	0.003	0.100	138.00	0.00	0.00	0.000	0.000
murres	4.2	0.009	0.100	129.00	0.27	0.00	0.000	0.000
gulls	4.1	0.002	0.120	122.00	0.00	0.00	0.000	0.000
orcas	5.0	0.001	0.020	11.15	0.00	0.00	0.000	0.000
toothed whales	4.4	0.052	0.070	28.85	0.09	0.00	0.000	0.000
sperm whales	4.7	0.037	0.020	6.61	0.55	0.00	0.000	0.000
harbor seals	4.4	0.004	0.084	17.44	0.70	0.01	0.000	0.001
sea lions	4.5	0.012	0.074	16.38	0.67	0.01	0.000	0.001
fur seals	4.5	0.006	0.091	39.03	0.80	0.00	0.000	0.000
grey whales	3.0	0.008	0.037	8.87	0.54	0.00	0.000	0.000
baleen whales	3.6	0.075	0.037	7.58	0.95	0.01	0.000	0.003
fishery offal	1.0	1.0	10.000	-	-	0.02	-	0.000
pelagic detritu	1.0	1.0	10.000	-	-	0.09	-	0.000
benthic detritus	1.0	1.0	10.000	-	-	1.09	-	1.000

Table 2.3: Parameter values for the 1990s NCC Ecopath model.

Group name	Trophic level	Biomass (t/km²)	Production/ Biomass	Consumption/ Biomass	Ecotrophic efficiency	Production/ consumption	Total catches	Accumulation (t/km²/year)
phytoplankton	1.0	55.150	120.00	-	0.40	-	0.000	0.000
infauna	2.0	35.700	2.50	12.0	0.84	0.21	0.000	0.000
amphipods	2.0	4.276	3.50	22.0	0.80	0.16	0.000	0.000
epibenthic	2.5	12.091	2.00	10.0	0.80	0.20	0.014	0.000
micro-zoop	2.0	3.693	100.00	300.0	0.80	0.33	0.000	0.000
copepods	2.2	15.614	14.00	70.0	0.80	0.20	0.000	0.000
euphausiids	2.1	25.238	8.00	40.0	0.80	0.20	0.000	0.000
carniv-zoops	3.1	7.136	2.00	10.0	0.80	0.20	0.000	0.000
small jellies	2.3	1.114	9.00	30.0	0.80	0.30	0.000	0.000
large jellies	3.2	1.035	3.00	12.0	0.80	0.25	0.004	0.000
pandalid shp	2.8	1.500	2.00	10.0	0.80	0.20	0.417	0.000
benthic shp	3.0	1.548	2.50	12.0	0.80	0.21	0.000	0.000
dungeness	3.5	1.028	0.75	3.8	0.64	0.20	0.180	0.000
tanner crb	3.0	0.761	0.30	1.5	0.80	0.20	0.000	0.000
cephalopods	3.6	1.954	2.00	6.0	0.80	0.33	0.001	0.000
forage fish	3.2	25.710	1.50	6.0	0.80	0.25	0.035	0.000
mesopelagics	3.2	6.550	0.60	3.0	0.80	0.20	0.000	0.000
benthic fish	3.3	3.706	0.50	2.5	0.80	0.20	0.000	0.000
macrourids	3.7	0.468	0.20	1.0	0.31	0.20	0.003	0.000
sardine	2.8	1.000	0.50	5.0	0.93	0.10	0.000	0.200
mackerel	3.5	1.780	0.35	6.0	0.15	0.06	0.000	0.000
salmon	4.1	0.418	0.93	5.8	0.73	0.16	0.104	0.000
hake	3.6	28.925	0.18	2.0	0.69	0.09	2.924	-2.900
skates	4.0	0.421	0.20	2.0	0.78	0.10	0.034	0.000
dogfish	4.1	1.000	0.20	2.5	0.39	0.08	0.028	0.000
sablefish	4.1	1.472	0.09	2.1	0.90	0.04	0.122	-0.040
juv rock	3.3	0.616	1.50	6.0	0.80	0.25	0.000	0.000
POP	3.3	0.298	0.08	2.1	0.72	0.04	0.021	-0.014
canary	3.2	0.214	0.11	1.7	0.78	0.07	0.038	-0.026
widow	3.5	1.486	0.16	2.2	0.43	0.07	0.122	-0.117
yellowtail	3.6	1.433	0.15	1.7	0.81	0.09	0.076	0.005
black	4.0	0.240	0.13	2.0	0.55	0.06	0.021	-0.018
shelf rock	3.7	0.828	0.13	2.2	0.66	0.06	0.059	-0.041
slope rock	3.3	0.585	0.06	1.9	0.86	0.03	0.037	-0.032
ssthorny	4.0	0.337	0.08	0.5	0.84	0.17	0.044	-0.023
lsthorny	3.7	1.720	0.06	0.4	0.89	0.16	0.052	0.000
juv thorny	3.4	0.414	0.50	2.5	0.80	0.20	0.000	0.000
juv round	3.2	0.234	1.50	5.1	0.80	0.29	0.000	0.000
lingcod	4.3	0.522	0.30	2.4	0.17	0.13	0.032	-0.020
juv flat	3.1	1.154	1.00	4.0	0.80	0.25	0.000	0.000
english	3.2	0.580	0.35	2.1	0.90	0.17	0.029	0.011
petrale	4.1	0.326	0.36	1.7	0.52	0.21	0.022	0.000
small flat	3.4	3.886	0.50	2.5	0.80	0.20	0.040	0.000
rex	3.1	0.400	0.50	2.1	0.82	0.24	0.009	0.006
dover	3.1	1.394	0.12	1.1	0.59	0.11	0.223	-0.072
arrowtooth	4.3	0.325	0.34	2.1	0.82	0.16	0.061	0.000
halibut	4.3	0.156	0.34	2.1	0.48	0.16	0.003	0.006
albacore	4.3	0.014	0.36	7.3	0.64	0.05	0.000	0.000
coastal sharks	4.4	0.050	0.18	2.8	0.49	0.06	0.000	0.000
shearwaters	4.2	0.003	0.100	138.0	0.00	0.00	0.000	0.000
murres	4.2	0.009	0.100	129.0	0.28	0.00	0.000	0.000
gulls	4.1	0.002	0.120	122.0	0.00	0.00	0.000	0.000
orcas	5.0	0.000	0.020	11.2	0.00	0.00	0.000	0.000
toothed whales	4.4	0.052	0.070	28.9	0.09	0.00	0.000	0.000
sperm whales	4.7	0.037	0.020	6.6	0.19	0.00	0.000	0.000
harbor seals	4.4	0.014	0.084	17.4	0.19	0.01	0.000	0.000
sea lions	4.5	0.038	0.074	16.4	0.22	0.01	0.000	0.001
fur seals	4.5	0.005	0.091	39.0	0.31	0.00	0.000	0.000
grey whales	3.0	0.033	0.037	8.9	0.14	0.00	0.000	0.000
baleen whales	3.6	0.160	0.037	7.6	0.22	0.01	0.000	0.001
fishery offal	1.0	10.000	-	-	0.02	-	0.000	
pelagic detritu	1.0	10.000	-	-	0.02	-	0.000	
benthic detritus	1.0	10.000	-	-	0.09	-	0.000	

Table 2.4a: Diet matrix for the first 20 components of the NCC 1960s model.

Prey \ Predator	infauna	amphipods	epibenthic	micro-zoop	copepods	euphausiids	carniv-zoops	small jellies	large jellies	pandalid shp	benthic shp	dungeness	tanner crb	cephalopods	forage fish	mesopelagics	benthic fish	macrourids	sardine	mackerel
phytoplankton	8	0.2		0.75	0.8	0.9	0.03	0.5											0.28	
infauna			0.43							0.25	0.4	0.4	0.792				0.3	0.15		
amphipods			0.02				0.02			0.02	0.04	0.025			0.01	0.03	0.18	0.05		0.01
epibenthic										0.05	0.4	0.2	0.118	0.009			0.4	0.15		
micro-zoop					0.2	0.05	0.03	0.25	0.03						0.1				0.02	
copepods						0.05	0.5		0.3	0.1				0.15	0.45	0.32			0.4	0.05
euphausiids							0.35		0.6	0.2				0.38	0.4	0.52			0.3	0.6
carniv-zoops									0.02	0.03				0.15	0.025	0.04				0.07
small jellies							0.05		0.05						0.01	0.045				
large jellies							0.02									0.02				0.01
pandalid shp														0.005			0.01	0.01		
benthic shp												0.2		0.005			0.04	0.04		
dungeness												0.005					0.005			
tanner crb																	0.002			
cephalopods												0.001		0.001	0.005	0.02	0.001	0.3		0.005
forage fish												0.1		0.2			0.01			0.2
mesopelagics														0.1		0.005		0.05		0.01
benthic fish												0.01						0.05		0.004
macrourids																				
sardine																				
mackerel																				
salmon																				0.001
hake																		0.05		
skates																				
dogfish																				
sablefish																				
juv rock												0.001					0.003			0.005
POP																				
canary																				
widow																				
yellowtail																				
black																				
shelf rock																				
slope rock																				
ssthorny																				
lsthorny																				
juv thorny																				
juv round												0.002					0.002			0.005
lingcod																				
juv flat											0.01	0.01					0.02			0.02
english																				
petrale																				
small flat												0.02					0.01			0.01
rex												0.001								
dover																				
arrowtooth																				
halibut																				
albacore																				
coastal sharks																				
shearwaters																				
murres																				
gulls																				
orcas																				
toothed whales																				
sperm whales																				
harbor seals																				
sea lions																				
fur seals																				
grey whales																				
baleen whales																				
fishery offal												0.02								
pelagic detritu		0.1		0.25				0.25												
benthic detritus	1	0.7	0.55							0.35	0.15	0.005	0.09				0.017	0.15		

Table 2.4b: Diet matrix for the second 20 components of the NCC 1960s model.

Prey \ Predator	salmon	hake	skates	dogfish	sablefish	juv rock	POP	canary	widow	yellowtail	black	shelf rock	slope rock	ssthorny	lsthorny	juv thorny	juv round	lingcod	juv flat	english
phytoplankton																				
infauna			0.02		0.02	0.009								0.05	0.16				0.575	0.34
amphipods	0.001		0.02		0.001	0.006	0.005	0.001	0.035	0.002	0.002	0.005	0.01	0.05	0.03		0.011		0.21	0.25
epibenthic		0.002	0.2	0.05	0.05	0.022	0.005			0.002	0.05	0.04	0.02	0.03	0.2			0.05	0.2	0.36
micro-zoop																				
copepods	0.001					0.39			0.002							0.2	0.818			0.04
euphausiids	0.1	0.575		0.2	0.06	0.44	0.78	0.92	0.3	0.55	0.1	0.35	0.8			0.5	0.123			
carniv-zoops	0.2	0.029			0.01	0.004	0.07	0.008	0.2	0.025	0.1	0.01	0.05	0.01		0.25	0.029			
small jellies	0.002				0.04	0.001		0.001	0.32	0.05	0.08			0.005	0.01	0.05				
large jellies	0.002			0.05	0.05				0.04	0.01	0.02		0.005							
pandalid shp		0.02	0.02	0.001	0.015	0.03	0.03	0.03	0.001	0.02	0.001	0.12	0.03	0.05	0.01			0.01		
benthic shp		0.007	0.2		0.002	0.075					0.042	0.01	0.01	0.15	0.25			0.01	0.015	0.005
dungeness			0.05	0.02	0.001						0.001							0.05		0.005
tanner crb			0.025		0.002	0.012								0.2	0.1					
cephalopods	0.01	0.005	0.01	0.005	0.05		0.03		0.005	0.025	0.01	0.005	0.015	0.025	0.05			0.15		
forage fish	0.612	0.324	0.05	0.2	0.25	0.004	0.01	0.02	0.015	0.2	0.5	0.25	0.04	0.02			0.019	0.105		
mesopelagics	0.002	0.016			0.03	0.004	0.06	0.02	0.035	0.05		0.1	0.02	0.02	0.1					
benthic fish	0.002	0.002	0.05	0.07	0.08	0.003	0.01			0.01	0.03	0.05		0.05	0.05			0.25		
macrourids					0.005									0.005						
sardine	0.01																			
mackerel																				
salmon					0.006						0.02									
hake	0.002	0.014	0.05	0.2	0.128				0.02	0.01				0.12				0.1		
skates					0.002															
dogfish																				
sablefish																				
juv rock	0.025	0.002		0.01	0.02				0.02	0.03	0.02	0.015		0.05	0.015			0.024		
POP				0.001	0.003									0.001						
canary				0.001	0.002							0.001						0.005		
widow				0.001	0.01							0.005						0.01		
yellowtail				0.001	0.01							0.003						0.01		
black												0.001						0.01		
shelf rock				0.001	0.003							0.001		0.002				0.01		
slope rock				0.001	0.001									0.002						
ssthorny					0.005															
lsthorny					0.01									0.05						
juv thorny					0.05									0.05						
juv round	0.01		0.02	0.01	0.025				0.002	0.002	0.004	0.004						0.004		
lingcod				0.001	0.001															
juv flat	0.01		0.05	0.02	0.003				0.002	0.002		0.005						0.022		
english			0.02	0.01	0.001						0.001	0.005						0.04		
petrale			0.005	0.005														0.01		
small flat	0.01	0.004	0.15	0.12	0.02				0.002	0.012	0.018	0.02		0.007	0.005			0.1		
rex	0.001	0.001	0.03	0.01	0.002				0.001		0.001			0.001				0.02		
dover			0.02	0.01	0.001									0.001				0.01		
arrowtooth			0.01	0.002										0.001						
halibut																				
albacore																				
coastal sharks																				
shearwaters																				
murres																				
gulls																				
orcas																				
toothed whales																				
sperm whales																				
harbor seals																				
sea lions																				
fur seals																				
grey whales																				
baleen whales																				
fishery offal					0.03									0.05						
pelagic detritu																				
benthic detritus					0.001										0.02					

Table 2.4c: Diet matrix for the last 19 components of the NCC 1960s model.

Prey \ Predator	petrale	small flat	rex	dover	arrowtooth	halibut	albacore	coastal sharks	shearwaters	murres	gulls	orcas	toothed whales	sperm whales	harbor seals	sea lions	fur seals	grey whales	baleen whales
phytoplankton																			
infauna		0.15	0.55	0.85	0.001	0.006												0.025	
amphipods	0.005	0.1	0.3	0.03	0.001													0.95	
epibenthic	0.15	0.38	0.12	0.1		0.05					0.01				0.02	0.01		0.025	
micro-zoop																			
copepods		0.08								0.01									0.01
euphausiids	0.005	0.1			0.04				0.03	0.01	0.01								0.5
carniv-zoops		0.02			0.001		0.1		0.015		0.01								0.005
small jellies			0.005																
large jellies		0.01							0.005										
pandalid shp	0.02	0.01		0.01	0.04	0.025													
benthic shp	0.25	0.06	0.02	0.01	0.002	0.025													
dungeness	0.005	0.005			0.002	0.025		0.005							0.025				
tanner crb						0.001													
cephalopods	0.005	0.005					0.25	0.01	0.1	0.03	0.17	0.1	0.2	0.65	0.05	0.2	0.3		0.035
forage fish	0.1	0.05			0.3	0.15	0.3	0.35	0.75	0.817	0.579	0.11	0.35		0.35	0.259	0.26		0.35
mesopelagics					0.004		0.2	0.025		0.01	0.02		0.07	0.05		0.02	0.024		
benthic fish	0.19	0.01				0.05		0.025		0.002			0.01		0.05	0.02	0.011		
macrourids														0.025					
sardine							0.05	0.05		0.001	0.001	0.005	0.05			0.01	0.01		0.09
mackerel							0.08	0.025				0.005	0.03			0.021	0.021		0.01
salmon						0.05		0.05		0.01	0.01	0.1	0.02		0.1	0.05	0.07		
hake					0.5	0.45		0.25					0.15	0.05	0.1	0.22	0.148		
skates								0.01				0.04	0.005	0.025		0.02			
dogfish								0.01				0.04	0.005	0.025		0.02			
sablefish						0.01						0.1	0.02	0.05		0.01	0.02		
juv rock					0.002		0.01		0.085	0.094	0.082					0.015			
POP					0.001	0.01		0.005				0.002		0.02		0.005	0.01		
canary					0.001	0.004		0.01				0.005	0.002	0.005	0.005	0.001	0.01		
widow					0.001	0.004	0.005	0.01				0.01	0.023	0.015	0.005	0.02	0.036		
yellowtail					0.002	0.01	0.005	0.01				0.01	0.015	0.02	0.015	0.02	0.03		
black								0.005				0.005	0.001		0.01	0.01			
shelf rock					0.002	0.008		0.015			0.001	0.005	0.003	0.01	0.01	0.015	0.02		
slope rock					0.001	0.002		0.005			0.001			0.02		0.005	0.02		
ssthorny														0.01					
lsthorny																			
juv thorny																			
juv round					0.002	0.01		0.005	0.015				0.01		0.005	0.005	0.01		
lingcod								0.01							0.02	0.01			
juv flat	0.01	0.01			0.01	0.01				0.008	0.005								
english	0.02				0.005	0.003		0.01					0.005		0.075	0.01			
petrale					0.002	0.002		0.002							0.01	0.002			
small flat	0.21		0.005		0.06	0.035		0.06		0.008	0.015		0.025		0.14	0.02			
rex	0.025				0.01	0.01		0.01											
dover	0.005				0.01	0.02		0.01					0.001			0.002			
arrowtooth						0.01		0.008				0.05	0.001		0.01				
halibut								0.01				0.05	0.001	0.025					
albacore								0.005				0.005	0.001						
coastal sharks												0.01	0.002						
shearwaters																			
murres											0.001								
gulls																			
orcas																			
toothed whales												0.14							
sperm whales												0.018							
harbor seals												0.003							
sea lions												0.037							
fur seals												0.06							
grey whales												0.03							
baleen whales												0.06							
fishery offal											0.085								
pelagic detritu																			
benthic detritus		0.01				0.02													

Table 2.5: Estimated sources of predation between key predator (top) and prey assemblages (side) in 1000s of metric tons in the 1960s model.

	crustaceans	pelagics	salmon	hake	groundfish	seabirds	mammals	fisheries
euphausiids	197	644	11	2268	427	2	22	0
benthic fauna	634	0	0	139	947	0	24	43
crustaceans	0	0	0	85	79	0	0	42
forage fish	26	127	44	1209	207	97	62	2
other nekton	14	44	18	218	372	22	56	0
cephalopods	0	19	4	24	44	8	48	0
pelagics	0	0	0	42	0	2	13	0
salmon	0	4	0	0	2	1	6	7
hake	0	0	0	60	81	0	30	205
elasmobrch	0	0	0	0	0	0	4	4
roundfish	0	0	0	0	3	0	5	11
rockfish	0	0	0	0	13	0	13	30
small flat	6	0	0	36	59	1	7	21
large flat	0	0	0	0	0	0	1	6

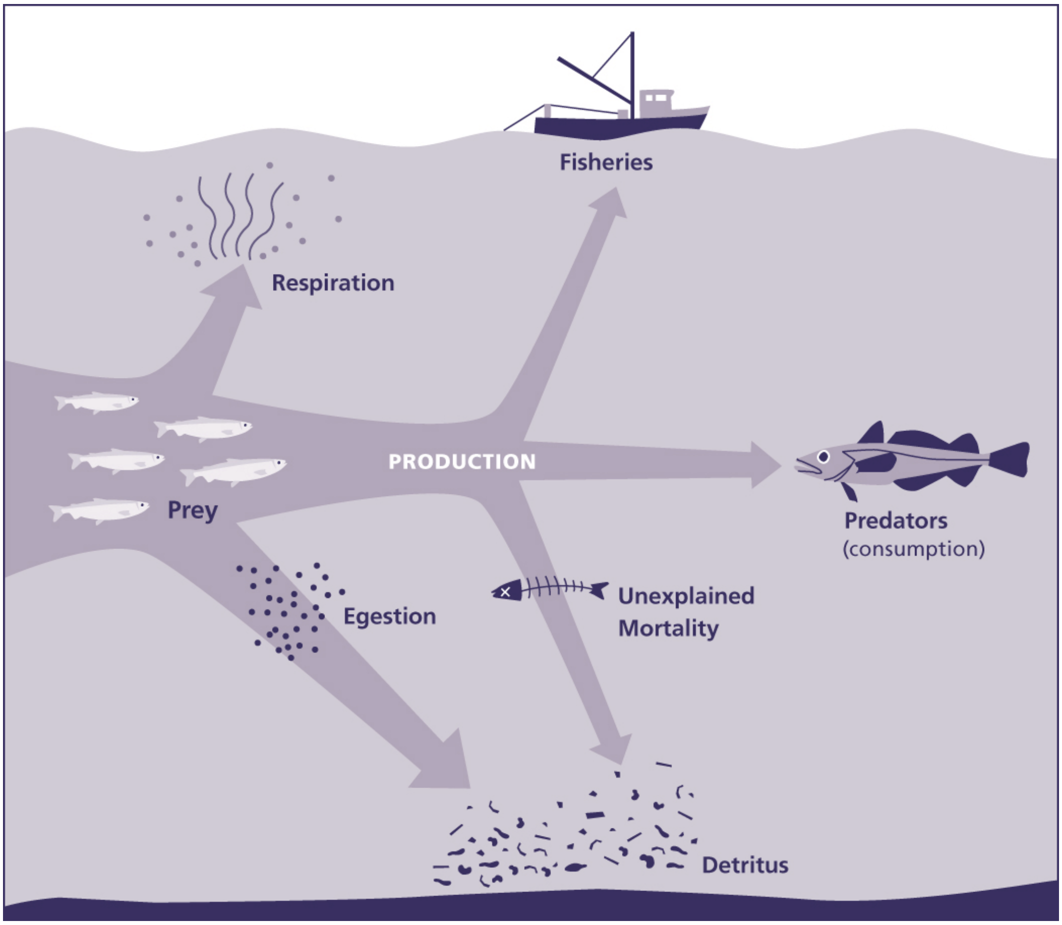

Figure 2.1: Graphic representation of the basic mass balance assumptions for Ecopath. Consumption is partitioned into respiration, egestion and new production. Production is partitioned into removals by fisheries, consumption by predators or unexplained mortality.

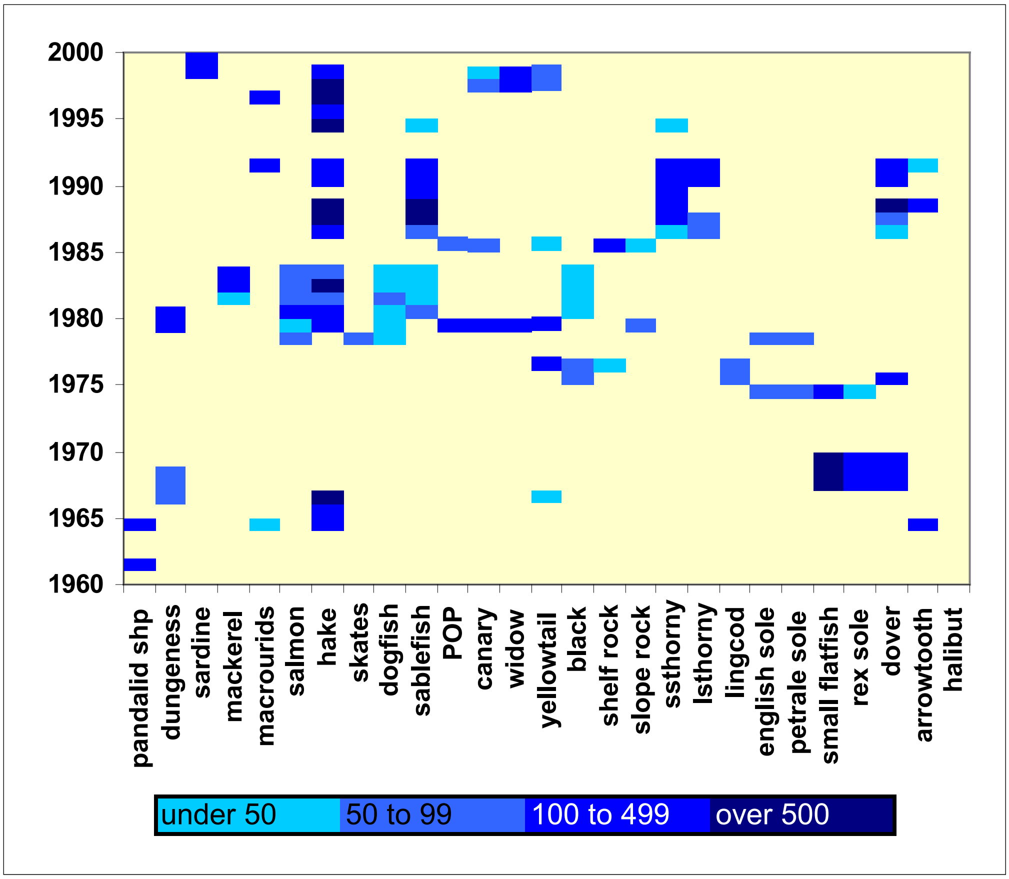

Figure 2.2: Approximate number and year of food habits data available for model groups

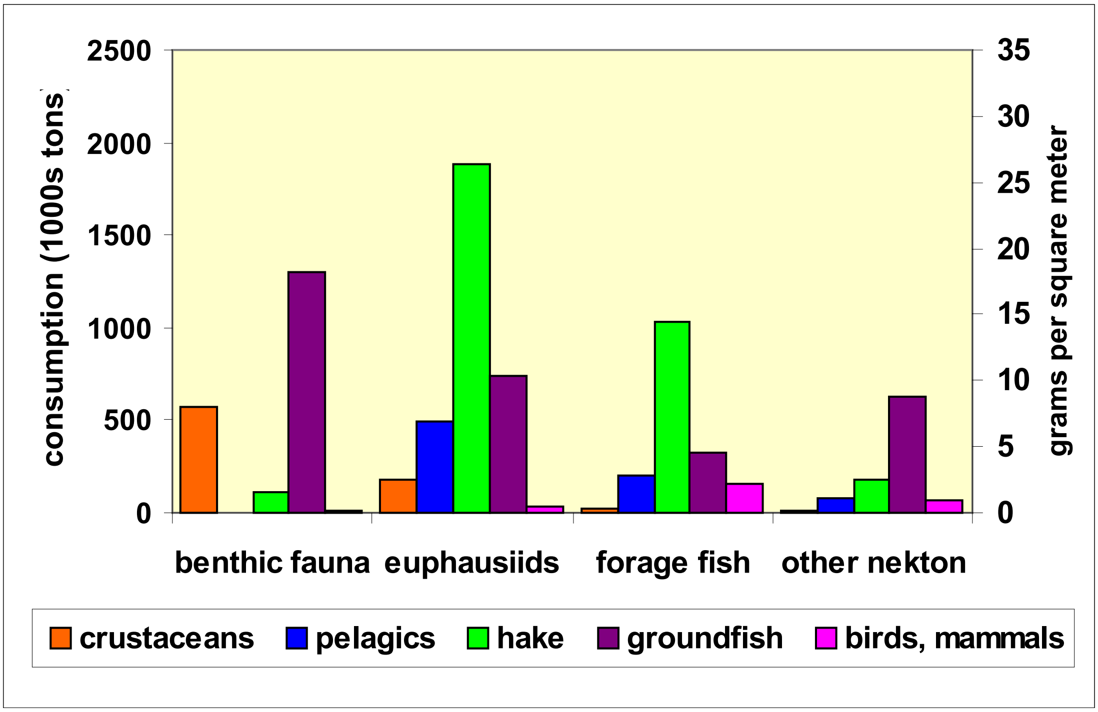

Figure 2.3: Estimated annual consumption of principal forage assemblages (benthic fauna, euphausiids, forage fish and other nekton such as cephalopods and mesopelagics) by generalized predator guilds (commercially important crustaceans, pelagics-including salmon, Pacific hake, groundfish and seabirds/marine mammals).

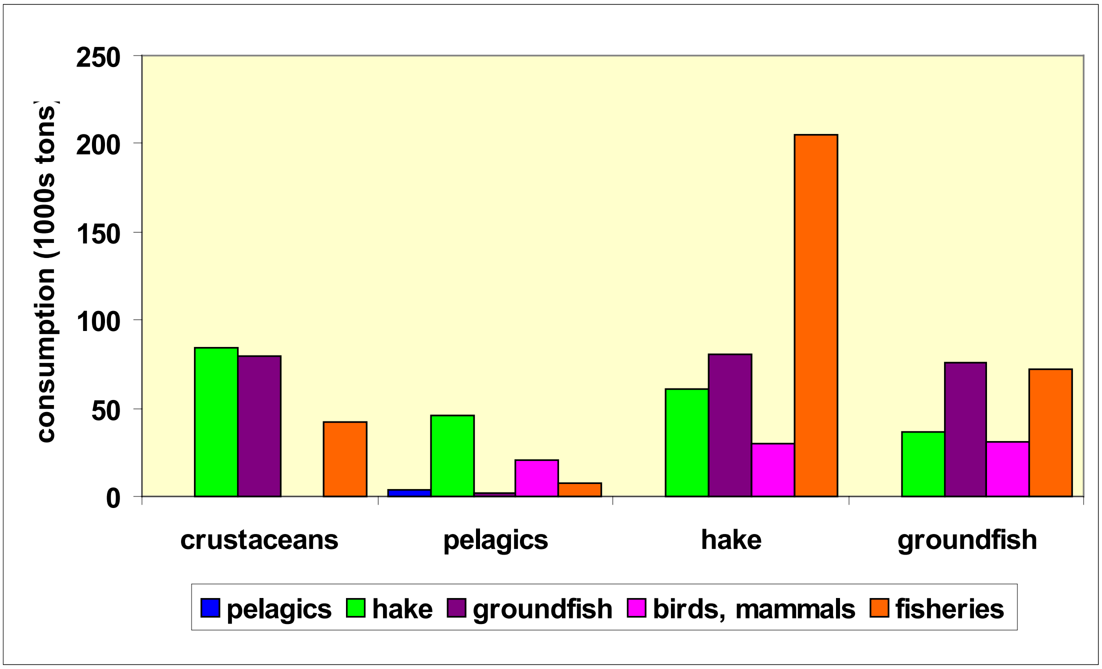

Figure 2.4: Estimated annual consumption of assemblages of commercial importance (commercially important crustaceans, pelagics-including salmon, Pacific hake, and groundfish) by generalized predator guilds (coastal pelagics, Pacific hake, groundfish, birds and mammals, and fisheries).

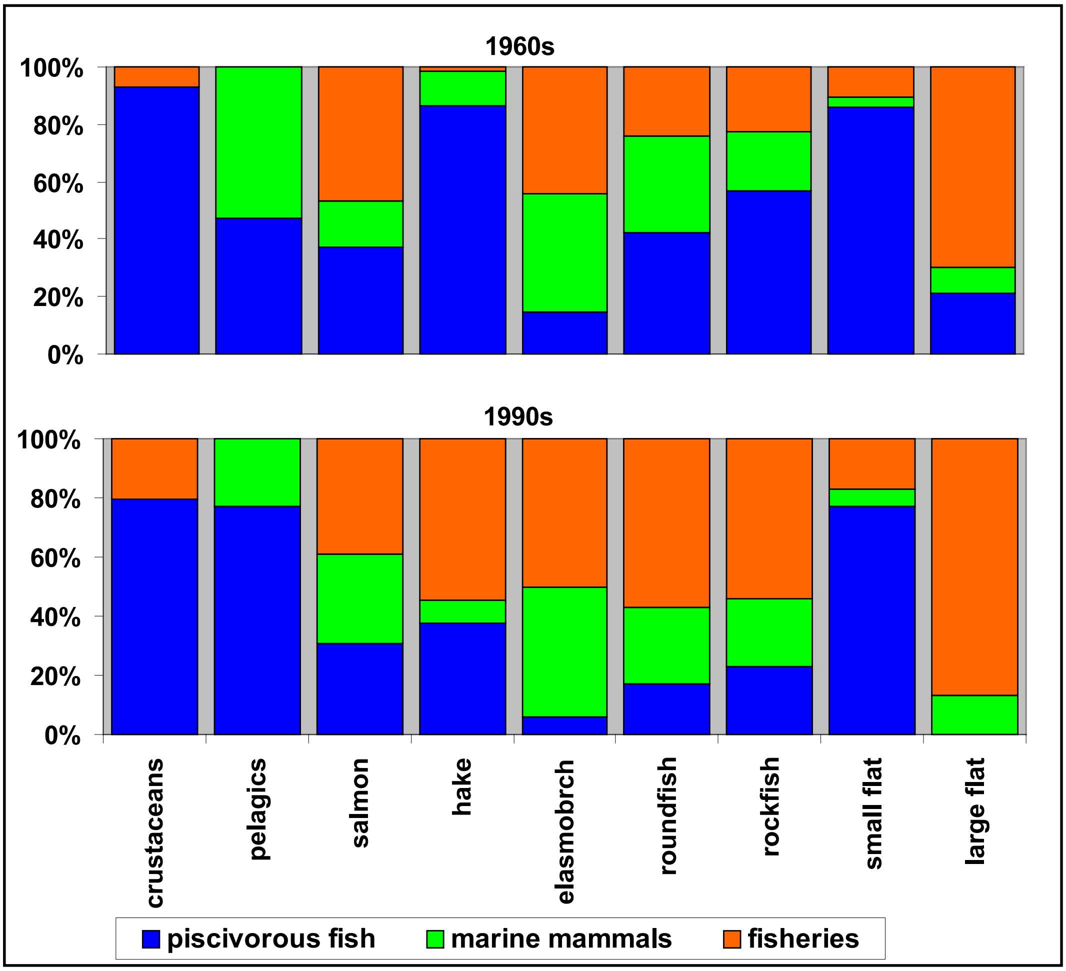

Figure 2.5: Principal sources of relative mortality for commercially important guilds in the 1960s (top) and 1990s (bottom).

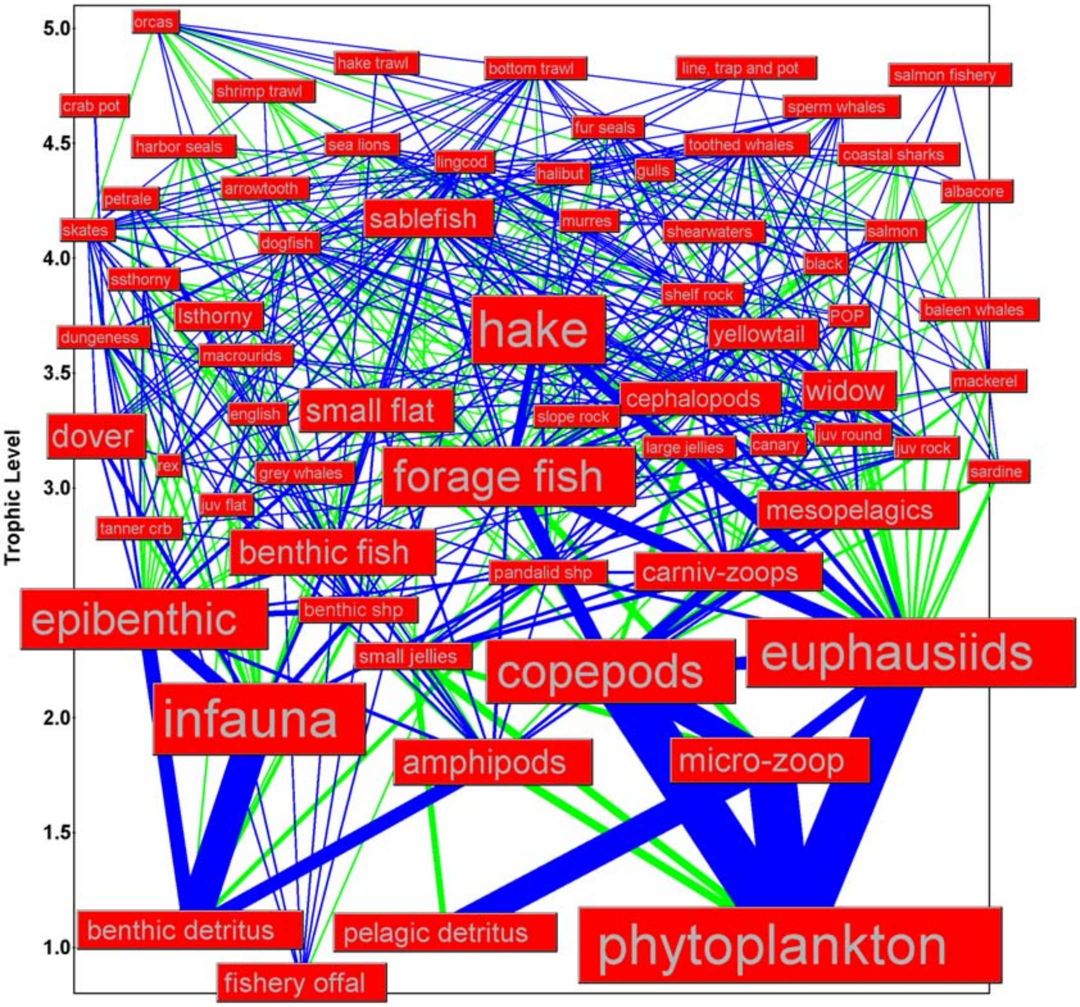

Figure 2.6: The significant food web of the Northern California Current.

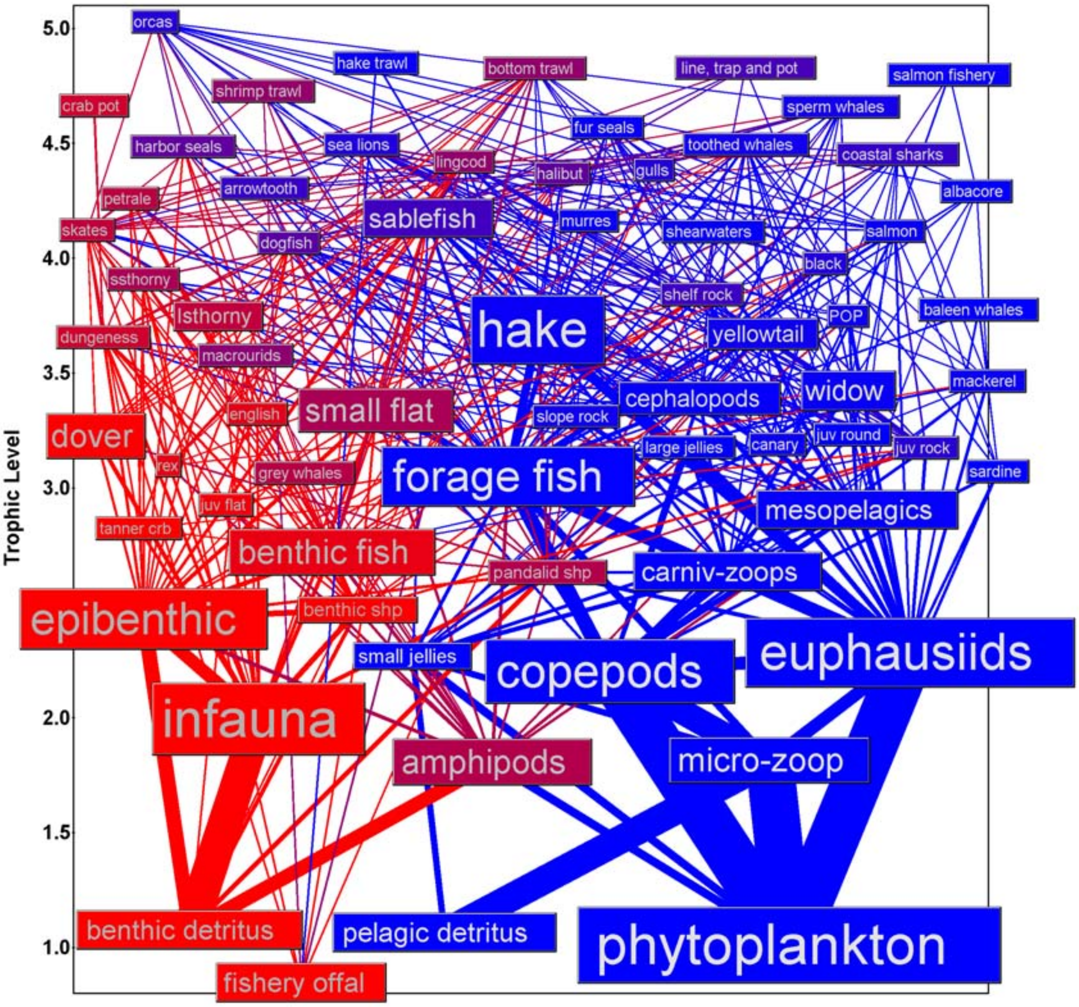

Figure 2.7: The significant food web of the Northern California Current, with blue representing pelagic energy pathways, and red benthic energy pathways.

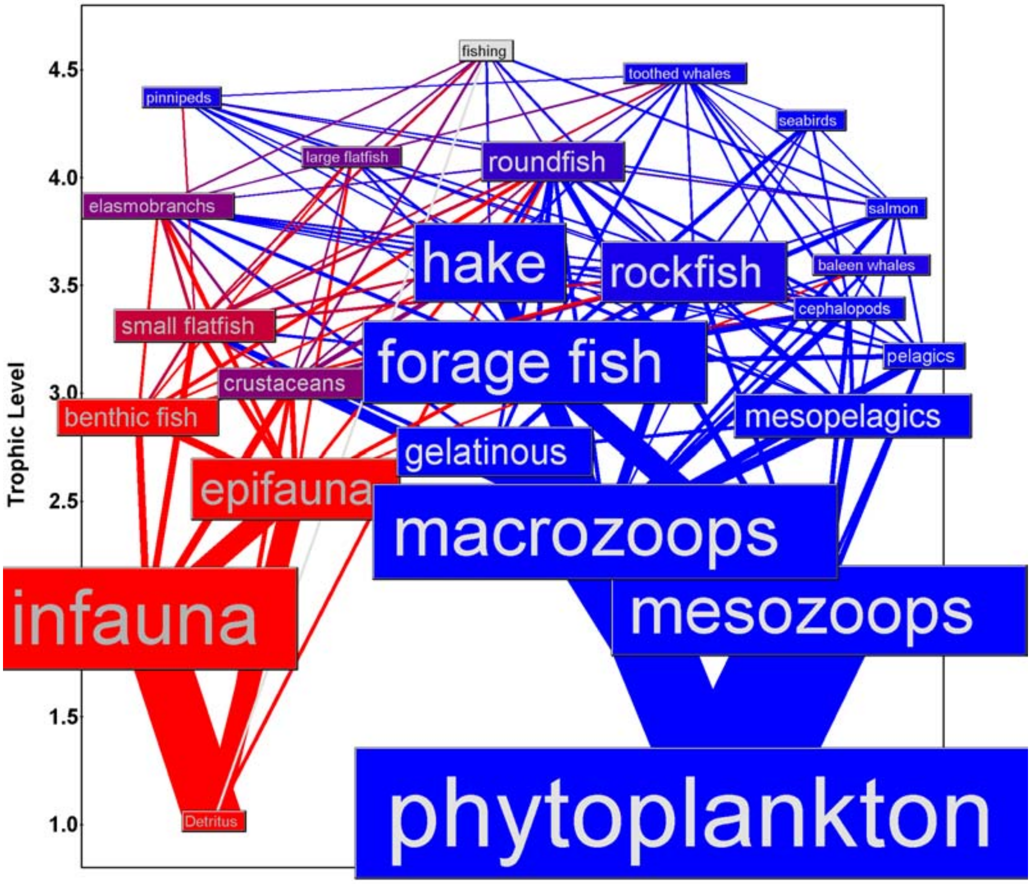

Figure 2.8: Simplified food web of the Northern California Current

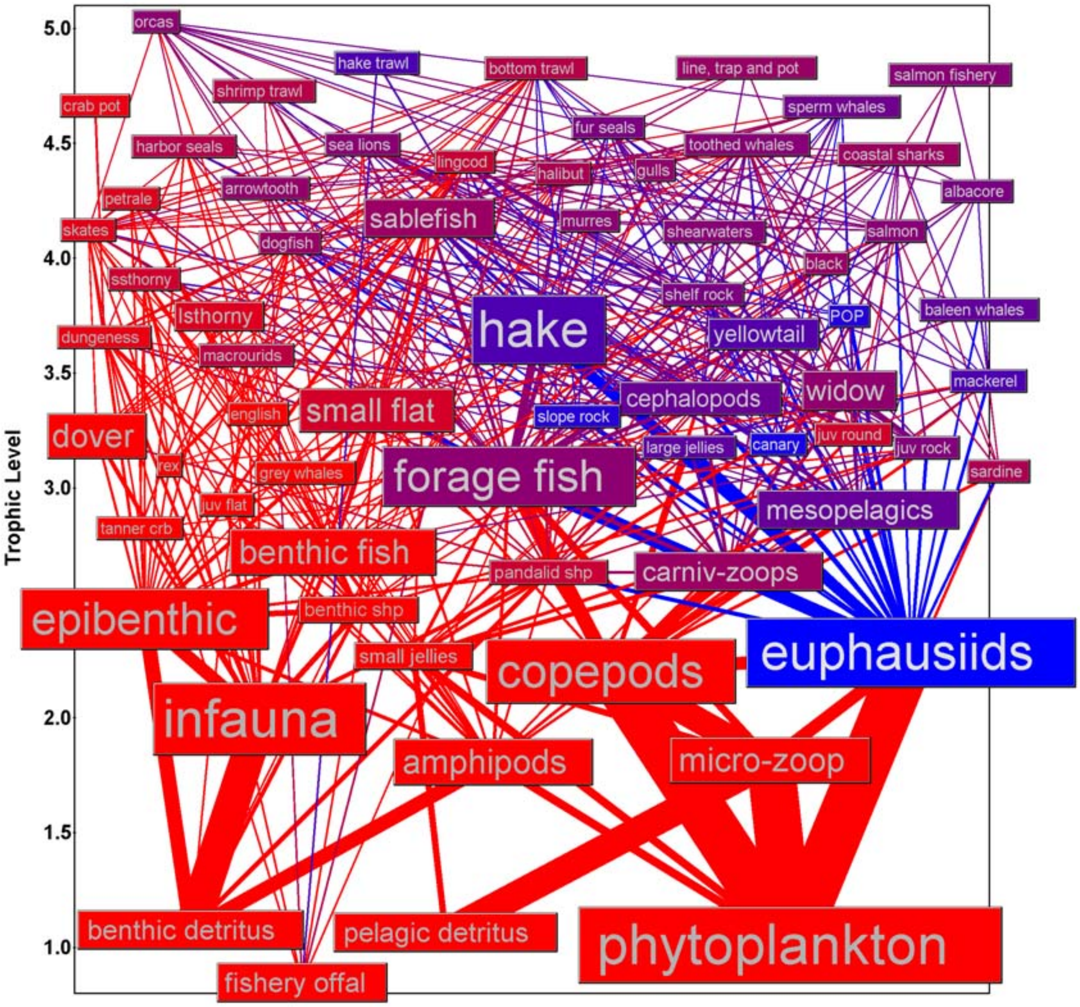

Figure 2.9: Dispersal of energy from euphausiids (in red) with respect to other intermediate energy sources in the Northern California Current.

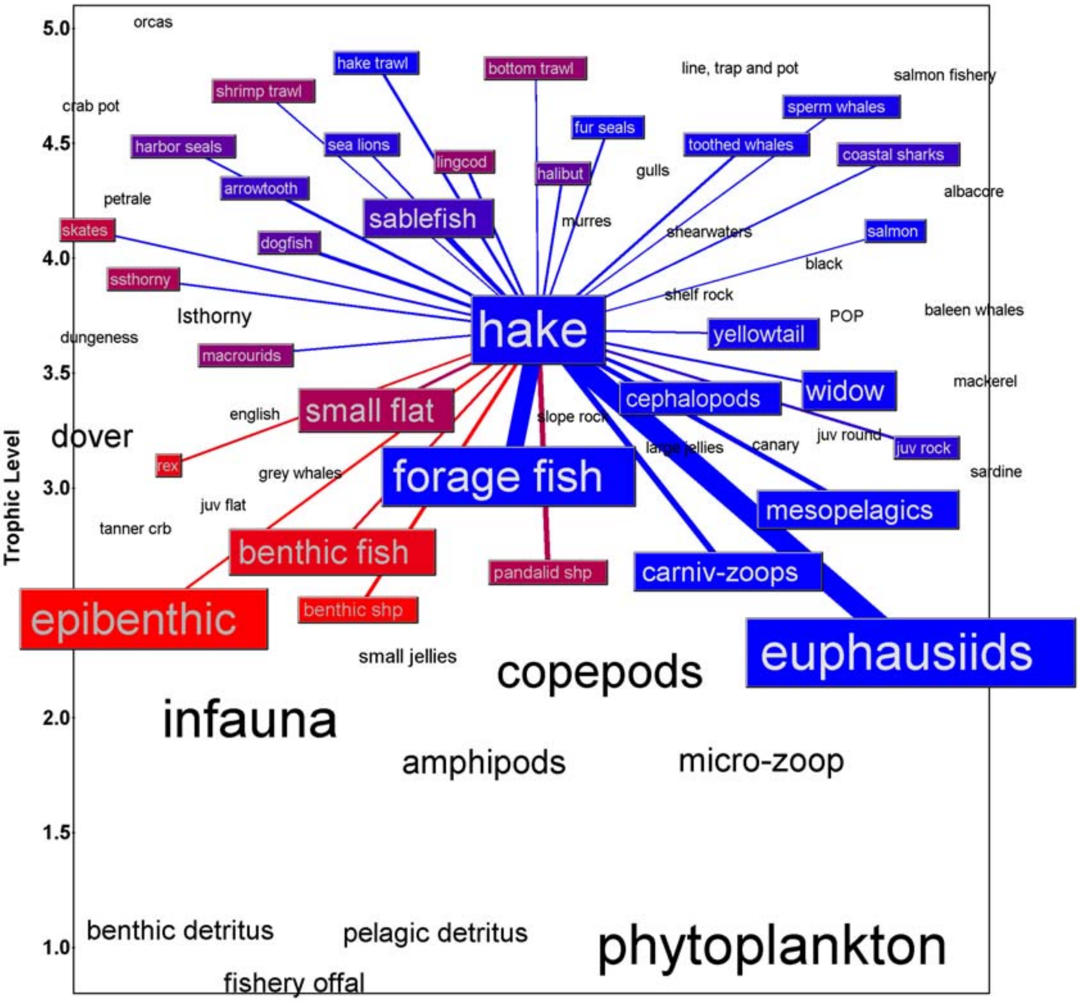

Figure 2.10: Isolated view of the trophic position of Pacific hake in the ecosystem relative to major prey (green flows) and predators (blue flows).

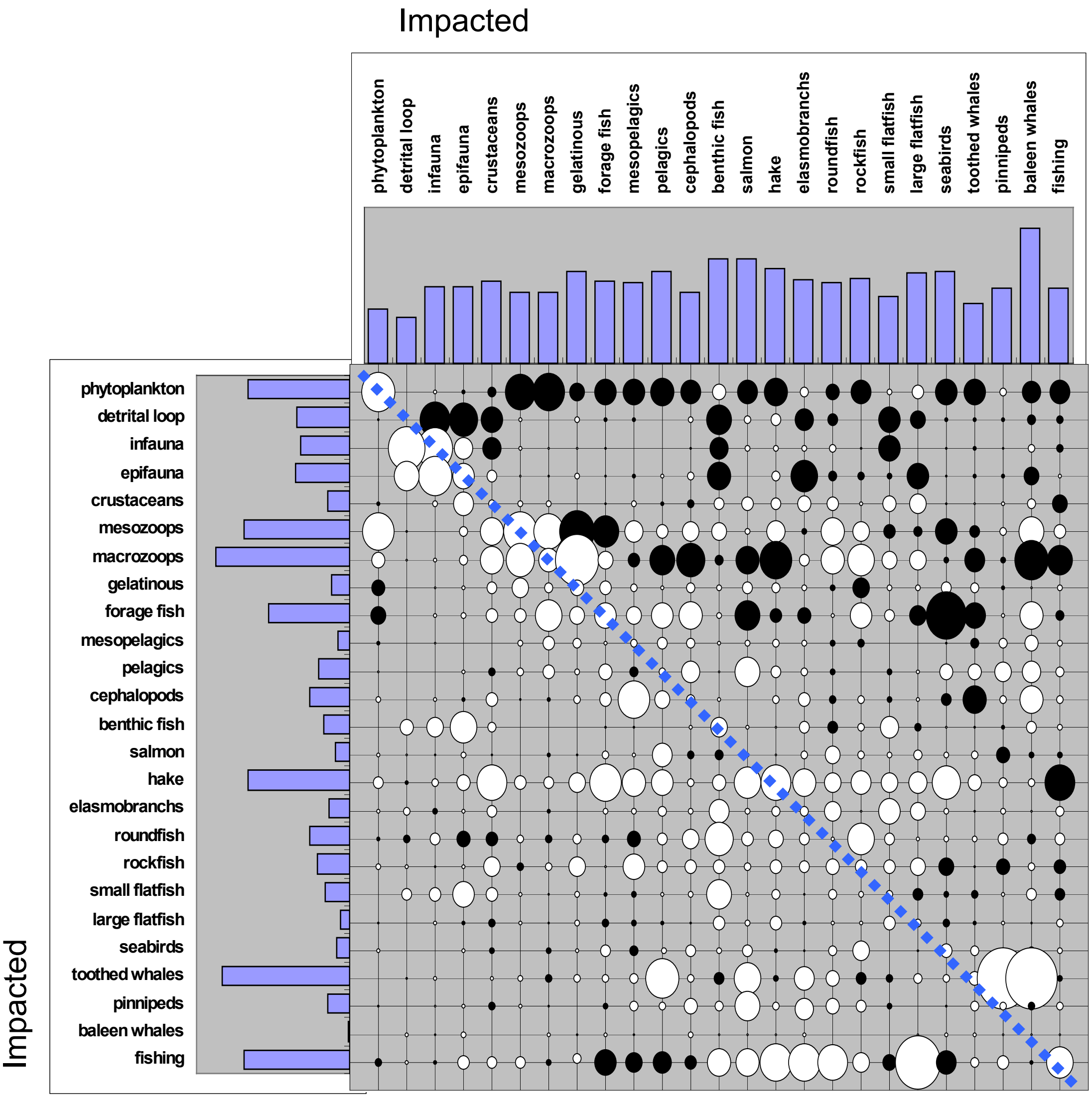

Figure 2.11: Trophic impact graph and indices for aggregated species assemblages in the 1990s NCC model. Impacting groups are on left, impacted groups are along top. The dashed line represents strict density-dependent effects (the effect of an increase in the abundance of an assemblage on itself).

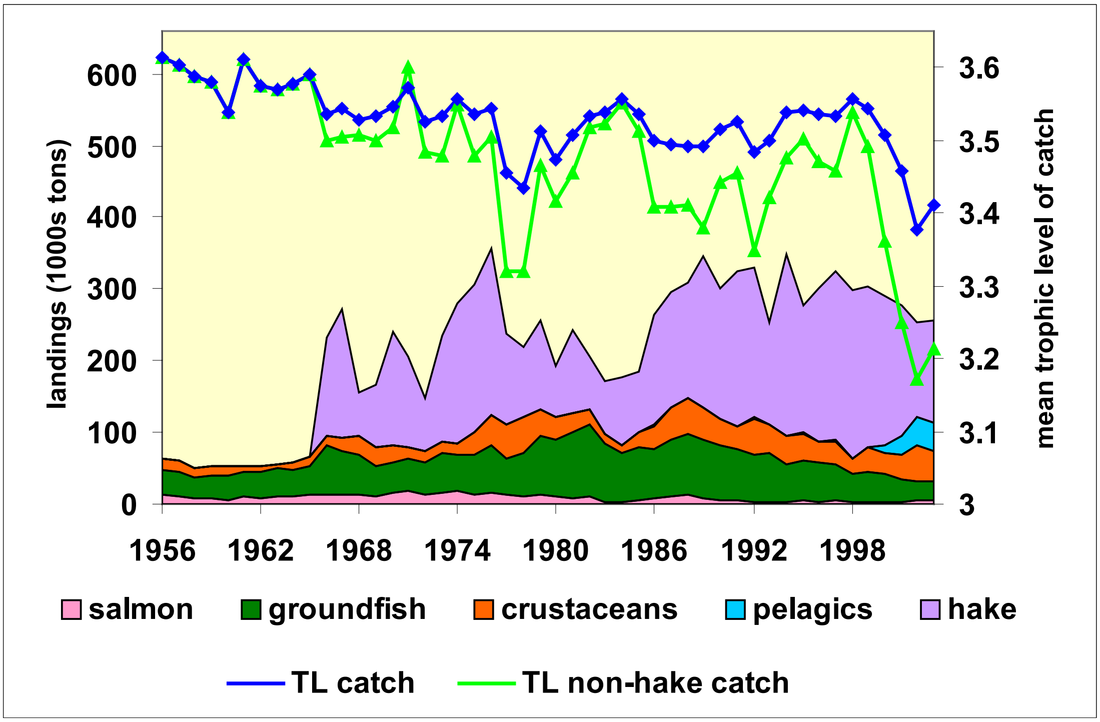

Figure 2.12: Landings and mean trophic level of the catch for the Northern California Current fisheries both with (blue) and without (green) hake.

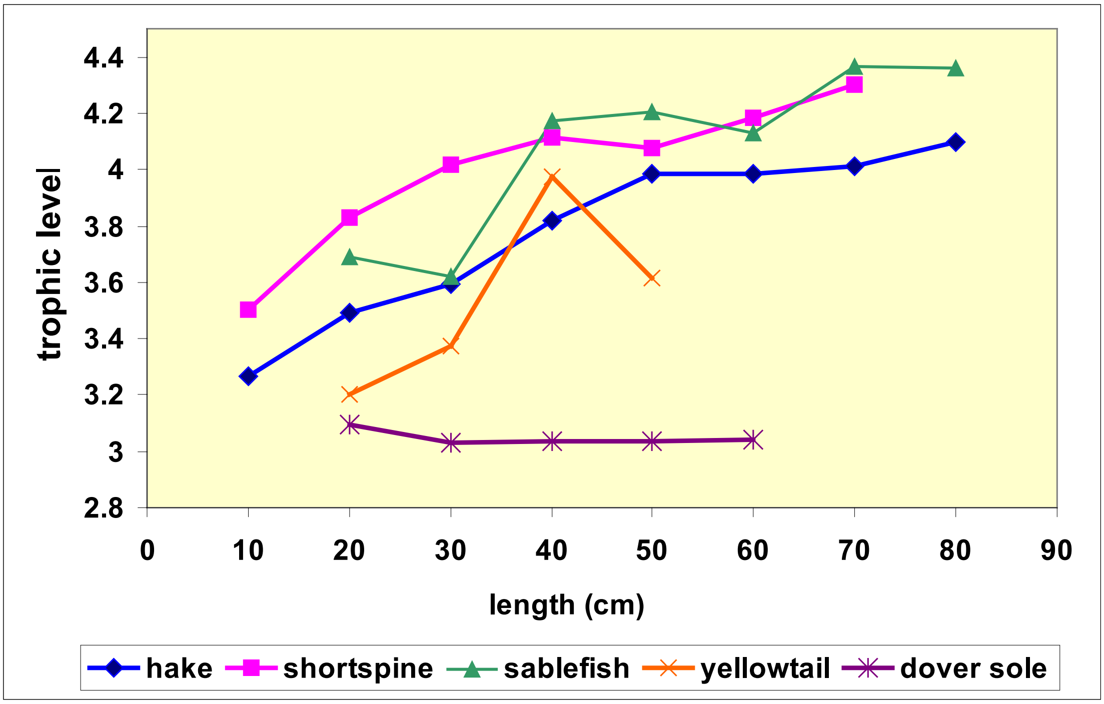

Figure 2.13: Estimated shifts in mean trophic level of size classes of important predators based on the model-estimated trophic level of prey.

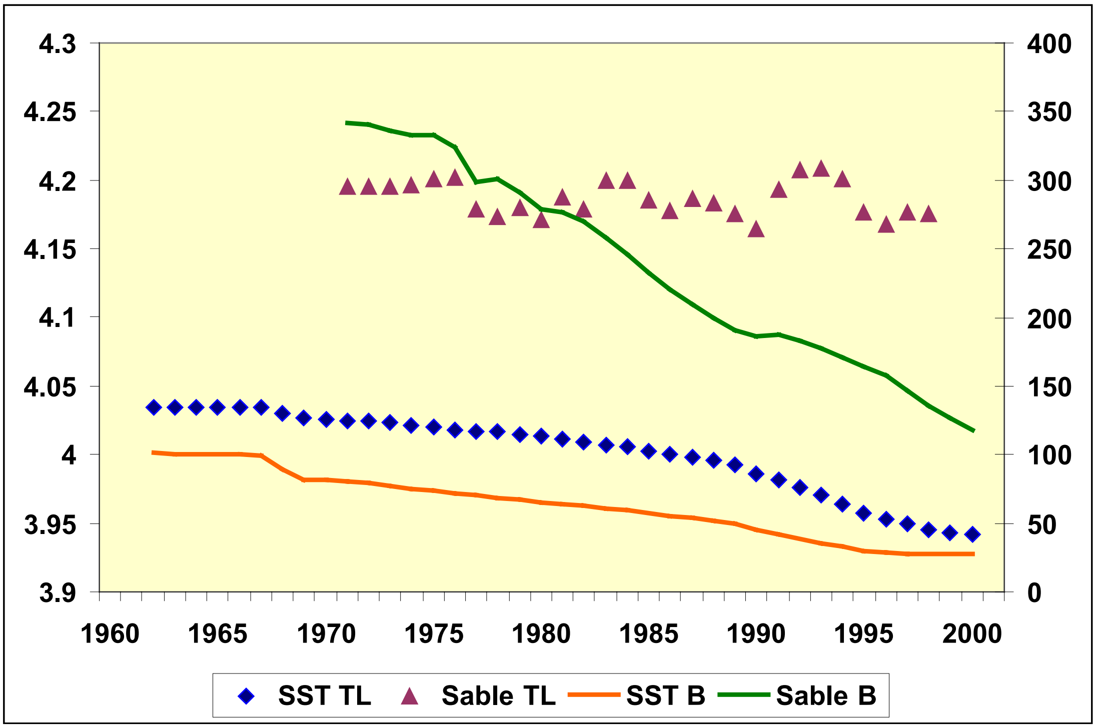

Figure 2.14: Reductions in population biomass and estimated impact to the mean trophic level (TL) of shortspine thornyhead (SST) and sablefish (sable) stocks inferred by changes in age and size distribution.

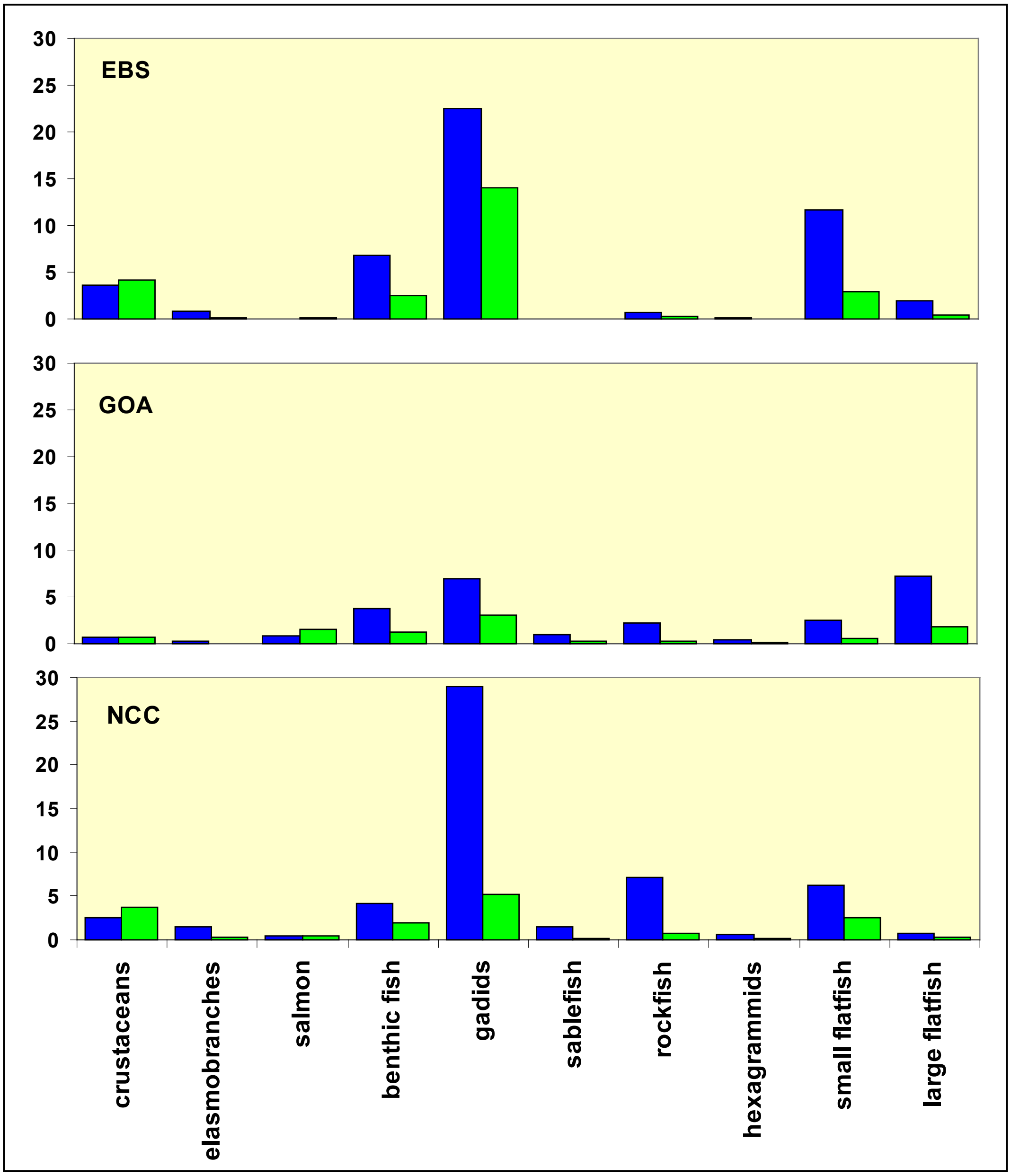

Figure 2.15: Comparing model estimates of standing biomass and productivity across the Northern California Current, Eastern Bering Sea and Gulf of Alaska ecosystems (units are metric tons per square kilometer).

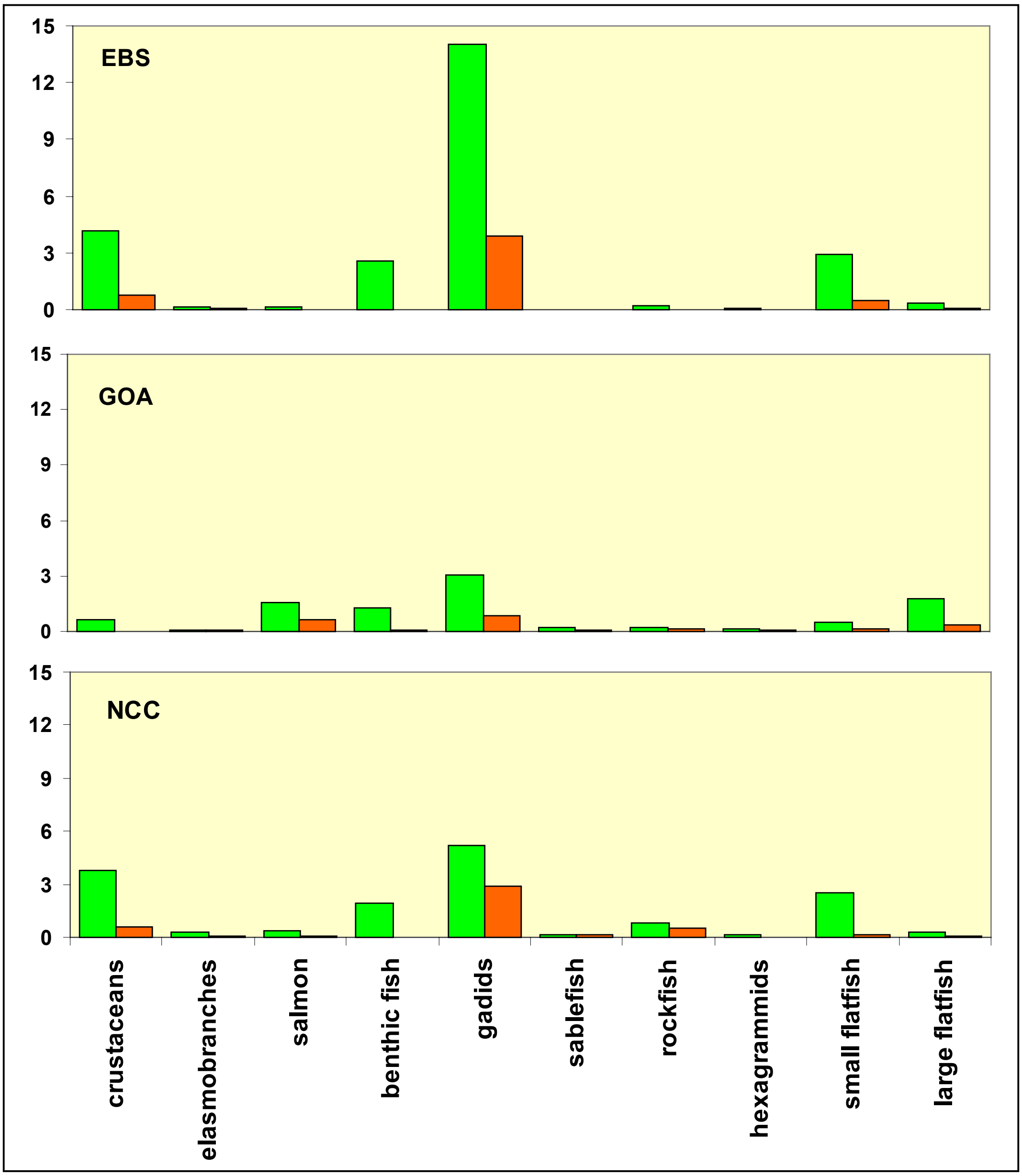

Figure 2.16: Productivity relative to total catches by guilds across the Northern California Current, Eastern Bering Sea and Gulf of Alaska ecosystems (units are metric tons per square kilometer).

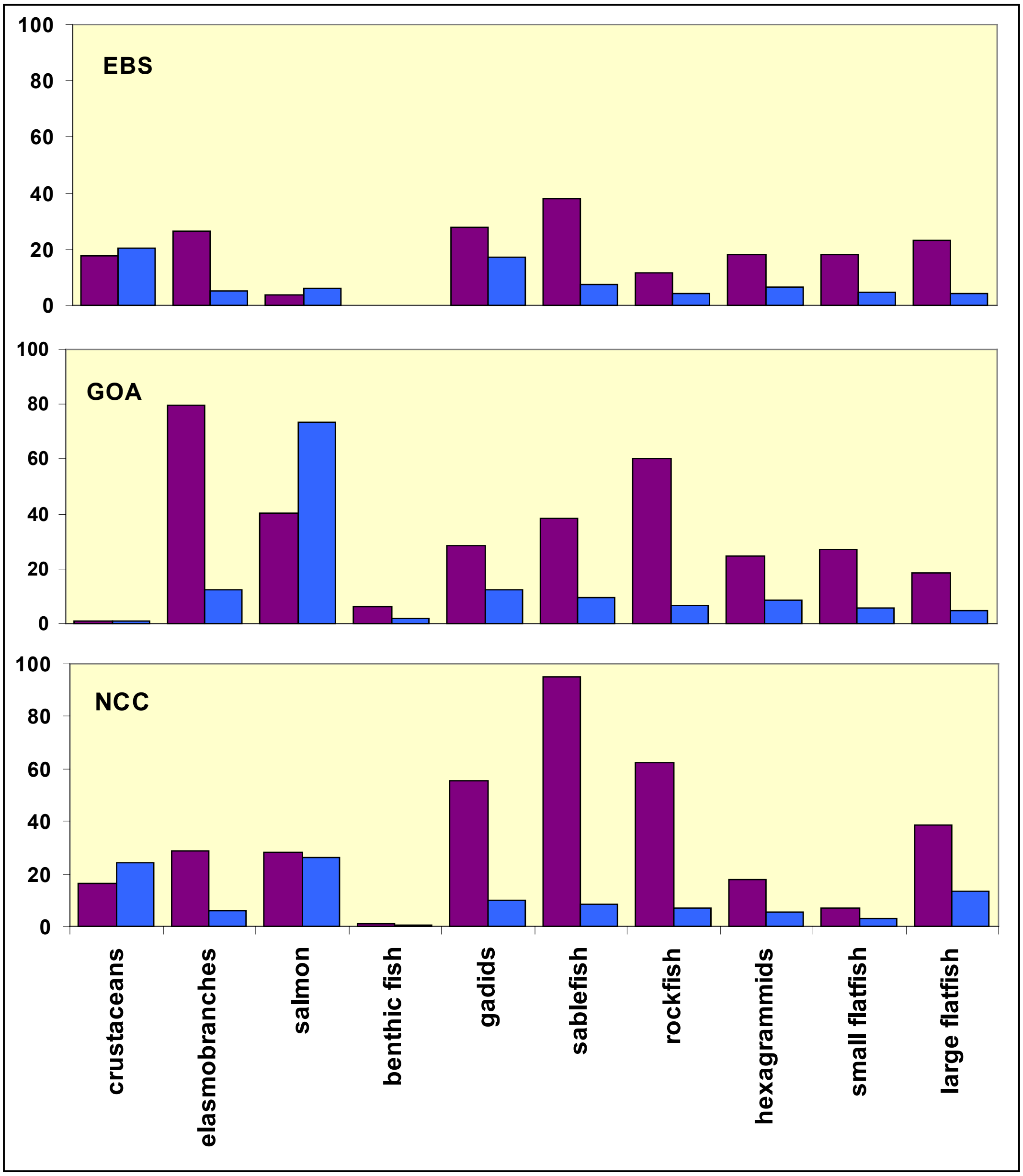

Figure 2.17: Fraction of standing biomass (B) and new production (P) removed by fisheries across the Northern California Current, Eastern Bering Sea and Gulf of Alaska ecosystems.

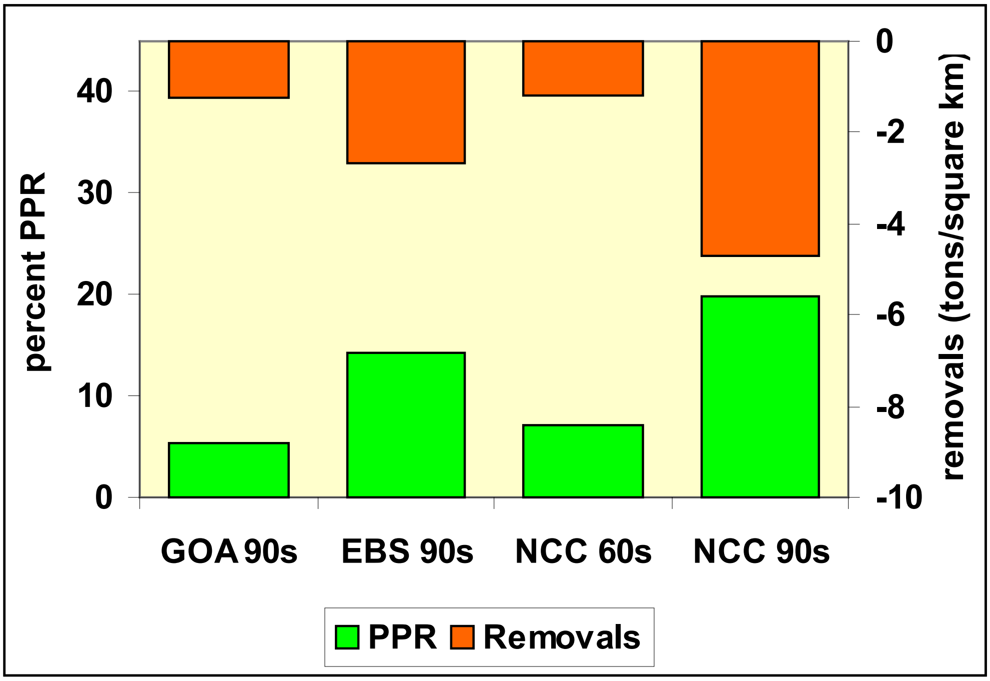

Figure 2.18: Mean system removals (right, upper axis) in metric tons per square kilometer, and corresponding percentage of primary productivity required (PPR, left, lower axis).

Chapter 3

Nature cannot be understood by pretending that it is simple (Elton 1927)

3.1 Introduction

The focus of this chapter is dynamic modeling of the NCC based on the Ecopath with Ecosim framework. This effort will use the static models presented in Chapter 2, driving them forward in time with estimates of fisheries effort, fishing mortality and climate, and fitting to stock assessment results and survey information. Ecosim is a dynamic version of Ecopath (Walters et al. 1997, Walters et al. 2000) that can be best described as a multi-species biomass-driven predator/prey surplus production model. Although the modeling framework is limited in its ability to account for some important ecosystem processes, in particular age structure, the relative simplicity of model behavior suggest that it is a useful tool for integrating available data and knowledge in dynamic simulations. The approach is particularly relevant to evaluating whether observed trends and results from single species assessments are consistent with commonly held notions of ecosystem abundance, productivity, interactions and behavior. The approach taken in this chapter will be to provide a brief review of ecosystem modeling approaches and insights, describe the Ecosim model equations, assumptions and dynamics used here, present fits to historical trends within the NCC over the past 40 years using both fishery and climate forcing, and, ultimately, consider the potential for dynamic models with regard to gaining insights about future ecosystem dynamics.

3.2 Interactions between Fisheries and Ecosystems

The current management paradigm for marine fisheries in the United States, and indeed throughout most of the world, is based on the assumption that exploited fish and shellfish populations are capable of sustaining a long-term harvest as a result of compensatory population dynamics. Although such processes tend to be varied, complex and often poorly understood, compensatory production is generally defined as surplus production in a single-species context, in which populations at abundance levels below their (generally theoretical) carrying capacity are capable of both growing at faster rates and producing more young, or recruits, than is necessary to maintain the population (Russell 1931, Rose et al. 2001). As discussed in Smith (1994), Schaefer (1954) was among the first to actually estimate this surplus production, by using the logistic growth curve to define the relationship between a given level of fishing effort and the resulting population production that would just balance the catch. Ultimately Schaefer's methods provided a means of estimating the level of fishing effort that would produce what he called the maximum sustained yield (MSY). This allowed fisheries biologists to arrive at a definition of overfishing, which was "fishing so hard that the total sustainable yield begins to decline."

The Schaefer method was quickly applied to many heavily exploited populations, including fisheries for the great whales, and achieving maximum sustainable yield became the mantra of sustainability for fisheries the world over.[1] Although the Schaefer model has been largely replaced by more complex age structured models, a key assumption since that time has been that fish stocks and populations (and presumably the ecosystems in which they exist) are healthy if they are maintained close

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[1] Schaefer's methods were developed in what has often been referred to as the "heyday" of fisheries science. Ricker (1977) called this a period that "crackled with new information and new ideas. The solidification of the concept of MSY, its application to fisheries here, there, and everywhere, was just under way." Similarly, Beverton (1998) recalled this period as a time when "We were carefree in the sense that we felt we were doing good and valuable things and, if we did not yet have all the answers, we were on exactly the right track to get them."

to the levels that provide MSY. However there is a growing body of ecological, genetic and theoretical evidence that suggests that this may not necessarily be so. Genetic, demographic and other life history changes, measurement errors, poor management decisions, impacts to food webs, and large-scale variations in productivity associated with climate variability all complicate efforts to remove "as much as we can," often leaving stocks, and ecosystems, in jeopardy. As Mangel et al. (2000) state "single-species management is based on the assumption that stocks can be viewed out of the context of their role in the ecosystem, that density dependence is the main regulating factor in population dynamics, and that if one simply knows enough about the vital information of the stock, then it is possible to fully control the trajectory of the stock." This presumption is increasingly recognized as an oversimplification, and fisheries science is gradually acknowledging that the impacts and consequences of fishing, climate, and other perturbations have widespread, complex and important impacts to both fisheries resources and the ecosystems in which they exist. The challenge today is whether the effects of ecosystem-scale perturbations can be modeled or otherwise accounted for to provide useful advice to managers.

The Ecosystem Principles Advisory Panel (EPAP 1999) suggested that when fishing is examined from an ecosystem context the rationale for surplus production is unclear, since before the advent of fisheries all production was recycled within ecosystems. Interpretation of this statement must be made with caution, as the intent was to infer that the consequences of any fishing include some level of ecological changes among competitors, prey and predators, and that such consequences are not explicitly accounted for in single-species estimates of surplus production. While it is true that any fishing activity can be expected to have some impact on an ecosystem, the focus of the report was in reference to the potential for ecosystems to shift into vastly different, potentially unproductive alternative states of stability following massive perturbations. Large scale shifts in community structure have been widely documented in polar to tropical coral reef ecosystems, and particularly throughout the world's temperate continental shelf communities (Hall 1999, Jennings and Kaiser 1999). The recognitions that dramatic, and perhaps irreversible, ecosystem changes and impacts may result from even “sustainable” levels of fishing is a key impetus for implementing ecosystem-based approaches towards managing fisheries.

One of the greatest challenges facing those who seek to model ecosystem dynamics is that both single species and ecosystem models generally rely on the same (or similar) equilibrium theory to govern model behavior. In single species models the logistic is generally replaced by spawner-recruit curves, which tend to be as poorly defined (if not more so) as surplus production curves. In models such as Ecosim the simulations are based on a series of linked biomass dynamic equations, where behavior is highly sensitive to numerous parameters that are perhaps more difficult to predict or measure. As such, ecosystem models are neither designed nor intended to replace single species models or modeling approaches in the near or foreseeable future. Instead, their key strength is that they provide a framework for evaluating what is known about ecosystem structure, productivity and interspecific interactions, including the compatibility of single species models and other sources of data. As Christensen and Walters (2004) suggest, ecosystem models are generally not appropriate to considering the tactical questions that face fisheries managers, such as how much of a stock to harvest in the next management cycle. However, they are useful tools for addressing strategic management issues, such as the potential long-term effects of harvesting some stocks at MSY (or proxies thereof) while others are untouched, or of depleting select components of the ecosystem in short time periods. The challenges and data limitations that face those trying to build, run and evaluate ecosystem models are tremendous, and results have often been treated with deserved skepticism. Yet this is no less true for those trying to estimate the “unexploited biomass” levels of many stocks that exist in highly dynamic ecosystems, particularly those known to have long histories of extreme climate and anthropogenic disturbances. Consequently, despite their theoretical (model assumptions) and empirical (data) limitations, dynamic ecosystem models are increasingly recognized as an important compliment to more traditional single species models for evaluating observed and potential impacts of altering the flow of energy in marine ecosystems.

Ecosystem impacts have often been inferred as a result of trophic cascades, in which declines of high trophic level species (keystone predators) have cascading impacts through food webs to the abundance, productivity and species diversity of lower trophic levels. Clear examples of trophic cascades appear to be more common for semi-enclosed ecosystems such as lakes and environments with interactions on two-dimensional surfaces such as intertidal or sub-tidal environments (Paine 1966, Carpenter and Kitchell 1993, Tegner and Dayton 2000). One often cited example is the case of sea otters in the Aleutians, in which the vast majority of the population was removed first by man (Simenstad et al. 1978) and more recently (perhaps) by increased predation from orcas (Estes et al. 1998). In both instances, these removals led to an increase in abundance of a key prey item, sea urchins, which in turn resulted in a decline in kelp cover. The loss of kelp negatively affected the communities dependent upon kelp for both forage and cover, leading to a substantial restructuring of species interactions both within and beyond the kelp forest community. As one ventures further from enclosed or highly structured environments, the evidence for trophic cascades becomes slightly spottier. Van der Elst (1979) reported one very convincing example of top-down control of a coastal ecosystem off of the Natal Coast in South Africa. In this case, the use of shark nets to protect bathers increased the mortality of large sharks, which subsequently caused an apparent increase in the abundance of smaller dusky and milk sharks on which they fed. The increase of smaller sharks led to declines in several populations of teleost fishes that were both commercially and recreationally important to coastal communities in the region. The potential for trophic cascades in the Eastern Bering Sea, associated with the large-scale removal of whales in the 1950s and 1960s, has also been extensively explored, and will be discussed in greater detail shortly.

As top-level predators, marine mammals figure prominently in scenarios of trophic cascades or top-down forcing. Marine mammal populations around the world have begun to recover from past exploitation, often to dramatic levels. As a result, there have been growing calls to consider the culling of such predators in order to increase food production.[2] While such proposals may seem repugnant for reasons of changing societal values and conservation, they may be more dangerous in light of their assumption that the consequences of (again) depleting top predators in large marine ecosystems can be easily predicted or controlled. In fact, such control may not be realistic given the many unknowns that remain in understanding behavior and interactions in complex ecosystems. For example, Punt and Butterworth (1995) evaluated the potential responses to the culling of fur seals in the Benguela Current ecosystem, and found that likely impacts ranged from neutral to detrimental for the hake fisheries. This unexpected result was based on tightly coupled interactions between the two species of hake in this ecosystem, both of which were important in the diets of marine mammals and one of which was the principal source of predation on the other.

3.3 Ecosystem Modeling

As Hollowed et al. (2000) state, the role of all fisheries models, whether single or multispecies, is to understand and inform decision-makers of the consequences of fishing or other activities to living resources and the ecosystem in which they exist. While there have long been attempts to model the interspecific and community dynamics of ecosystems (Laevastu and Favorite 1976, May et al. 1979), there has been a resurgence in efforts to do so in recent years in an effort to improve our understanding

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[2] Yosdis (2001) describes discussions of this issue at a recent meeting of the International Whaling Commission (IWC), in which estimates were made that marine mammals consume between 280 and 500 million metric tons of fish and invertebrates annually. The implication was that culling would release some or much of this food for use by humans. However, Yosdis also makes the point that if top predators do indeed compete with fisheries, then it is equally true that fisheries compete with top predators (such as threatened or endangered marine mammals whose recoveries may be mandated by law), and in fact the latter is more likely given the powerful technology and lack of ecological feedback mechanisms.

of interspecific interactions, estimate changes in natural mortality (predation) and recruitment, evaluate potential impacts of environmental variability and change, and consider the potential cascading effects of fishing and other ecosystem impacts (Hollowed et al. 2000, Pauly et al. 2002, Fulton et al. 2003). Yet because top-down and bottom-up interactions in ecosystems are so complex, and strong assumptions are required to model such interactions, the predictability of ecosystem consequences resulting from fishing (or other) activities is often fairly low. This is due both to the simplicity of model assumptions (despite their similarity to those of single species models) and the lack of adequate data or knowledge to parameterize such models.

Yet it is equally clear that the abilities of these models are evolving rapidly, as the need for understanding complex interactions becomes increasingly apparent. Clearly, without at least modest data and understanding of ecological dynamics, making any inferences with such models could be extremely misleading, and where data collection and ecosystem level information is improving, finding an appropriate level of model complexity is crucial (Plagányi and Butterworth 2004). Where an appropriate level of data does exist, these models will undoubtedly have a useful role to play in the future of marine resource management. In their short term, their principal objective may be little more than forcing managers and decisionmakers to explicitly address the fact that exploited fish populations sit within complex food webs, and that selective removals by fishing have the potential to result in undesirable consequences to both target species as well as entire ecosystems. Ultimately however, such models will have a more valuable roles, and could contribute both to improvements in single species assessments and to strategic analysis of fisheries management strategies and objectives over longer time scales.

Hollowed et al. (2000) have categorized and evaluated dynamic multispecies and ecosystem models used in fisheries, and trace both the development and the differences between these models back in time. Among the earliest were the dynamic multispecies models, or multispecies virtual population analysis (MSVPA) models of Anderson and Ursin (1977) and Ursin (1982); a more recent examples includes Jurado-Molina and Livingston (2002). The MSVPA is an age-structured model that uses similar data to single species models, but allows for retrospective changes in natural mortality (predation) rates by species and age class related to changes in the abundance of predators. However such feedback is generally limited to other exploited species included in the model. Ecosim is included in a family of aggregate systems models, which began with the models of Laevastu and Favorite (1977) and Polovina (1984), but is currently represented by the Ecopath with Ecosim models of Walters et al. (2000). A third major class of models includes dynamic systems and process models. These have more detailed interactions between physical forcing and biological interactions, higher levels of detail at the species life history level, and the ability to account for greater temporal and spatial resolution in species interactions. Examples include individual based models (IBMs) of Hermann et al. (2001), the physically forced nutrient-phytoplankton-zooplankton-fish models of Robinson et al. (1993) and Robinson and Ware (1999), and the biogeochemical systems models reviewed in greater detail in Fulton et al. (2003). Thus, there exists a wide range of modeling frameworks, of varying complexity, with which to consider the importance of human, climate and food web interactions on exploited species and systems. The model of choice will depend upon the data and knowledge available to parameterize the model, as well as the nature of the questions that are to be addressed.

Few of these models have been actively used to inform or persuade decisionmakers, or guide management decisions. However a growing body of literature demonstrates the versatility of the modeling framework and the nature of insights that can be gained from modeling exercises that are tempered with appropriate caution and uncertainty. Many of these insights are with regard to the nature of functional responses, in particular the extent to which predators (such as marine mammals) can adjust their feeding habits to compensate for changes in the availability of prey (such as commercially important groundfish). For example, we can consider a scenario in which a stock of fish is highly vulnerable to a marine mammal predator, such that predators can fully compensate for stock declines and continue to consume the same volume of fish they would have eaten otherwise. In such a scenario, relative natural mortality of the fish stock would increase, stock assessment model assumptions of constant mortality would be violated, and the stock would be at greater risk of collapse. This mechanism has been referred to as a "predator trap", and Bundy (2001) constructed a model of the Newfoundland-Labrador ecosystem to evaluate such potential interactions between harp seals and cod in this heavily exploited system. Her results suggest that although the decline of cod was the result of overfishing, the recovery may be hindered by the increasing natural mortality rate associated with a nearly constant per capita consumption of cod by harp seals and concurrent increases in seal abundance.[3] Although her model did not fit all of the trends in stock trajectories estimated by single species models, it did suggest that the decline in cod and several other heavily fished species may have resulted in the increase of shrimp and other large crustaceans, an outcome supported by Worm and Myers (2003).

A different type of insight seems to have been gained from ecosystem modeling exercises in the Eastern Bering Sea in an attempt to explain the rapid decline in Steller sea lion abundance in the late 1960s and early 1970s, and its apparent failure to recover. The NRC panel on the Bering Sea ecosystem (NRC 1996b) had suggested the possibility of a trophic cascade in that ecosystem, in which increases in pollock and declines in forage fish may have been a result of a reorganization of the Bering Sea ecosystem following both the massive removals of marine mammals during the 1950s and 1960s and changes in climate patterns that occurred in the mid 1970s. A key

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[3] Bundy evaluated the interactions under scenarios of bottom-up, intermediate, and top-down control (essentially by using alternative values of the parameters that determine the vulnerability of prey to predators in Ecosim, these are discussed in greater detail in the next section) and found that harp seals had negative impacts on the recovery rates of cod under top-down and intermediate control. An example of the converse is given in Jennings and Kaiser (1999), who suggest that declines of grey seals by starvation in the Barents Sea were directly related to the collapse of capelin stocks following intensive fishing.

impetus for that effort had been to explore in detail potential causes of ongoing Steller sea lion declines, responses to which have continued to complicate fisheries management efforts. The NRC report resulted in the initiation of major efforts to model food web interactions in the Northeast Pacific, although most subsequently failed to replicate sea lion population declines (Trites et al. 1999, S. Gaichas pers. com.). A later NRC Committee established to review the scientific integrity of hypothesized causes of Steller sea lion mortality (NRC 2003) revisited the use of Ecosim models to consider potential trophic mechanisms for Stellar sea lion declines. Yet even when allowing annual deviations in bottom-up production to float as "free parameters" over time, the panel was unable to develop scenarios that might predict the short period of rapid decline observed during the late 1970s and early 1980s. While acknowledging that model and data constraints prevented fully ruling out trophic cascades as a mechanism for Steller declines, the Committee expressed serious doubts that further, more detailed modeling exercises could suggest otherwise.

Such insights demonstrate the utility of ecosystem modeling in formally evaluating whether "word models" of ecosystem change are consistent with the "mechanized deductions" that such models are capable of addressing (Walters et al. 2000). However there are problems with assuming that the mechanistic deductions of quantitative models are exclusively superior to those of qualitative models. Among the most recent mechanisms to be proposed for the Stellar sea lion decline is a slight permutation of the original cascade hypothesis, in which the removal of baleen whales left a void in the diet of the whale's major predator, the orca. Under this hypothesis, orcas subsequently engaged in the systematic devastation of pinniped and other marine mammal populations throughout the Bering Sea and Aleutian Islands. Although it can be argued that such prey could not alone have satisfied the caloric requirements of orcas, the hypothesis is at least reasonably consistent with what is known about the sequential declines in whales, harbor seals, fur seals, sea lions and sea otters in the region (Springer et al. 2003). In simulation models, the deterministic nature of "prey switching" may contrast considerably to the widely acknowledged uncertainties regarding the nature of prey selectivity and predation behavior, particularly for such a highly advanced top predator. Thus it is reasonable to expect that simulation modeling capable of repeating such dynamics would be extremely challenging, if not impossible.

In the Newfoundland-Labrador sea model, the results alone may not provide sufficiently rigorous evidence to guide policy, but are informative for policy makers, especially where consistent with more empirical evidence of ecosystem changes. In the Eastern Bering Sea example, the model and modeling approach allowed for a rigorous examination of a working hypothesis (trophic cascades) that ultimately suggested that such a hypothesis is inconsistent with what is known about the timing and nature of past ecosystem change. This too is informative for policy makers, as at a minimum it suggests that trophic interactions, at least to the limited degree that we are able to understand them, may not be the principal cause of the Steller sea lion decline. Yet this in turn does not preclude such interactions as a factor in the absence of a recovery, nor exclude the possibility of a combination of trophic interactions and climate variability or change contributing to the decline.

Other modeling efforts have met with some success using climate as a driver to replicate past ecosystem dynamics, including the Central North Pacific (CNP) and Eastern Tropical Pacific (ETP). There, interactions between fleets of different nations and fishing strategies are leading to conflicts over the direction of future management (Cox et al. 2002, Olson and Watters 2003). All of these examples help to set the context for interpreting and using information and insights from ecosystem models. Perhaps more importantly, they demonstrate that multispecies models are currently the only reasonable models available with the ability to at least address questions related to trophic and climate interactions.

3.4 Model Equations and Assumptions

Ecosim was initially developed by Walters et al. (1997) as a dynamic version of Ecopath, and later revised by Walters et al. (2000) to address some important inconsistencies in the dynamics of linked split-pool groups. The basic equations, and many of the associated assumptions and technical details, are reviewed in detail in Walters et al. (2000), Aydin and Friday (2001), Christensen and Walters (2004) and Plagányi and Butterworth (2004). Essentially, Ecosim turns the static energy flows of a given Ecopath model into dynamic, time-varying predictions by using coupled differential equations derived from the basic Ecopath equation (Equation 2.1), such that:

Equation 3.1 $$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i$$

Where dB_i/dt is the growth rate (in units of biomass) of the group i during the time interval *dt*, g_i is the growth efficiency (defined in Chapter 2 as production, P/B, over consumption, Q/B), Q_{ji} represents predation by group i on group j, Q_{ij} represents predation on group i by group j, I_i is the biomass immigration rate, $M0_i$ is the nonpredation mortality, F_i is the fishing mortality rate, e_i is the emigration rate, and B_i is the biomass of i at the previous time step. More simply, the instantaneous change in biomass of a given group i is dependent upon the difference between the prey that *i* consumes (the Q_{ji}, multiplied by growth efficiency) and how much of that group is consumed by predators (the Q_{ij}), taking into account non-predation mortality (M0), fishing (F), immigration (I) and emigration (e). The differential equations are solved in Ecosim using an Adams-Basforth integration routine (default) or a Runge-Kutta fourth-order routine (Walters et al. 2000).

The biomass accumulation (BA_i) term build into the static (Ecopath) model becomes especially important in the dynamic version, as this accumulation is taken into account when M0 is estimated in the static model from the Ecotrophic Efficiency. This term reflects the population trend, or lack of equilibrium, in components known to be either increasing (such as many marine mammal populations in the NCC) or decreasing (such as many exploited finfish populations in the NCC). Without accounting for such trends, Ecosim will behave as if the energy flow in the system is sustainable, which can lead to severely flawed model behavior in scenarios where the baseline fishing mortality is responsible for ongoing population declines.

Similarly, the unexplained mortality, M0, becomes an increasingly important factor in the dynamic model. In the static model, M0 reflects the difference between the estimated production rates of prey and consumption rates of predators. As Aydin and Friday (2001) demonstrate, in the dynamic version of Ecosim the difference between 1-growth efficiency and 1-ecotrophic efficiency (described in Chapter 2 as the proportion of production directly utilized in the system) essentially represents passive metabolism costs from a bioenergetic point of view. Decreasing the ecotrophic efficiency, while increasing growth efficiency, can result in similar static balances, but alter dynamic behavior as a result of greater passive metabolic costs. These differences may alter the manner in which declines in predation (or fishing) rates result in compensatory population growth. It is generally assumed that these effects are insignificant in groups with rapid turnover (most forage species), where biomass estimates are rare and top-down balances common. Higher trophic level groups typically have (or are assigned) lower EE values that may suggest more "realistic" passive metabolism costs, although data to estimate or tune these values rarely exists.

The most important interactions in the dynamic model are the biomass flows between compartments, the consumption rates (Q_{ij}) themselves. These flows are calculated by the "foraging arena" concept (Walters et al. 1997, Walters et al. 2000, Walters and Martell in press), which assumes a quasi-defined heterogeneous environment, in which the biomass of a model component is partitioned into vulnerable and non-vulnerable (to predation) states. The transfer rate, v, between these two states determines whether control is top-down (Lotka-Volterra), bottom-up (primary productivity) or intermediate. The non-vulnerable state is intended to represent mechanisms that prey use to avoid predation, such as daily vertical migrations, schooling, or the use of limited habitat for avoiding predation (particularly for juveniles); behaviors that can lead to strong competitive interactions between predators even when the biomass of prey is large. By contrast, MSVPA and other multi-species models assume that predators are always able to consume their daily rations of food (Plagányi and Butterworth 2004). In such scenarios there is little density dependence in the absolute consumption of prey by a predator, and thus greater potential for prey increases associated with predator declines.

For example in the study by Bundy (2001) referred to earlier, results indicated a strong top-down effect of harp seals on cod when vulnerability parameters were set at either high (implying top-down control) or intermediate (default) values. When they were set to low (bottom-up) values, strong top-down effects did not occur. In this instance, high vulnerability is likely to be a reasonable assumption, particularly as marine mammals and other animals with high passive metabolism costs typically do not have the option of lowering consumption rates relative to prey availability. By contrast, a low vulnerability implies weak top-down control on a prey biomass (closer to ratio-dependent predation rates), to the extent that control is bottom-up and production does not significantly increase with predator declines. In the first version of Ecosim (Walters et al. 1997), the consumption rates of a prey *i* by a predator *j* (Q_{ij}) were determined by the equation:

Equation 3.2
$$Q_{ij} = \frac{v_{ij} a_{ij} B_i B_j}{\left(v_{ij} + v'_{ij} + a_{ij} B_j\right)}$$

Where a_{ij}, is the search rate for prey i by predator j, v_{ij} and v'_{ij} are the movement rates between the vulnerable (v_{ij}) and invulnerable (v'_{ij}) prey behavior states (with default settings $v'_{ij} = v_{ij}$, see Walters et al. 2000),[4] and B_i and B_j are the biomass of prey and predators respectively. The values for search rates (a_{ij}) are inferred from the maximum consumption rate, C^{max}, which is relative to C_{ij} in the Lotka-Volterra case such that $a_{ij}=C_{ij}/(B_iB_j)$. The default value for C^{max} is 2, which translates into the expectation that if predator *j* numbers were very high, their maximum consumption rates of prey i would be twice the (Ecopath) base case. Thus, as with vulnerability, the estimated values for C^{max} can have an influence on model dynamics, with a high ratio of C^{max}_{ij} to C_{ij} implying strong top-down control and a low ratio implying bottom-up control. As with the vulnerability parameters, these parameters are difficult to estimate, measure or otherwise derive, although their influence on model dynamics is generally less than the influence of setting vulnerabilities. The general approach here has been to use default values unless otherwise noted.[5] In the most recent version of Ecosim (Walters et al. 2000), which is the version used for all simulations in this Chapter, consumption is described in nearly identical, albeit more elaborate equation, in order to facilitate opportunities to manipulate consumption rates dynamically, such that:

Equation 3.3

$$Q_{ij} = \frac{a_{ij} v_{ij} B_i B_j T_i T_j S_{ij} M_{ij} / D_j}{v_{ij} + v_{ij} T_i M_{ij} + a_{ij} M_{ij} B_j S_{ij} T_j / D_j}$$

Where a_{ij} and v_{ij} are as in the previous equation, T_i and T_j represent the relative feeding time of prey and predators respectively, S_{ij} is a user-defined seasonal or long-term forcing effect, M_{ij} is a parameter representing mediating forcing effects, and D_j

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[4] The vulnerability rates chosen in the software package are scaled to range from 0 to 1 with a default of 0.3, however the values used in the computations are rescaled such that the computational v_{ij} is equal to exp(2*[exp($\acute{\upsilon}_{ij}$)-1] where $\acute{\upsilon}_{ij}$ is the value chosen by the user. The $\acute{\upsilon}_{ij}$ chosen by the user range in a continuum between 0 and 1, with 0 representing "bottom-up" control, 1 representing "top-down" control, and 0.3 serving as the default value for mixed control.

[5] For the simulations shown throughout this Chapter, default values were used such that the maximum relative P/B was set to 2, the maximum relative feeding time to 2, the feeding time adjustment rate 0.5, the predator effect on feeding time to 0, the density dependent catchability to 1, and Q/Bmax/Q/B0 (for handling time) to 1000, and the fraction of "other" mortality sensitive to changes in feeding time to 0. This is consistent with other approaches to these parameters (Bundy 2001, Cox et al. 2002), although Olson and Watters (2003) vary the fraction of other mortality sensitive to feeding time by trophic level, setting it to 0 for large predators, 0.5 for medium-size fishes and 1 for forage components.

represents the effects of handling time as a limit to consumption rate as a function of handling time. The effects of the handling time parameter (D_j) on model dynamics is discussed in detail in Walters et al. (1997, 2000), furthermore Plagányi and Butterworth (2004) found that handling time limitations did not appear to restrict consumption rates, which generally remain a linearly increasing function of prey abundance. Both S_{ij} and M_{ij} default to 1, but can be used to increase or decrease vulnerability with season, habitat change, climate or other factors. The examples Christensen and Walters (2004) use are of organisms whose behavior alters the availability of prey to other predators, such as tuna driving forage fish to the surface making them more available to birds, or the use of corals or other benthic habitat as cover for juvenile fishes. In the NCC, the ability to mediate the vulnerability of prey to predators dynamically is an important feature that will be used to mimic some of the impacts of climate variability on the spatial distribution of some ecosystem components.

One of the more recent developments in Ecosim is the ability to handle ontogenetic shifts in life history characteristics with "split-pool" juvenile and adult groups for model components, a model feature that has evolved considerably since early attempts to account for these changes. The split-pool approach (Walters et al. 2000) is based on a Deriso-Schnute delay difference model (Deriso 1980, Schnute 1987) that tracks the number of juveniles or recruits and the number and size of adults, allowing for greater representation of changes in growth, mortality and recruitment in model dynamics. More recently, Christensen and Walters (2004) have described ongoing efforts to model multiple stanzas for species with more complex ontogeny than simply "juveniles" and "adults." The stanza model is based on von Bertalanffy growth assumptions, and consequently not appropriate for invertebrates, seabirds or marine mammals. Despite this, the stanza model is a tremendously important step in moving the potential abilities of ecosystem models to more accurately account for important ontogenetic shifts in growth rates, growth efficiencies, production to biomass rations, and prey preferences.

Such potential, however, is only meaningful if there exists data with which to refine life history stages and stanzas. Although versions of the NCC models were constructed with species-specific juvenile and adult pools, the lack of data on abundance, consumption, production and prey preferences made effective implementation of a split-pool model unfeasible in the first round of modeling. Instead, juveniles of similar species have been pooled together, as rockfish, flatfish and roundfish juveniles, based on what predation could be reliably inferred from diet studies (where juveniles as prey are very rarely identified beyond genus or family level) and inferences from the literature and other models regarding plausible production and consumption rates. Thus, while the behavior of NCC models has been preliminarily explored using juvenile pools, and the final models are "primed" for the incorporation of linked juvenile/adult stages for some species, the application of the split pool and stanza modeling features are not discussed here.

3.5 Model Behavior and Sensitivity

As this modeling framework is sensitive to a wide array of parameters, assessing model sensitivity and behavior is essential. Shannon et al. (2000) estimated model behavior with a range of vulnerabilities, representing top-down, bottom-up and middle-out, or "wasp-waist" control in the Southern Benguela current ecosystem off of western South Africa and Namibia.[6] Their definition of wasp-waist control was characterized by top-down control on zooplankton, and bottom-up control of predatory fish, seabirds and mammals by small pelagic forage fish (primarily sardine, anchovy and round herring). The authors then perturbed the system with sustained and pulsed fourfold increases in

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[6] The idea of "wasp-waist" control was first suggested by Rice (1995) and developed in greater detail in Cury et al. (2000). The premise is that the low species diversity often observed in the middle of many upwelling ecosystems results in a vast majority of the energy in the food web flowing through coastal pelagic species such as sardine, anchovy and mackerel. Many of these seem to feature "weak links" in their life cycles related to sensitivity to climate forcing, such that climate conditions determine the productivity of these stocks, and indirectly drive the dynamics of both higher and lower trophic levels.

fishing mortality on these coastal pelagics, and evaluated the consequent impacts through the ecosystem. Not surprisingly, under the bottom-up scenario the effects of pulsed fishing are relatively small and dampened. Following a five year long pulse in which fishing mortality was doubled, all components of the ecosystem recovered fully within ten years. Coastal pelagics recovered very rapidly, their predators lagging by several years. With mixed control the impacts to both predators and prey were greater, although most components recovered fully within 15 years of the perturbation being removed. However under the assumption of wasp-waist control, the fluctuations were considerably greater and many groups (including the coastal pelagics themselves) had yet to fully recover 35 years after the perturbation had been removed.

Although the work of Shannon et al. (2000) did not “test” whether one type of forcing versus another resulted in a better fit to historical population dynamics, it served as a valuable example of the sensitivity of Ecosim to assumptions about vulnerability and the nature of trophic interactions. As such, it is worth presenting a similar sensitivity test here, done using the scaled down (simple) 1990s model of the NCC.[7] Figure 3.1 shows the sensitivity of several of the key model components to top-down and bottom-up perturbations following an initial five year startup period under varying assumptions of vulnerability (v). For the top-down example, the perturbation comes in the form of a doubling of fishing mortality for a five year period, after which mortalities were returned to their starting values and the model was run out for another 35 years to equilibrate. The bottom-up example was a five year pulse of 50% greater primary production, followed by a return to equilibrium levels.

In both of these simple examples, one can see dynamically the same result predicted by the mixed trophic impact figure in Chapter 2 (Figure 2.11), with the magnitude of increase or decline in prey, predators or competitors associated with a perturbation. For

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[7] Note that for this exercise, the biomass accumulations that reflect declining or increasing population trends were removed to suggest equilibrium conditions.

example, with increased fishing mortality there is a release of forage fish and other prey that fuels an increase in the abundance of seabirds (which feed primarily on forage fish) but little increase in pinnipeds (which feed on a mixture of forage fish and commercially important groundfish). There were also initial (although modest) declines in crustaceans and small flatfish resulting from increased fishing mortality, that immediately shifted to increases in abundance due to decreasing predation by higher trophic level groundfish following the return to baseline levels of fishing mortality. Similarly, in the bottom-up perturbation, forage fish and crustaceans increase tremendously, nearly three fold for the default vulnerability model within a year of the perturbation. Yet these then decline to below equilibrium levels as soon as the perturbation is removed, as a result of the greatly increased mortality associated with an increase in (slower turnover) predators.

It is also interesting to notice that the wavelength of the perturbation is much longer on the top-down forcing (impacting the longer lived species, but not lower trophic level groups), but the amplitude is much greater on the bottom up forcing (although it is dampened for groups with lower P/B). More importantly, both the amplitude and the wavelength of the perturbations increase significantly with an increase in the vulnerability parameters, to the extent that that it takes only ten years to equilibrate from the top-down, low vulnerability perturbation while it takes over forty to equilibrate from the high vulnerability scenario. Walters et al. (2000) suggest that modeling in low vulnerability scenario is comparable to the compensatory responses considered in contemporary single-species management. However Aydin (pers. com) has pointed out that the nature of compensation in Ecosim comes from increased per-capita consumption (at the expense of other species) rather than from the increasing growth rates (and conversion efficiencies) of relatively younger fish as older individuals are removed from the population in a single-species catch-at-age model.

Perhaps one of the most vexing characteristics of the Ecosim model is that model behavior is constrained by equilibrium processes, such that a perturbed model will always return to it's starting equilibrium following the removal of perturbations such as changes in fishing mortality or bottom up forcing (given sufficient time). Although this is not entirely true when modeling under very high vulnerability scenarios, which can lead to erratic and at times chaotic behavior (users are cautioned against setting vulnerability values too high), even here the usual result is a return to starting conditions after long time periods. Walters et al. (1997, 2000) identified this as a weak, albeit necessary, characteristic of the model, particularly as this equilibrium generally precludes the possibility of prey switching by predators. Hollowed et al. (2000) noted that these constraints reduce the utility of such models in evaluating the consequences of species outbreaks, as well as the introduction of exotic species.

Rice (2001) attacked this stability even further, arguing that "explanations and models that focus on changes in carrying capacity and contest competition for food are not going to apply to the systems recovering from an environmental crunch or species whose abundances are controlled by a top-predator." By contest competition, Rice is referring to the typical assumption in food web theory, in which many individuals share a limited resource, and small differences in their ability to access or control access to that resource affect their survivorship and reproduction (Milne 1961). Rice suggested that an alternative form of competition, which he describes as scramble competition, occurs when resource availability changes abruptly for reasons other than usage by consumers, and all individuals simultaneously experience either a sudden shortage or a sudden abundance of food or other resources. Such variability is often an integral feature of coastal upwelling ecosystems, for example, which are characterized by variability in physical conditions and productivity over multiple time scales. Differences in the rate at which populations can react to the new food supply rate determine future survivorship and reproduction, and can thus result in differing patterns of species abundance and dominance over time.

In an effort to address these shortcomings, a new refinement to the basic model assumptions was developed by K. Aydin (pers. com) and shows promise for generating alternative model scenarios, in which rule changes can occur and ecosystems do not return to equilibrium conditions following the removal of a perturbation. This refinement uses the concept of scramble competition as defined by Rice (2001) and based on the ideas of Milne (1961), in which resource availability changes abruptly, independent of changes in consumer abundance, with life history adaptations and characteristics being a partial determinant of the winners or losers in competition for resources. Operationally, this is little more than the re-arranging of the consumption equation from Ecosim (using the simple version for clarity), such that:

Equation 3.4

$$Q_{ij} = \sum \frac{v_{ij} a_{ij} B_i B_j}{2v_{ij} + \sum a_{ij} B_j}$$

Here, the functional response of predator's consumption rates are based on the biomass levels of all predators simultaneously, rather than solely that of a given predator *i* at the previous time step, such that all predators simultaneously affect each of the terms for all other predators. It is not necessarily clear that this change represents "true" scramble competition, and it has been suggested that instead it may be a form of competitive exclusion. However, this change dramatically alters model behavior in terms of the shape of the functional response (consumption against biomass), from a fairly predictable response based on prey abundance (the slope of which is a function of the vulnerability parameters), to a highly sensitive response based on the abundance of competitors (and predators) in the ecosystem.

Figure 3.2 is arranged similarly to Figure 3.1, with simulated biomass levels of different model components under different model assumptions. The first is simply the default (v=0.3) scenario, the second is with high (v=0.7) vulnerability, which leads to severely unstable, and one would presume unrealistic, behavior. The third is scramble competition (with v set to 0.3), in which wavelike or regime-like behavior in the form of decade-long trends in abundance seem to be the response to either pulses of mortality (fishing) or production anomalies (bottom-up forcing). Longer-term simulations in which traditional (contest) competition was replaced by scramble competition and small amounts of white noise seem to suggest very similar patterns of 'regime-like' behavior even in the absence of perturbations (K. Aydin pers. com.), and under moderately heavy fishing mortality (based on a proxy for MSY) the behavior seemed to be even more erratic and variable. The problem is there is rarely evidence for one form of competition over another; either type of interaction may be wrong or right some, or all, of the time. However this in turn would suggest that scramble, or some similar, unstable form of competition, is just as likely to be the "correct" form of interaction as the traditional "contest" form upon which most single species and ecosystem models are based. Evaluating the behavior of the model under both contest and scramble competition may provide an interesting reassessment of the consequences and interactions between fisheries and variability in ecosystems.

3.6 Modeling Environmental and Ecosystem Dynamics in the NCC

In any dynamic modeling, one of the most important tasks is to somehow "validate" model behavior by reproducing, as well as possible, observed trends in a system. For the NCC, the primary objective of such validation has been to attempt to use the 1960s model of the NCC as a starting point for running simulations, and to fit this model to available time series (stock assessments, survey data and catch indices) between 1960 and the present. A key challenge in doing so has been determining how best to incorporate climate impacts and forcing processes into model dynamics, an effort that requires numerous simplifying assumptions in order to accommodate the modeling framework. Although climate forcing has in the past been integrated into other Ecosim simulations, it has typically been through relatively straightforward bottom-up processes, such as the relationship between El Niño and primary production in the Eastern Tropical Pacific (Watters et al. 2003), or by assuming the environment to be process error that is addressed by minimizing objective functions with free parameters referred to as “primary production anomalies” (Christensen et al. 2000, NRC 2003).

Climate is well known to affect productivity and dynamics both from the bottom up (through short and long term variability in primary and secondary productivity) as well as from the top-down (through variability in the spatial distribution of key middle and top trophic level predators such as hake, sardine and mackerel) in the NCC. A plethora of environmental indicators exist that have been associated with climate variability on multiple time scales, from local physical indices such as upwelling, sea surface temperature, and transport, to basin scale indices such as the ENSO and the PDO. The interactions between physical forcing and biological production are complex and nonlinear, and the representations of interspecific interactions modeled in these simulations were not designed nor intended to include biophysical processes. Instead, such models are generally fisheries specific, and focus in detail on the level of interest to fisheries scientists, managers and stakeholders.[8] Conversely, despite the “sketchy understanding” of physical and biological ocean processes, biogeochemical and physical oceanographic models are increasingly well developed to the level of phytoplankton and zooplankton, although considerable challenges have faced those who have sought to extent such models beyond these lower trophic levels (deYoung et al. 2004). The challenges involved in developing fully integrated biophysical process models with higher trophic level (including fisheries) ecosystem models are tremendous, and not likely to be overcome in the near future.

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[8] As discussed in Chapter 2, and earlier in this Chapter, the spatial and temporal scale of most such models matches those of greatest significance to stock assessment and management, although the models are unavoidably biased in aggregating the considerably diversity of lower, and often higher, trophic levels. As such, they are built on the same foundation as single species assessment models, and provide a pragmatic template for using available data, albeit with considerably less detail in population structure.

However, we can explore the extent to which incorporation of various means of climate forcing, that are consistent with our conceptual model of climate and ecosystem dynamics discussed in Chapter 1, complement or contrasts with observed trends. For example, we can evaluate the extent to which forcing lower trophic level production with physical indices improves the fit of model dynamics to the known or inferred trends, relative to the fit obtained by running the model with no variability in bottom-up forcing. To attempt to validate the model performance, a series of simulations were run in which the 1960s model was projected to 2004. Fishing was represented by using fishing mortalities based on stock assessments and known catches (for hake and most groundfish), estimated changes in effort (pandalid shrimp and Dungeness crab)[9] and in one case a simplified assumption of constant fishing mortality (Pacific salmon) where attempting to estimate either fishing mortality or effort are impractical. The model was run forward first under the assumption of a constant environment, then forced dynamically with several climate indices. Although several indices were tentatively explored as forcing functions, only select results are shown and discussed in detail here. The indices discussed here include upwelling wind indices, indices of southward Ekman transport, the Pacific Decadal Oscillation index (PDO), and an index of predicted Oregon coastal coho salmon survival based on a suite of nonlinear fits to physical ocean data (Logerwell et al. 2003). The upwelling winds index and the coho survival index represent “local” climate impacts, and are shown in Figure 3.3. The PDO and southward transport represent large-scale indices, and are shown in Figure 3.4.

Upwelling wind indices were generated by the average of monthly offshore Ekman transport indices at 42, 45 and 48° N, as obtained from the Pacific Fisheries Environmental Laboratory (PFEL) Live Access Server (www.pfeg.noaa.gov).[10] These

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[9] Both estimates of effort are simplistic, but seem to be reasonable. Relative effort for the shrimp fishery was based on dividing the total annual catch by observed measures of shrimp catch per unit effort described in Hannah et al. (1997) and provided by R. Hannah (pers. com). Effort for the crab fishery was based on the number of Dungeness crab landings based in data provided by D. Colpo (pers. com).

[10] Methods for deriving upwelling and other transport indices are based on estimates of offshore Ekman

were converted to standardized anomalies, with seasonality removed, by subtracting monthly means from monthly values and dividing by the monthly standard deviation over the time period. To set the baseline reasonably close to the mean the starting period of the model runs, all of the indices (with the exception of the coho survival index, which begins in 1969) were converted to standardized anomalies based on a climatology of 1950 to 1964. The southward Ekman transport and the Pacific Decadal Oscillation (PDO) [11] indices were chosen to represent the significance of large-scale environmental conditions on the abundance and dynamics of key predator stocks in the NCC. As discussed in Chapter 1, it has long been hypothesized that the magnitude of southward transport in the California Current system is closely linked to physical conditions and secondary productivity in the California Current (Chelton et al. 1982). As with the upwelling indices, estimates of southward transport were obtained from the PMEL Live Access Server. Transport estimates were averaged over a greater spatial area (36 to 51° N) than the NCC itself, in the expectation that this would better represent larger scale patterns of spatial distribution, migration and production that might respond to transport indices. Similarly, the PDO is widely recognized to reflect basin scale patterns in SST variability, which, in turn have been strongly linked to the production and distribution of hake, sardine and other species.

The predictive index of Oregon coastal coho marine survival index was developed by Logerwell et al. (2003) is based on a conceptual model of the principal environmental

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transport driven by geostrophic wind stress, detailed methods and illustrations are available on the PFEL website, as well as in standard oceanography texts such as Mann and Lazier (1996). The PFEL upwelling indices are calculated for 15 standard locations on the west coast at both monthly and 6-hour intervals, based on geostrophic winds derived from observed atmospheric pressure fields, and are widely acknowledged to be the best available information on upwelling variability over time (aside from very limited *in situ* data from monitoring programs). However it is obviously important to recognize that upwelling alone is not a linear driver of primary production, as the physical qualities (temperature, salinity, nutrients, oxygen) of the source waters and depth of the thermocline, as well as the intensity, duration and frequency of upwelling events, are just a few of the many mechanisms that also contribute to variable production rates in upwelling systems.

[11] As discussed in Chapter 1, the PDO represents the leading principal component of monthly sea surface temperature (SST) anomalies in the North Pacific (north of 20° N). Values for the PDO are from the JISAO/SMA Climate Impacts Group (http://tao.atmos.washington.edu/PNWimpacts/).

processes thought to influence marine smolt-to-adult survival rates, as estimated by hatchery releases and adult returns in the coastal areas of the Pacific Northwest.[12] Logerwell et al. used a general additive model (GAM) to predict survival based on winter sea surface temperatures prior to migration (a "preconditioning" index), the date of the spring transition, relative sea level during the spring of smolt migration, and winter sea surface temperature the year after smolt migration. More importantly, their model was based on sequentially evaluating conceptual and quantitative models that integrate key physical ocean processes that have long been known to complex, sequential and non-linear relationships with biological indices (Gargett 1997). Their resulting model explains 75% of the variability in coho survival between 1969 and 2000, including both monotonic declines in survival evident since the mid-1970s and high interannual variability throughout the period of the study. The use of this index here is based on the assumption that the survival of coastal coho salmon is highly indicative of system-wide variability in physical ocean conditions and consequent productivity. In support of this argument is the observation by Peterson and Schwing (2003) of a high degree of correlation between coho survival and indices of copepod biomass off of the central Oregon coast. This further demonstrates that coho salmon survival is a suitable indicator of interannual, and perhaps longer-term, variability in coastal ocean conditions and production.

All of the indices (with the exception of the coho survival index, which begins in 1969) were converted to standardized anomalies based on a climatology of 1950 to 1964, to set the baseline reasonably close to the mean the starting period of the model runs. Table 3.1 shows Pearson correlation coefficients for each of the four time series used to drive model dynamics. Note that the PDO and upwelling winds are poorly correlated, reflecting the difference between basin scale (PDO) and local (upwelling-favorable

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[12] As a result of severe declines in freshwater habitat quality, most coho salmon smolts in the Oregon Production Index (OPI) area (which includes coastal rivers and tributaries in northern California, Oregon, and southwest Washington) are produced in hatcheries. As a result it is widely held that the abundance of adult returns is related to variability in ocean survival during the first few months that coho spend at sea, in the coastal ocean habitat off of Oregon and Washington.

winds) physical processes. The PDO and transport are strongly correlated, suggesting that transport tends to reflect large scale processes, an observation further supported by the weak correlation between transport and upwelling winds. Very interesting is the observation that all of the physical indices are moderately to strongly correlated with the predicted coho survival index. This should not be surprising, given that the index itself is a reflection of non-linear relationships between multiple (local) physical indices that are themselves functions of both local and basin-scale processes. Instead, this is encouraging, as it suggests that the coho survival index is an integrated indicator of a suite of physical conditions, and as such may be an appropriate proxy for a physical forcing factor in this model.

The climate indices were used here in two ways. The first, most comprehensible, manner in which they were used was as simple, “bottom-up” forcers of primary production over time. In other words, the indices were scaled to range between 0 and 2 and used to drive the relative biomass of primary producers in the model. The second way in which indices were used were as “top-down” forcing mechanisms that mediate the predatory impact (consumption), and consequently production pathways, of mid-trophic level consumers by altering the vulnerability of their prey to predation. The intent is both to represent the effect of an increase in predator abundance (and thus predation) associated with changing spatial distributions of migrant species (hake, sardine and mackerel) during warm/low southward transport periods, as well as to reflect greater reproductive success of salmon, rockfish and other species during cool/high southward transport periods. This is done by creating a dummy biomass pool in the model, that is driven deterministically by the climate time series. This biomass pool in turn is used to “mediate” the vulnerability of prey to select predators, such that the value M_i in equation 3.3 in any given time step is equal to the value of the input climate time series (scaled between 0.5 and 1.5, such that a value of 1 would have no effect). Although this is not strictly a “top-down” mechanism in the sense that it is driving changes in the very top of the food chain (marine mammals, seabirds, piscivorous fishes, fisheries), it is driving massive changes in the community behavior, and possibly structure, very close to the top of the food chain by increasing the consumption (and consequently, the production) of select model components at the expense of others. While a more appropriate moniker for this forcing might be "middle-out" in the sense of Cury et al. (2000), for the purposes of this exercise we will maintain the terminology of "top-down" climate forcing.

This application of climate indices to drive the model is consistent with the conceptual model developed in Chapter 1. In particular, Dorn (1995a), Ware and McFarlane (1995) and Swartzman and Hickey (2003) have all clearly demonstrated a high sensitivity of the northerly extent of hake distribution to sea surface temperatures (which tend to occur in periods of low transport) in the northern part of the California Current, a characteristic shared by Pacific sardine and mackerel (Emmett and Brodeur 2000, McFarlane 2002). Consequently, there is greater predation by hake in such years, presumably to the detriment of other elements of the ecosystem, which can be represented by increasing the vulnerability of euphausiids, forage fish and other hake prey to predation. By contrast, Mantua et al. (1997) showed that many west coast salmon populations are more productive during cooler conditions (negative phases of the PDO), Hare and Mantua (2000) demonstrated that recruitment for many west coast groundfish stocks, particularly rockfish (*Sebastes*) species, respond similarly (poor recruitment during warm conditions), and Ralston (pers. com) has demonstrated that rockfish reproductive success (as indexed by juvenile abundance) is extremely poor during periods of low transport in the California Current.[13]

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[13] Over twenty years of midwater trawl surveys for juvenile rockfish along the central California coast suggests that year class strength is set early in the pelagic stage, that abundance of pelagic juveniles can vary by three orders of magnitude, and that there is strong synchrony in relative abundance among species (Ralston and Howard 1995). Ralston (pers. com) have also used these data to demonstrate that year class strength is strongly correlated to environmental conditions, as manifest through the large-scale flow patterns in the California Current, such that the abundance of juveniles is greatest when equatorward geostrophic flow is strong, as indexed by depressed relative coastal sea level measured by tide gauges. Since 1999, ocean conditions for many of these species have improved considerably, and it is progressively obvious that good recruitment years are associated with cool coastal ocean temperatures,

Little is certain regarding the interactions between most NCC flatfish and climate, although both Hare and Mantua (2000) and Hollowed et al. (2001) found that recruitment and productivity of many flatfish in the Gulf of Alaska seems to be greater during positive PDO conditions. The strongest relationship for flatfish came from Clark and Hare (2002), who found a link between Pacific halibut recruitment and the PDO throughout the range of halibut, a trend consistent with survey and catch data for halibut in the NCC. Taken with survey and stock assessment trajectories for many other flatfish species in the California Current, this would suggest that many NCC flatfish populations may also be positively correlated with PDO anomalies. While a split-pool or stage-based model would be more appropriate for building a climate mechanism through increasing juvenile production, for our purposes the direct connection to raw biomass will suffice. Most importantly, this is done in a manner consistent with both the evidence and the conceptual models that have been used to describe the role of these species in this region.

The simulations were compared with the data (stock assessment results, survey information and catches) for 24 of the model components most significant in commercial fisheries by using a negative log likelihood estimator. Likelihoods were estimated in the following manner. First, abundance data were scaled to the model output by computing a relative abundance factor q, where:

Equation 3.4
$$q = \log \frac{B_{obs}}{B_{pred}}$$

for each year, where B_{obs} is the observed data and B_{pred} is the model biomass prediction. The average q over all years was then estimated to be the scaling factor, such that

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high equatorward transport, and enhanced productivity throughout much of the California Current System.

Equation 3.5 $$B_{adj} = \frac{B_{obs}}{\exp(\overline{q})}$$

Negative log likelihoods for each simulation were then generated by estimating the mean likelihood error (MLE) for each time series, estimating the likelihoods with a probability mass function (done in Microsoft Excel using the *normdist* function) for each observation, and taking the negative log of that value. The negative log likelihoods are summed across all years for each group, and across all groups to get a total negative log likelihood for the simulation.

Total negative log likelihoods for the key model runs, are reported in Table 3.2. These include a run with no climate, runs with a single bottom-up index, runs with a single top-down index, and runs with both a bottom-up and a top-down index,. The results demonstrate that adding some of the climate indices as a forcing factor improves the fit modestly to substantially, an obvious exception being the addition of upwelling as a bottom-up forcer. The resulting likelihoods were further evaluated using a likelihood ratio test (Hilborn and Mangel 1997) in which the number of parameters was assumed to be equivalent to the number of years of climate indices included in the model. The likelihood ratio assumes that the more complicated model would fit the data better, such that $\mathbf{L}\{Y|M_A\}>\mathbf{L}\{Y|M_B\}$, and the significance can be evaluated with

Equation 3.6: $$R = 2[\mathbf{L}(Y|M_A)-\mathbf{L}(Y|M_B)]$$

Where R has a chi-square distribution with the degrees of freedom equal to the difference in the number of parameters between models B and A. Although the climate indices themselves are not free parameters, but rather fixed values based on *a priori* assumptions of their significance to ecosystem dynamics, this approach to measuring the relative improvement in model fit among models of differing complexity is appropriate. The results of the likelihood ratio tests are given in Table 3.3, and discussed in greater detail throughout the remainder of this section.

A selection of the resulting simulations are shown as Figures 3.5 through 3.13. In these figures, the first panels show the 24 model components that were used to estimate fits, all but three being assessment or survey abundance estimates. As abundance estimates are non-existent for pandalid shrimp, Dungeness crab or salmon, reported catches (absolute, not relative) were compared to predicted catches for these groups. Additionally, the second panel for each run shows the behavior of another 9 model components as “indicators” of how different trophic levels behaved throughout the simulation. In these panels, select indices of relative abundance from a range of sources were shown for scale only (these were not used in estimating likelihoods), with the intent being to show which simulations capture different modes of variability better than others. The lower trophic levels included were copepods, for which recent (1996-2003) relative abundance estimates by Peterson (pers. com) were used for scale; euphausiids, for which model estimates from the simulation for the La Perouse Bank region (Ware and Robinson 1999) were used for scale; forage fishes, for which relative abundance estimates from the triennial groundfish trawl survey were used for scale, and cephalopods, for which no even moderately informative index exists. Also shown are sardines, with the (dramatic) trend from the most recent coastwide assessment by Conser et al. (2003) shown for scale; murres, for which no relative abundance index is available; harbor seals, with counts reported in Carretta et al. (2002) included for scale; sea lions, with pup counts from southern rookeries of California sea lions shown for scale, and baleen whales, with estimates of California Current wide humpback whales shown for scale.[14]

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[14] Recall that many marine mammal populations (including all of those pictured in the figures) had increasing trends built into the 1960s starting values, such that the 1990s biomass estimates approximated biomass estimates for that period; however even these increases pale in the face of the dramatic increase of the California sea lion in southern waters, shown for scale in the sea lions box despite the fact that the vast majority of the population is distributed south of Cape Mendocino.

The second panel for each run also shows are the observed and predicted catches for the 21 model components for which biomass estimates were used for fitting. Note that the “observed” catches here represent only reported landings for unassessed species (they include assessment estimates of discards for assessed species), the discrepancy between the observed and predicted landings in the unassessed groups (shelf and slope rockfish, small flatfish, rex sole, arrowtooth flounder, skates and dogfish) is based on the catches of those species being forced by their bycatch relative to total landing. These are estimated based on observed bycatch rates (relative to total catch) from the Pikitch et al. (1988) bycatch study, which were incorporated into the catch composition of the fishing fleets at the beginning of the simulation. Note that neither the model groups nor the catches from the second panel were included in estimating likelihoods. Instead, they are shown solely for informative purposes. For most species, it is clear that predicted catches are very similar to observed catches, which is not surprising given that simulations are run with fishing mortality rates based on the assessments themselves. For several, such as small flatfish, rex sole, skates and dogfish, “catches” are substantially higher than landings, reflecting the high discard rates observed by Pikitch et al. for these groups. Interestingly, catches and reported landings for dogfish and skates in particular do seem to converge in later years, as limited fishing opportunities and increasing market opportunities may have led to increased retention.

The first run (Figures 3.6 and 3.7) are simulations with only fishing mortality and effort as a factor, and the result makes it clear that fishing mortality is the principal top-down forcing function for most of the groups in this simulation. This is particularly true for rockfish, roundfish (sablefish and lingcod) and Dover sole. There are also suggestions of the observed increases in other flatfish, such as English sole, rex sole and others, that may be associated with decreasing predation on these species by sablefish, lingcod, hake and other piscivores. The fit of Pacific hake is notably poor, which is not necessarily surprising given that hake are a coastwide migrant in which recruitment is largely a function of processes outside the NCC. While the fits to pandalid shrimp and

Dungeness crab landings are not remarkably poor in light of the nature of the forcing function (poorly defined units of effort), they do lack some of the highly variable patterns exhibited by these stocks in actual landings (and presumed abundance). Furthermore, the near tripling of salmon landings (which are a model index of biomass, based on a constant mortality rate) is clearly unrealistic; although this is largely a reflection of the inability of the model to account for salmon life history patterns (iteroparity and migratory behavior) adequately.

If we run the model with bottom-up forcing, running the model with upwelling only actually decreases the fit (total negative log likelihood increases from –329 to -192), and clearly does not improve model performance. Given that the wind-driven upwelling index excludes so many relevant factors to productivity (such as ocean temperature, depth of the mixed layer, and nutrient concentrations), this result is not terribly surprising.[15] Yet running the model with the Oregon coho survival index improves the fit substantially (from –329 to –369, Figures 3.8 and 3.9), and more important, significantly based on the likelihood ratio test. Much of the improvement in likelihood is observed in the highly dynamic indices for shrimp, crab, salmon and lingcod. Interestingly, some components show reduced fits, particularly the long-lived and slow growing species (canary rockfish, sablefish, dover sole), for which abundance would be expected to change little in response to high frequency climate signals.

Running the model with the top-down climate forcing also results in substantially greater improvements to model fits. With top-down (but no bottom-up) forcing, southward transport improves the likelihood from –329 to –337, but is not significant

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[15] Another explanation, beyond simply the disconnect between singular indices physical forcing and biological productivity, might be based on the observations of Mendelssohn et al. (2003, and references therein). They point out that although wind-driven upwelling seems to have increased in parts of the California Current over the last several decades, this increase has occurred in concert with overall warming trends throughout the Northeast Pacific (including the California Current) that has likely been associated with a decrease in the nutrient content of (upwelling) source waters. In other words, greater stratification, a deeper thermocline and warmer source waters may have (in a very general sense) resulted in declines in primary and/or secondary production, despite increases in upwelling winds over time.

with respect to the likelihood ratio test. By contrast, the PDO improves the likelihood to –389, the best likelihood estimate among all of the simulations, and with regard to AIC (Figures 3.10 and 3.11). Interestingly, likelihood for both transport and the PDO decreases in both cases when upwelling is added as a bottom-up index, resulting in likelihoods greater (poorer) than the simulation with no climate whatsoever. When transport is also run with the coho index (Figures 3.12 and 3.13), the likelihood improves (from –337 to –364), but the large number of parameters associated with using two indices immediately suggests that this simulation does not pass the likelihood ratio test. Interestingly, when the PDO and coho survival are run together as top-down and bottom-up respectively, the overall likelihood is greater than when the model is run with the PDO alone; suggesting this model is a poorer fit than using either index independently.

It is interesting that the top-down indices seem to improve the model fit considerably more than bottom-up forcing. This suggests that large-scale physical changes in the dynamics of the NCC may be more important than local forcing, as widely acknowledged to be true based on the review in Chapter 1. However, a scenario that includes both bottom-up and top-down forcing is more consistent with what is known about the system, particularly given the magnitude of bottom-up variability suggested by not only coho survival, but by observations on significant year to year variability in secondary production throughout the California Current as described by Chelton et al. (1982), McGowan et al. (1998), Peterson and Schwing (2003) and many others. Another problem is the lack of appropriate time series. If adequate data and resolution of lower trophic model elements (zooplankton, forage fish, cephalopods) existed, it would be quite reasonable to expect that bottom-up forcing could likely result in significantly greater model performance. In either event, providing a reasonable range of model scenarios and forcing functions might be likened to the practice common in single-species stock assessments, in which a suite of models using a range of estimates for natural mortality, catchability, or other key parameters are presented to managers and decisionmakers.

Despite this, the model run with top-down (PDO) climate forcing on predators seemed to provide the best fits to the available time series. Select results from this model will be discussed as examples of the types of inferences that these efforts can address. First, however, we consider a final visual image of the results of the dynamic model. Figure 3.14 shows the significant food web of the NCC, as shown in Chapter 2, with changes in biomass in 2003 relative to starting (1960) conditions represented by color. Red boxes indicate model elements that have declined relative to their starting values, green boxes indicate elements that have increased (flows between boxes are modeled the same way). The end year 2003 was chosen as it represents a year of high productivity, such that most forage groups are very abundant. A fair number of commercially important species are green as well, including salmon, shrimp, sardine and many flatfish. Many marine mammals (harbor seals, sea lions, and baleen whales) are at significantly greater levels of abundance as well. However many rockfish and roundfish are slightly to very red, representing a significant fraction of the low-turnover, mid-trophic level biomass that has been removed by fishing. Clearly, a large group of stocks in this ecosystem no longer fill the functional role that they used to. Graphic outputs such as these are useful in evaluating, even simply appreciating, the consequences of fishing and other impacts on the structure of marine communities.

3.7 Select Model Results

That much of the variability observed in single species models and dynamics can be replicated in this multi-species modeling approach is both encouraging and informative for several reasons. Perhaps most important is the finding that model performance can be improved significantly when climate is introduced as a driving force, given the *a* *priori* assumption that climate variability on multiple scales are key variables in determining productivity and dynamics in this ecosystem. In one sense, these model fits are slightly incestuous, as most of the parameters for assessed species in the ecosystem model are based on the results of the assessment models to which ecosystem model trajectories are compared. Yet this may be insightful in its own right, as convergence implies that there do not appear to be obvious changes in ecological structure that have resulted in strong interspecific interactions (predation, competition) between most of these species. This makes sense for many of the rockfish, roundfish and longer-lived flatfish, where low mortality rates are indicative of low predation rates and trophic interactions. Stronger interactions are more likely to be observed in species such as shrimp, salmon and small flatfish where there is high turnover and high predation coupled with substantial changes in many of their key predators (hake, sablefish, marine mammals) over the last forty years.

The first example is a modest snapshot of what appears to be largely competitive interactions between hake and salmon. Both prey heavily on euphausiids and forage fishes; hake more so on the former, salmon more so on the latter. However both the biomass and landings of hake dwarf those of the much less abundant, yet proportionately more economically important salmon. Figure 3.15 shows the trajectories of both stocks estimated by the model, simulated with and without the observed historical fishing effort on hake (corresponding to the simulation shown in Figure 3.10 and an unfished ecosystem respectively). Throughout the modeled period there is a slight increase in the estimated biomass of salmon with the existence of a hake fishery, relative to that without a hake fishery, which can be attributed to the decreased competition for forage (similar responses are observed for other competitors). What is especially interesting is the extremely rapid response of salmon to the increased productivity throughout the food web following the shift in ocean conditions in 1999. With the hake fishery maintaining high fishing mortality during a period of sharp declines in biomass in the late 1990s, the “fished” biomass is between one half and one-third the “unfished” biomass at the initiation of the regime shift. The response of salmon under the two scenarios is similar, salmon increase immediately after 1999 in both models, but respond faster, and with a much greater magnitude, when the hake biomass is low as a result of fishing. With their much faster turnover rates, salmon are well suited to take advantage of short-term boosts in productivity, an advantage that is considerably enhanced when the abundance of other species has been reduced. The flip side to the equation is the observation that migratory hake and slow growing groundfish fill a role in stabilizing the system, by dampening what might otherwise be even greater responses to rapid changes or short-term bursts in production (Apollonio 1994).

The second example also considers the impact of hake, as well as fisheries, on the pink shrimp (*Pandalus jordanii*). Many studies have either suggested or demonstrated a strong interaction between hake and shrimp (Gotshall 1969, Rexstad and Pikitch 1986, Hannah 1995), and the results of this evaluation also suggest that hake represent one of the principal sources of mortality for shrimp. Figure 3.16 shows the model estimated total mortality, relative biomass, and relative sources of mortality over time for ocean shrimp. The starting conditions suggest that hake accounted for slightly less than half of total shrimp mortality, although errors in the diet composition estimates (or consumption rates) of hake or other predators could obviously bias this result. Furthermore, the total mortality of shrimp seems to be very responsive to the abundance of hake, increasingly dramatically in the mid 1980s when the hake biomass nearly tripled. This, in turn, contributed to the low biomass levels of shrimp throughout most of the 1990s. By contrast, the total mortality from fishing would seem to be at least somewhat modest in contrast to that of hake. Fishing likely accounted for roughly 20% of the total shrimp mortality over time, generally less than half that of hake, even during the period when landings first peaked (then declined) in the late 1970s. In this instance, the fishery may indeed be behaving similar to a top predator, even appearing to stay within the frequency distributions of predation rates by other species in the sense of Fowler (1999).

The next example revisits one of the balancing issues from the initial Ecopath model, the interaction between sablefish as predators of longspine thornyheads (*Sebastolobus altivelis*). As described in section 2.3, the observation that thornyheads (of both species, but primarily *S. altivelis*) are a key prey item of sablefish, as suggested by several food habits studies, is inconsistent with the estimated abundance, consumption and production of both of these species. Although careful evaluation of the food habits data from the two principal food habits studies on this coast demonstrates that net feeding is at least partially responsible for overestimating the importance of thornyheads, a strong interaction is still indicated by the available data. Even more true is the observation that sablefish represent the major source of predation on longspines, with modest predation by shortspine thornyheads, and limited predation of pelagic juveniles by hake, salmon and other predators (accounted for in the juvenile rockfish group in this model).

Figure 3.17 shows the estimated trend in predation and fishing mortality for longspine thornyheads, as well as the estimated model biomass for longspine and its two primary predators, sablefish and shortspine thornyheads. Essentially the model suggests that natural mortality rates for thornyheads have fallen by nearly fourfold over the past forty years, to less than 25% of the 1960s level, coincident with the decline in predator abundance. While this has been associated with a substantial increase in fishing mortality, especially since the late 1980s, total mortality has declined significantly with recent reductions in fishing mortality. While the 1996 stock assessment, assuming a constant natural mortality rate, predicted declines in longspine abundance beginning in the early 1990s, the consequences of reducing their major predators suggests that the biomass should have been largely stable, or increasing, over recent time. The lack of any discernable trend in the slope survey data that exists for the 1990s lends support to this hypothesis. At a minimum, this is a consideration that could be qualitatively, if not quantitatively, taken into account in future both future stock assessments and in future consideration of the impacts of fishing on community structure.

The next two examples address the issue of fisheries/marine mammal interactions, which are undoubtedly issues that fishermen, fisheries biologists and many other stakeholders identify with ecosystem interactions. Throughout the California Current, pinniped populations have increased substantially over the past four decades, following nearly two centuries of intensive hunting and culling. However both the total abundance, and the rate of population increase, have been modest north of Cape Mendocino, relative to the south. These increases were parameterized into the starting conditions of the NCC model, in order to arrive at abundance levels equivalent to marine mammal assessment estimates of abundance in the 1990s. Although the relative impact of marine mammal predation on forage fish, cephalopods, and other lower trophic level groups seems to be fairly low in contrast to that of other predators, marine mammals (particularly pinnipeds) represent an important source of mortality on commercially important stocks of roundfish, rockfish, flatfish and migrants such as hake. A logical assumption to make would be that the increase in marine mammal abundance over recent decades may have resulted in an increase in natural mortality rates from predation, this during a time when fishing mortality rates were (generally) increasing dramatically as well.

Figure 3.18 shows the total (model) biomass of five key stocks of rockfish in the NCC over the last 42 years, along with estimates of the total sources of mortality for these stocks. In the 1960s, other piscivorous fishes (principally sablefish, lingcod and other species of rockfish) represented the greatest source of mortality for rockfish, with marine mammals and fisheries also comprising a substantial fraction. In the 1980s, fishing mortality clearly surpassed natural mortality, which correspondingly declined as other predators of rockfish were themselves substantially depleted. Interestingly, the simulation suggested that the total amount of mortality resulting from marine mammals stayed roughly constant, implying a decline in the relative consumption of rockfish as the rockfish stocks declined and pinniped stocks increased. The extent to which marine mammals may have shifted their diet preferences relative to the impacts of fishing on minor components of their prey is explored in Figure 3.19. This figure shows the model predicted changes in total pinniped biomass, which more than doubled over the duration of the model, and the composition of the total estimated biomass of pinniped prey over the same period. Food habits, based principally on studies from the 1960s, show that commercially important groundfish make up only a modest proportion of most pinniped diets. With declines in many of these species, particularly rockfish, the model would suggest a modest shift away from groundfish and towards increased forage fish and cephalopods (the principle "non-target" species, which also includes mesopelagic fishes). One exception might be predation on small flatfish, which seem to have increased significantly over the last twenty years, and increases in salmon predation in very recent years. Although these results are based on poorly quantified (and somewhat dated) food habits, as well as uncertainties in the nature of prey switching by pinnipeds, this would suggest that the direct impact of marine mammal recoveries on rockfish and other commercially important pinniped prey is negligible.

The final example is intended to cast light on the tremendous uncertainties in both data, the ecosystem, and in model dynamics. From the earliest versions of Ecosim, Walters (1997) has acknowledged the challenges inherent in representing prey switching by predators, particularly in ecosystems characterized by extreme changes in physical conditions and the abundance of highly variable species. This is especially true where diet composition data may be used that is not representative of the time period being modeled (Plagányi and Butterworth 2004). For the NCC, only sporadic food habits data exist for most species, but the most important predator in the ecosystem, Pacific hake, is an important exception. For hake, quantitative food habits data exist for the mid 1960s, and most of the 1980s and 1990s. As discussed earlier, early food habits studies did not suggest high levels of cannibalism, but in the late 1980s and through the 1990s, cannibalism was widespread, and data suggest that an average of 30%, and in some years as much as 70%, of hake prey by volume was other hake. As Figure 3.20 shows, the simulated prey composition was unable to capture this change in food habits. Several factors may have led to this, including the anomalous nature of climate conditions and widely recognized low levels of production throughout much of this period, as well as the absence of split-pool groups in modeling juvenile-adult interactions. A stage-based, or even fully age-based model of hake and other key predators and prey might be able to improve on our understanding of such interactions, particularly if accompanied by climate drivers that replicate the low productivity and perhaps changes in spatial distribution of juvenile and adult cohorts. However it is clear that equally important instances of prey switching and diet shifts may have occurred for species in which no long term diet data exist. Consequently, the interpretation of trophic interactions and predictions need always be tempered with the limitations of data, knowledge and inference regarding the stocks and species being modeled.

These examples of model insights are typical of the finer scale insights that can be inferred from ecosystem modeling, as well as typical of the limitations in doing so. Such insights could be useful in developing qualitative scenarios of interacting ecosystem consequences of fishing, climate forcing, and marine mammal recoveries. In all of these results however, one certainly appreciates the considerable uncertainty in such scenarios, in particular the very subtle changes over time that govern prey selection and are unavoidably unrealistic with regard to a multitude of aspects in foraging behavior and the relative importance or abundance of prey. To a large extent, this is model uncertainty that simply cannot be overcome in this class of models, however there is an element of uncertainty in the parameter values themselves that can be addressed and confronted quantitatively. Doing so may allow us to determine which types of ecosystem impacts we might feel “confident” in predicting, versus those for which there simply is not sufficient data nor evidence to consider realistic.

3.8 Addressing Parameter Uncertainty

Multispecies and ecosystem models are confounded by data limitations not simply in biomass, catchability and growth rates, but in consumption rates, transfer efficiency, diet composition, and functional responses throughout a complex and poorly documented food web. That uncertainty envelops all model parameters (observation and parameter uncertainty), as well as the behavior of the model itself (model uncertainty) is unavoidable. However, Aydin et al. (2003) have demonstrated that some of the unavoidable parameter uncertainty in models such as this can be confronted quantitatively, and in doing so it can often be demonstrated that the direction and magnitude of effects from perturbations (be they climate, fishing or other) is at times consistent over a wide range of starting parameter values. In such instances, a greater degree of confidence can be expressed in the direction and magnitude of change for some of the more poorly known components of the ecosystem.

The approach taken by Aydin et al. (2003) is summarized here, and three simple examples of the insights that might be gained by using such an approach are presented. The first step is to assign coefficients of variation as indices of the estimated error for each input parameter (B, P/B, Q/B, diet compositions, and catch ratios by fleets). These estimates typically range between an error index of 10% of the point estimate (for a parameter with low uncertainty) to 80% (for a parameter with high uncertainty). As actual estimates of error are nonexistent for the vast majority of model parameters, this data grading is done qualitatively, based on a standard set of criteria developed explicitly for the purpose of evaluating the confidence in a given parameter. For example, a biomass point estimate from an age-structured stock assessment model might be given a high degree of confidence (10 or 20% error), a biomass point estimate based on raw survey biomass point estimates might be given a moderate degree of confidence (50% error), and a biomass estimate generated by the model (in the top-down balance) might be given a very low degree of confidence (80-90% error). A predetermined number of "potential" ecosystems (usually between five and twenty thousand) is then generated by drawing randomly from uniform distributions around each parameter and interaction term; the details of how diet compositions and other co-varying parameters are selected is given in greater detail in Aydin et al. (2003).

The resulting ecosystems are not in equilibrium, there are generally biomass accumulations for all groups in response to the changing abundance of their predators and/or prey. However, because the uncertainty in the base of the food web is considerably greater than that for (most) higher trophic level model components, the higher uncertainty associated with estimates of lower trophic level abundance and productivity leads to a high percentage of models in which lower trophic level production is simply too low to support the rest of the foodweb, and consequently a subset of functional groups tend to "die-out" over a moderately short (30 year) time period. To address this "thermodynamic inconsistency," Aydin et al. (2003) subsampled the resulting ecosystems by discarding those ecosystems in which at least one group had increased, or decreased, by more than 1000-fold over a 30 year period from the base model output. The result is that only parameter sets that allow ecosystems in which all species can persist over a reasonable time frame are retained. Perturbations can then be applied to the resulting subset of models, such that the difference between the baseline (no perturbation) simulations and the perturbed simulations can be evaluated to assess whether there are consistent responses of given model components to perturbations across a wide range of parameter values. Where such perturbations tend to result in consistent responses, there can consequently be greater (albeit by no way perfect) confidence in the direction and magnitude of ecosystem impacts to some elements of the food web.

Three simple examples of responses to perturbations for components of the NCC model are shown here, as examples of the potential utility of this approach. Table 3.5 shows the same model parameters as table 2.2, but color-coded to reflect the "base uncertainty" given to each of the model parameters in the 1960s model (green represents a CV between 0.1 and 0.3, yellow between 0.4 and 0.6, and orange a CV between 0.7 and 0.9). Five thousand potential ecosystems were generated, the first 1200 accepted ecosystems were considered for this example. The perturbation applied to these 1200 ecosystems was the changes in fishing mortality rates and fleet effort trajectories for the period between 1960 and 2003, with fishing mortality rates driving the dynamics of the assessed species, and changes in fleet effort driving the dynamics of unassessed species (with the caveat that the relative catch ratios for the unassessed species were resampled over their range of uncertainty, which are reflected as the color-codings on the "total landings" column of Table 3.5). The trajectories of biomass estimates from 44 years of simulations for the baseline runs was removed from the trajectory of biomass for the perturbed runs to arrive at a difference between the baseline and the perturbed run for each sample ecosystem.

Figure 3.21 shows the results of the first 200 resulting trajectories for the small flatfish group in the NCC, providing both a vision of the variability in trajectories as well as a sense of the consistency in the direction of change among them. In all of the trajectories the result of the perturbation of historical fishing effort was to increase the total biomass of the small flatfish box, despite generally greater fishing pressure on this model component overall (in a large part related to the growth of the shrimp trawl fishery over this period). In essence, this suggests that the release of predation pressure, as many of the more significant predators of small flatfish declined as a result of fishing, was sufficient to overcome changes in fishing mortality over time and resulted in an increase in abundance for this functional group. Although this functional group really consists of a wide range of species, including many that may themselves prey on the more abundant species of small flatfish, the general result would appear to be consistent with the increase in many small flatfish species (including species such as English sole and Petrale sole) that has been suggested by the triennial survey data over the last 25 years (see Appendix A for more details). The median level of increase in this example is 30%, with the 5th and 95th percentiles suggesting 16 and 90% increases in relative abundance respectively. Although changes in survey design and target assemblages, as well as either local or basin-scale climate conditions, may also be relevant to the observed survey trends (in particular, early surveys were explicitly intended to sample rockfish populations), this exercise suggests that trophic interactions may be an important factor in explaining these trends.

Figure 3.22 shows a slightly more complex example, based on the early described interaction between sablefish and longspine thornyheads. In this example, the trajectory of longspine thornyheads only is shown, in which the relative abundance tends to slowly increases from the baseline over the first 25 years of the simulation, declines sharply between 1985 and 1995, then rebounds back to an increasing trajectory after 1995. This could be explained by the decline in predation rates on longspine thornyhead between 1960 and 1985, when both sablefish and shortspine thornyhead populations were declining as a result of fishing, followed by an increase in fishing mortality in the mid- and late- 1980s when increasingly limited fishing opportunities and growing markets resulted in an increase in fishing effort for the deepwater complex (sablefish, dover sole, short- and longspine thornyheads), followed by the combined effects of reduced fishing mortality and predation when fishing pressure eased (despite remaining significant) in the mid to late 1990s (as shown in Figure 3.17). Also shown in this figure are the trajectories from the 1997 stock assessment by Rogers et al. (1997), and the most recent (1998-2002) point estimates of biomass from Northwest Fishery Science Center surveys. Note that the early biomass estimates from the most recent assessment were based not on survey data, but rather on model estimates of unfished biomass; there is no evidence to suggest either a downward or upward trajectory in early slope survey biomass estimates. Similarly, whether the results of recent survey estimates truly suggest an upward trajectory is unclear, the uncertainty around these estimates (not shown) is significant. However it seem reasonable to expect that substantial declines in predation mortality have occurred for this species, and may offset, at least partially, increases in fishing mortality associated with the changes in fishing strategies in recent decades.

The final example, Figure 3.23, is simply meant to illustrate that even with statistically vigorous efforts to confront at least some of the many sources of uncertainty in models such as these, there still may be instances where the insights generated by such models are limited. The figure shows the trajectories for both "perturbed"' and baseline scenarios for all pinnipeds in the NCC model (as a reminder, all of these had a baseline "biomass accumulation" term to reflect observed population increases over the last 45 years), in which it is clear that there is no clear signal with regard to the impact of increased fishing on pinniped population behavior. This in no way is to infer that fishing has had either a negative, or positive, impact on these groups; rather to illustrate that within the limitations of the models structure and behavior, there is no clear impact of fishing on these model components. As shown in Figure 3.19, the model would suggest that as the commercially important pinniped prey populations have declined as a result of fishing (rockfish, roundfish, hake in the late 1990s), pinnipeds are likely to have switched to a greater proportion of forage fish, cephalopods and small flatfish. Whether such prey switching is feasible or realistic, or indeed even energetically efficient, are clearly issues that must be addressed with more focused studies rather than models that have little or no resolution with regard to the relative foraging costs or caloric value of alternative prey when evaluating scenarios such as this. Yet despite such shortcomings, this approach to addressing a significant amount of the uncertainty that we know exists is a useful one, and is clearly one that could be more appropriate with regard to evaluating past or future impacts of fishing and predation on some of the more poorly understood elements of the ecosystem.

3.9 Modeling Plausible Scenarios of the Future

There is generally consensus that science is not in a position to make reliable forecasts about the behavior of complex systems, such as global or regional climate dynamics, ecosystem behavior or disease outbreaks (Levin 1998, Mantua and Mote 2002, Gunderson et al. 2002). With climate in particular, we have been repeatedly cautioned to avoid the expectation that the climate conditions of the future will resemble those of the past (Mantua and Mote 2002, Bond et al. 2003). Consequently, this final exercise promises results which are little more than plausible scenarios that, one would hope, serve to at least bracket a reasonable range of climate and fishing futures in this ecosystem. They are meant to illustrate the nature of these models as a strategic, rather than a technical, predictive tool in evaluating potential interactions between climate and fishing into the future.

It is often said, and generally believed among fisheries biologists, that single species models have predictive value while multispecies models do not (Goodman et al. 2002, NRC 2002). As both are ultimately based on similar assumptions of surplus production and compensatory behavior, this can be a difficult charge to make. Berkes et al. (2003) discuss a similar contradiction when they demonstrate that despite the fact that most ecologists or population biologists have recognized as myth the notion of the balance of nature, most continue to view single species and ecosystem behavior as quantitatively predictable, at least in theory, given more data and research. The implications of believing in one worldview versus the other is critically important to the nature by which we manage natural resources. As Barry (2000) puts it, believing that either species or ecosystem behavior is predictable in theory is dangerous, for “As soon as a mystery is scheduled for a solution, it is no longer a mystery; it is a problem. The most tyrannic of all reductions has thus been accomplished; a self-aggrandizing science has thus asserted its “proprietary sense of the future.” Similarly, when model predictions are treated as expectations rather than plausible scenarios (be the model ecosystem, single species, climate, economics or other), those with the responsibility for making decisions may be lulled into believing that the behavior of such systems is nearly understood, and that future dynamics can consequently be effectively predicted.

Such predictability would reduce the extent to which we would worry about the inherently unknowable and unpredictable catastrophes of the future, for we will be able to see them coming, and can steer ourselves away from them. However such predictability is also a fallacy in complex systems. As opposed to the (relatively) immovable laws of physics, systems such as climate, ecosystems and national or global economies behave in nonlinear and complex ways that are, and will remain, difficult to quantify (Levin 1998). Yet if this is true, than how can any of these models be useful in conveying the potential consequences of impacts to such complex systems to decisionmakers? Without at least a moderately tangible product, prediction, or trajectory to respond to, policy or decisionmakers are not likely to react. Similarly, presenting a range of highly qualified model results and behaviors passively and indecisively is little more than an offer to ignore any results or insights that may be meaningful. It is also true that overselling a prediction or belief in a model result can be equally dangerous; both in terms of the potential consequences of the decision if the result is wrong and the confidence in the science for future predictions. This dilemma is an important one, and one that should not be far from the mind of anyone involved with developing, delivering or evaluating model predictions based on such complex systems. Clearly, the ultimate objectives are to engage managers and stakeholders in a meaningful dialogue that emphasizes the likely or plausible consequences of management decisions, and allows them to thing strategically about species interactions, and ecosystem dynamics.

The general approach is based on repeating historical patterns of climate deterministically as a first order evaluation of possible consequences and interactions with fishing mortality. The best fitting model from the previous section (using PDO as a top-down forcing mechanism) was run forward to 2020 with fishing set to approximate 2003 mortality and catch rates. The three runs shown as Figures 3.24, 3.25 and 3.26 were run under assumptions of PDO neutrality (equivalent to no climate forcing) positive PDO conditions (resampling the 1978-1998 index), and negative PDO (resampling the 1960-1977 index) respectively. Although the differences between these three runs are subtle, they are significant with respect to catches and population trends. While some stocks undergo rapid recoveries and population increases, note that these are associated with extremely low catch levels; the catch of widow rockfish is on the order of 1/100th the catch in 1981, and even yellowtail rockfish catches (one of the healthier stocks) are minimal. Despite minimal fishing mortality for canary rockfish, recovery is extremely slow; and note that while the trend for Pacific ocean perch looks encouraging, the (1980) benchmark already represented a decline to less than 20% of the historical abundance. Interestingly, in these simulations sablefish and Dover sole population trends are downward, and while catches remain modestly high initially (at least relative to declining catches of rockfish), they taper off slowly as stocks decline. Whether this is real or a model artifact is unclear, but this result is consistent with ongoing declines estimated in recent assessment and the relatively high catches that have been maintained for these species as other fishing opportunities have waned. Hake catches are low relative to historical catches as the fishing mortality rate in 2003 was extremely low, in response to low biomass levels.

To bracket these examples, two alternative scenarios are offered. In the first (Figure 3.25), all fishing is halted in 2004 and stocks rebuild or increase on a variety of trajectories. Most might be expected to rebound to or above 1980 levels over a relatively short (5 to 10 year) time period, although for some (canary, sablefish and Dover sole) recovery is considerably slower. By contrast, Figure 3.26 shows model trajectories and estimated landings under estimated 1990 harvest rates. In this run, nearly all of the groundfish undergo substantial to devastating declines, and although catches are initially closer to 1990 levels for many stocks, they are substantially lower for others, and become lower still as many stocks decline. Dungeness crab and shrimp do remarkably well in this scenario, likely due in part to the very low levels of abundance for many of their major predators. It is perhaps a more difficult sell to believe that salmon would prosper as much as they do in this scenario, in no small part due to the inability to account for any freshwater processes, however this may represent a plausible accounting of the increased availability of food to salmon independent of freshwater habitat impacts.

Obviously, these alternatives reflect only general differences in fishing pressure, which varies from stock to stock, fishery to fishery. Considerably greater resolution at the fleet level, together with alternative catch and mortality ranges that reflect actual trade-offs between target assemblages and gear types, could make the evaluation of scenarios such as these a useful tool for managers and stakeholders coping with decisions that cut across fisheries and ecosystems. These particular scenarios are meant solely to illustrate the potential for generating more focused investigations of potential future interactions between climate, fishing and the ecosystem, based on recent patterns of fishing activity. At a minimum, the modeling framework provides an opportunity to compare single species trajectories with those that result when climate and multispecies interactions are included, to evaluate the potential for additional sources, or releases, of mortality or competition that might influence a stocks single species trajectory.

The resilience inferred to all of these stocks is troubling, as the model will allow any stock to recover from any level of fishing mortality, given time and removal of the perturbation. Yet this too is a fault shared with single species models. In presenting rebuilding plans, simulations such as these, or other model estimations it is critical to emphasize to those who consume such information as a guide that nature is not this simple. Actual outcomes may diverge substantially from those that might be expected with simplistic models, and the results could be ecologically devastating. In considering ecosystem-based approaches to management, we need far more than simply ecosystem models and scenarios, we need management options that are both cognizant of ecology and robust to uncertainty on multiple levels. Models have a critical role to play, by allowing the management community to relate to the consequences of their decisions, but neither single species nor ecosystem models alone should be the sole determinant of management strategies and alternatives.

3.10 Chapter Summary

The insights gained dynamic simulations of the NCC were encouraging given that much of the variability from landings and from single species assessments could be replicated over recent decades. Of particular interest was the confrontation of the dynamic model with various indices of climate forcing, which in turn improve the performance of the model. As with the results of the static model, dynamic simulations suggest that strong interspecific interactions have not played a tremendous role in determining the dynamics of many components in the NCC food web. This makes sense in a community dominated in part by long-lived groundfish, where low mortality rates are generally indicative of low predation rates and weaker trophic interactions. In addition to a very strong interaction between sablefish and thornyheads, significant interactions were observed in groups such as shrimp, salmon, hake and small flatfish, where high turnover rates and predation mortality is coupled with substantial changes in many of their key predators (hake, sablefish, marine mammals) over the last forty years.

Future modeling efforts would clearly benefit by the inclusion of split-pool or stage-based modeling of many commercially and ecologically important species, particularly with regard to evaluating the potential role of cannibalism as a factor in the dynamics of Pacific hake, and juvenile predation by sablefish, lingcod and larger rockfish. Future efforts should also both expand and reduce the spatial scales being considered; clearly a model of the entire California Current system would be desirable at many levels.

However one might also gain considerable insight modeling unique habitats independently, such as deep-slope communities characterized by only modest interactions with shelf or pelagic communities but significant trophic interactions within clearly defined depth ranges (sablefish-shortspine-longspine interactions). With adequate data, caution, and considerable effort in confronting and conveying the associated uncertainty involved, ecosystem models can complement the insights gained from single species models through consideration of past and current biomass and productivity, and the potential for plausible expectations of future system trade-offs between management decisions and possibly climate dynamics.

Table 3.1: Pearson correlation coefficients for environmental forcing indices, shaded boxes indicate significant correlations (at 0.05 level).

Correlations among time series (1960-2003)			
	PDO	transport	upwelling
southward transport (annual)	-0.312		
spring-summer upwelling winds	-0.171	0.290	
Oregon coho survival index	0.365	0.449	0.462

Table 3.2: Total negative log likelihood estimates of simulations under alternative climate forcing scenarios.

	Top-down climate		
Bottom-up climate	none	PDO	transport
none	-329	-389	-337
upwelling	-192	-210	-197
coho index	-369	-374	-365

Table 3.3: Total negative log likelihoods for the four most significant runs under alternative vulnerability assumptions

	no climate	Logerwell index	PDO	Logerwell and PDO
v=0.1	-166	-285	-301	-307
v=0.3 (default)	-352	-389	-391	-379
v=0.5	-313	-339	-397	-354

Table 3.4: Total negative log likelihoods, and the results of likelihood ratio tests for four of the best fitting simulations

	no climate	Logerwell index	PDO	Logerwell and PDO
total negative log likelihood	-352	-389	-391	-379
likelihood ratio (relative to no climate)		73	78	53
d.f. (number climate years)		33	45	78
Chi square		0.0001	0.0017	0.9856

.

Table 3.5 Model parameter estimates with color-coded levels of uncertainty

Group name	Trophic level	Biomass (t/km²)	Production/ Biomass	Consumption/ Biomass	Food Habits	Total catches
phytoplankton	1.0	🟨 55.150	🟨 120.00			
infauna	2.0	🟨 35.700	🟨 2.50	🟧 12.0	🟨	
amphipods	2.0	🟧 4.380	🟧 3.50	🟧 22.0	🟨	
epibenthic	2.5	🟨 12.564	🟧 2.00	🟧 10.0	🟨	🟨 0.012
micro-zoop	2.0	🟧 3.947	🟧 100.00	🟧 300.0	🟨	
copepods	2.2	🟨 16.609	🟨 14.00	🟧 70.0	🟨	
euphausiids	2.1	🟨 27.037	🟨 8.00	🟧 40.0	🟨	
carniv-zoops	3.1	🟧 7.731	🟨 2.00	🟧 10.0	🟧	
small jellies	2.3	🟧 1.342	🟨 9.00	🟧 30.0	🟧	
large jellies	3.2	🟧 1.168	🟨 3.00	🟧 12.0	🟧	🟨 0.000
pandalid shp	2.8	🟧 1.518	🟨 2.00	🟨 10.0	🟨	🟨 0.000
benthic shp	3.0	🟧 1.608	🟨 2.50	🟨 12.0	🟧	
dungeness	3.5	🟨 0.843	🟨 0.75	🟨 3.8	🟧	🟨 0.000
tanner crb	3.0	🟨 0.975	🟨 0.30	🟨 1.5	🟧	🟨 0.000
cephalopods	3.6	🟧 2.059	🟨 2.00	🟨 6.0	🟧	🟨 0.000
forage fish	3.2	🟧 27.101	🟨 1.50	🟨 6.0	🟨	🟨 0.004
mesopelagics	3.2	🟧 7.575	🟨 0.60	🟨 3.0	🟨	🟨 0.000
benthic fish	3.3	🟧 4.110	🟧 0.50	🟧 2.5	🟧	🟨 0.100
macrourids	3.7	🟨 0.468	🟨 0.20	🟨 1.0	🟨	🟨 0.000
sardine	2.8	🟧 0.663	🟨 0.50	🟨 5.0	🟨	🟩 0.000
mackerel	3.5	🟧 0.286	🟨 0.35	🟨 6.0	🟨	🟩 0.001
salmon	4.1	🟧 0.367	🟩 0.93	🟩 5.8	🟨	🟩 0.014
hake	3.6	🟨 25.990	🟩 0.23	🟩 2.5	🟩	🟩 0.141
skates	4.0	🟨 0.421	🟨 0.20	🟨 2.0	🟧	🟨 0.046
dogfish	4.1	🟨 1.000	🟨 0.20	🟨 2.5	🟧	🟨 0.028
sablefish	4.1	🟩 2.756	🟩 0.06	🟩 2.0	🟩	🟩 0.011
juv rock	3.3	🟨 0.704	🟨 1.50	🟨 6.0	🟨	🟨 0.029
POP	3.3	🟩 1.217	🟩 0.07	🟩 2.0	🟨	🟩 0.000
canary	3.2	🟩 0.757	🟩 0.10	🟩 1.6	🟨	🟩 0.045
widow	3.5	🟩 2.828	🟩 0.14	🟩 2.1	🟨	🟩 0.008
yellowtail	3.6	🟩 1.966	🟩 0.11	🟩 1.6	🟨	🟩 0.027
black	4.0	🟩 0.407	🟩 0.09	🟩 2.0	🟨	🟩 0.020
shelf rock	3.7	🟨 1.179	🟨 0.10	🟩 1.9	🟧	🟨 0.006
slope rock	3.3	🟨 0.864	🟨 0.06	🟩 1.5	🟨	🟨 0.025
ssthorny	4.0	🟩 0.751	🟨 0.07	🟩 0.5	🟨	🟩 0.017
lsthorny	3.7	🟨 1.800	🟨 0.05	🟩 0.4	🟨	🟩 0.003
juv thorny	3.4	🟧 0.714	🟧 0.50	🟧 2.5	🟧	🟨 0.009
juv round	3.2	🟧 0.247	🟧 1.50	🟧 5.1	🟧	🟨 0.000
lingcod	4.3	🟩 0.522	🟩 0.24	🟩 2.2	🟧	🟩 0.012
juv flat	3.1	🟧 0.959	🟧 1.00	🟧 4.0	🟧	🟨 0.000
english	3.2	🟨 0.600	🟨 0.35	🟨 2.1	🟨	🟩 0.057
petrale	4.1	🟨 0.326	🟨 0.28	🟨 2.0	🟨	🟩 0.032
small flat	3.4	🟧 3.684	🟧 0.50	🟧 2.5	🟨	🟨 0.026
rex	3.1	🟨 0.400	🟨 0.50	🟨 2.1	🟨	🟨 0.020
dover	3.1	🟨 3.861	🟨 0.08	🟨 1.1	🟩	🟩 0.093
arrowtooth	4.3	🟧 0.321	🟨 0.34	🟨 2.1	🟨	🟧 0.027
halibut	4.3	🟨 0.089	🟨 0.34	🟨 2.1	🟧	🟩 0.003
albacore	4.3	🟧 0.014	🟨 0.36	🟨 7.3	🟧	🟧 0.000
coastal sharks	4.4	🟧 0.050	🟨 0.18	🟨 2.8	🟧	🟧 0.000
shearwaters	4.2	🟨 0.003	🟨 0.100	🟩 138.0	🟧	0.000
murres	4.2	🟨 0.009	🟨 0.100	🟩 129.0	🟨	0.000
gulls	4.1	🟨 0.002	🟨 0.120	🟩 122.0	🟧	0.000
orcas	5.0	🟧 0.001	🟧 0.020	🟩 11.2	🟧	0.000
toothed whales	4.4	🟨 0.052	🟨 0.070	🟩 28.9	🟧	0.000
sperm whales	4.7	🟧 0.037	🟨 0.020	🟩 6.6	🟧	0.000
harbor seals	4.4	🟨 0.004	🟨 0.084	🟩 17.4	🟨	0.000
sea lions	4.5	🟨 0.012	🟨 0.074	🟩 16.4	🟧	0.000
fur seals	4.5	🟨 0.006	🟨 0.091	🟩 39.0	🟧	0.000
grey whales	3.0	🟧 0.008	🟨 0.037	🟩 8.9	🟨	0.000
baleen whales	3.6	🟨 0.075	🟨 0.037	🟩 7.6	🟧	0.000
fishery offal	1.0	1.000	10.00	-	-	
pelagic detritu	1.0	1.000	10.00	-	-	
benthic detritus	1.0	1.000	10.00	-	-	

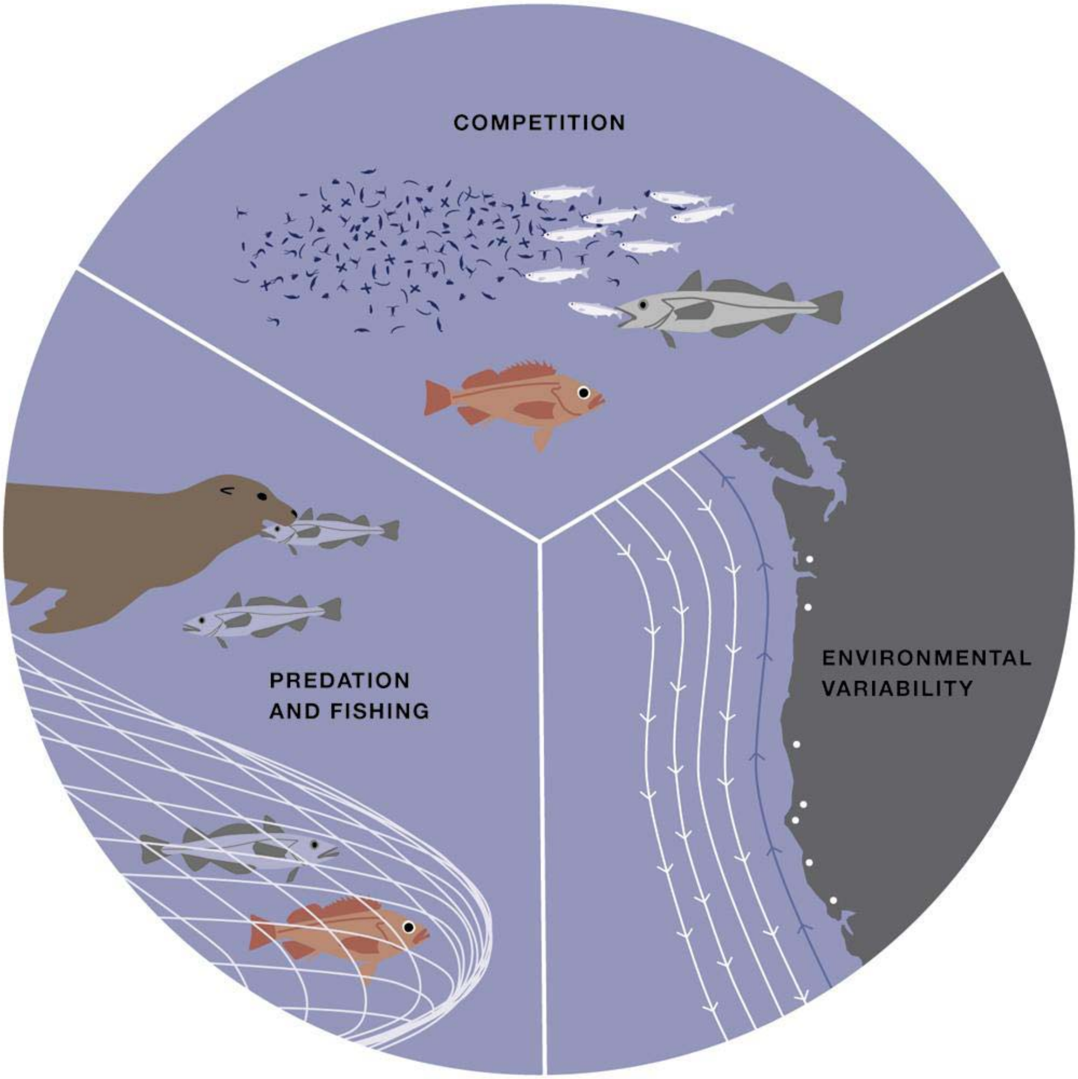


Figure 3.1: Graphic depiction of the three fundamental processes that shape population behavior; competition, predation (including fishing) and environmental variability.

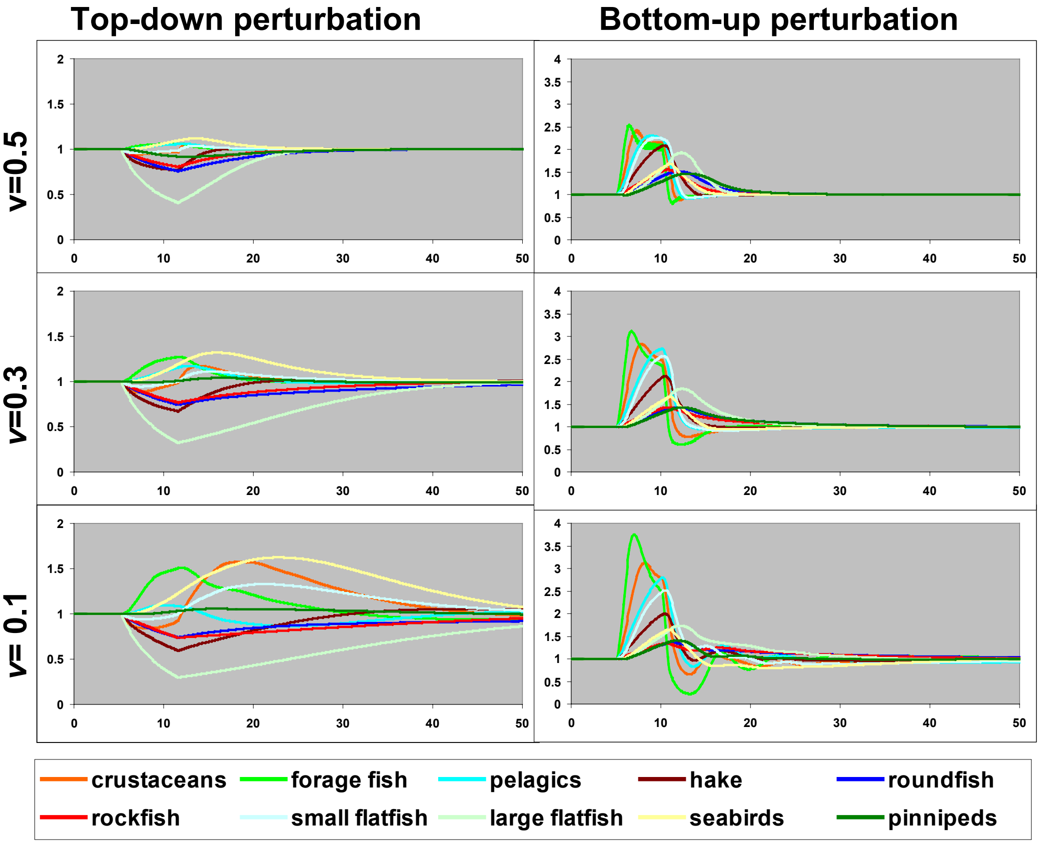


Figure 3.2: Sensitivity of model components to top-down (fishing) and bottom-up (primary production, note difference in scale) forcing under varying assumptions of vulnerability (v).

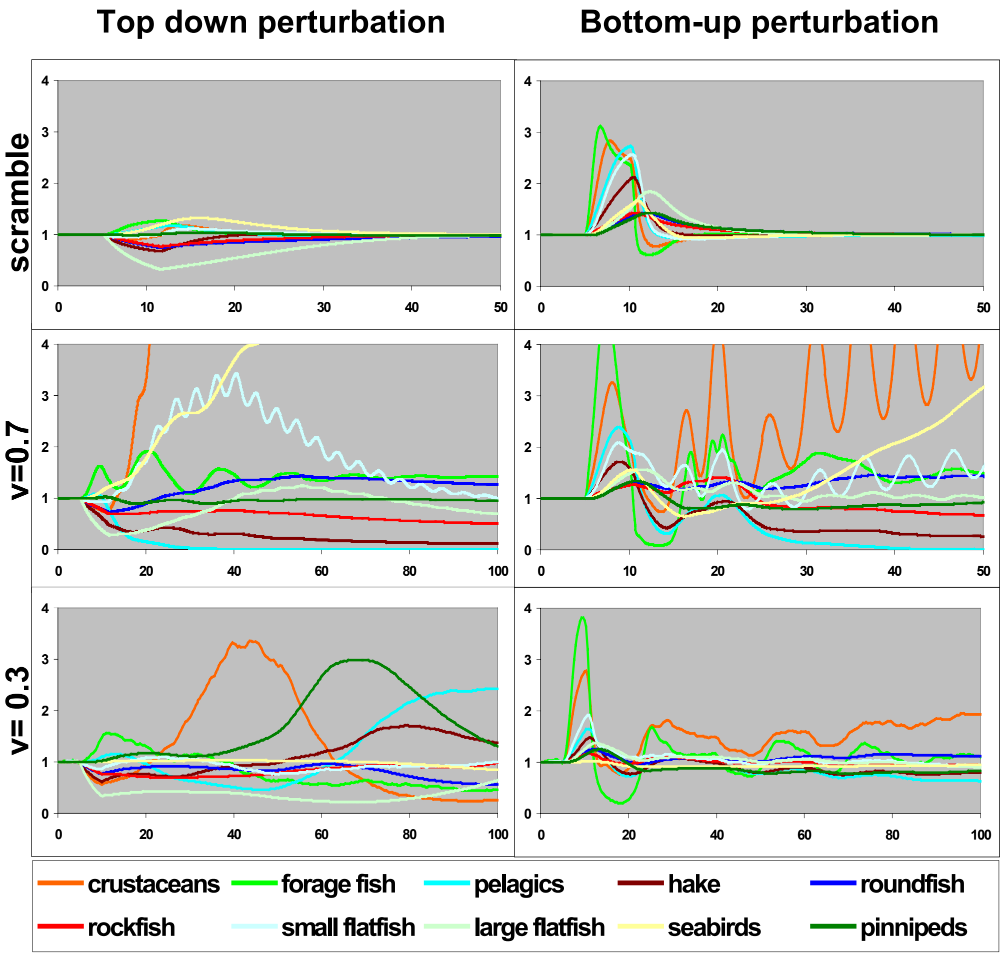


Figure 3.3: Baseline model behavior(v=0.3, top) contrasted to extreme examples (very top-down forcing and scramble competition) of non-equilibrium model dynamics with perturbations in both fishing mortality (left) and primary production (right).

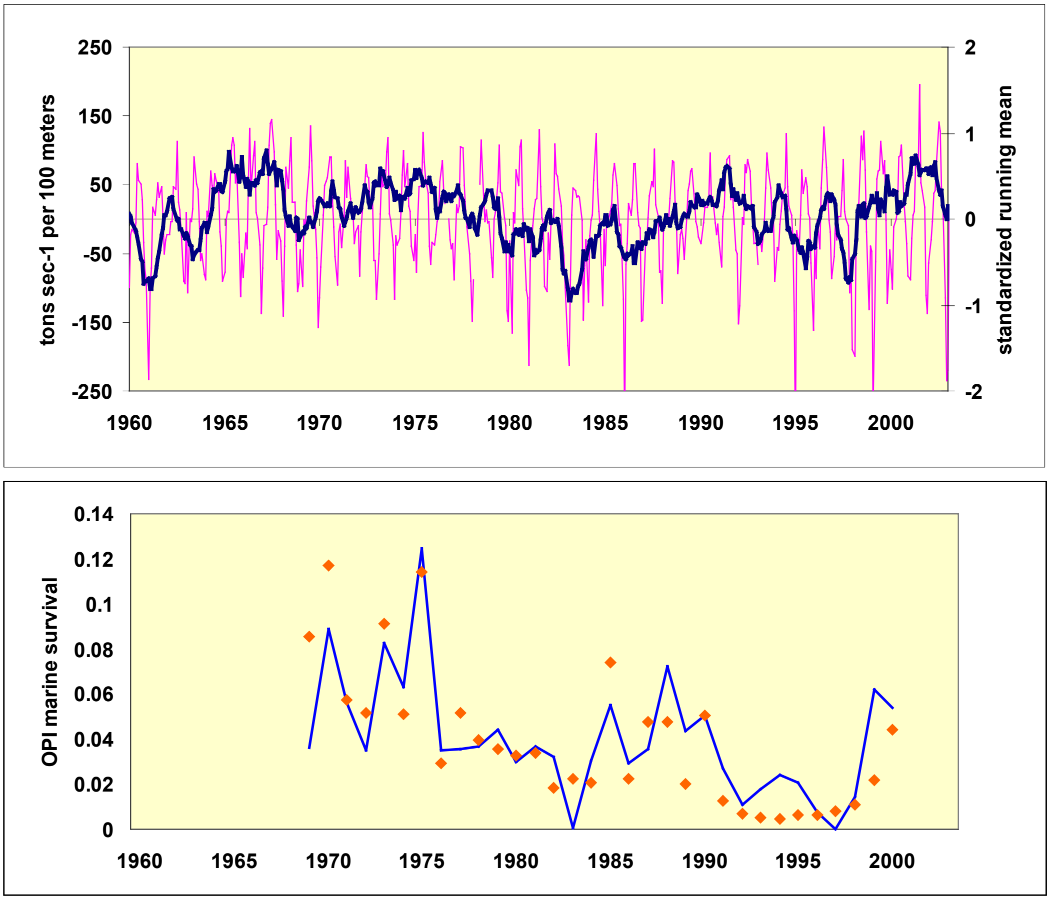
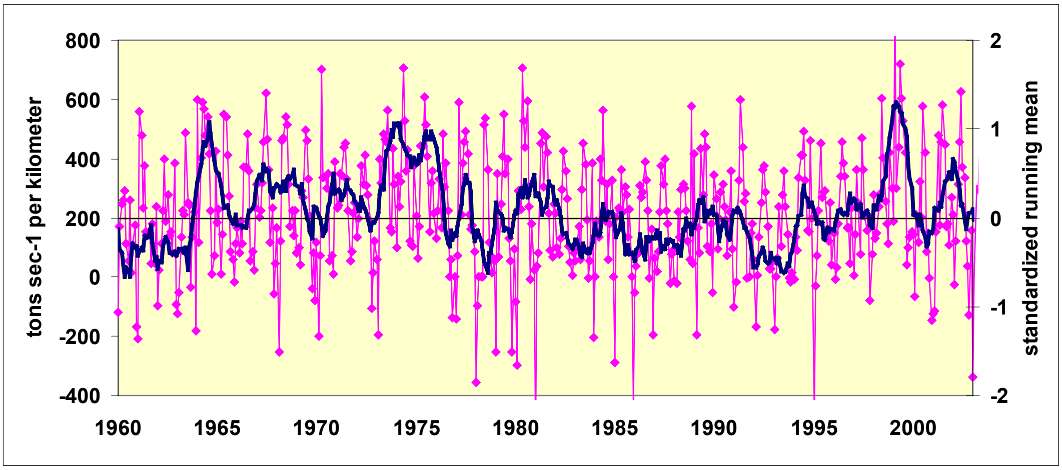


Figure 3.4: Bottom-up forcing mechanisms. Top, Averaged monthly upwelling indices for 42 to 48 N (pink) with a standardized 13 month running mean (blue). Bottom, observed (orange) and GAM predicted (blue) OPI coho ocean survival rates from Logerwell et al. (2003).



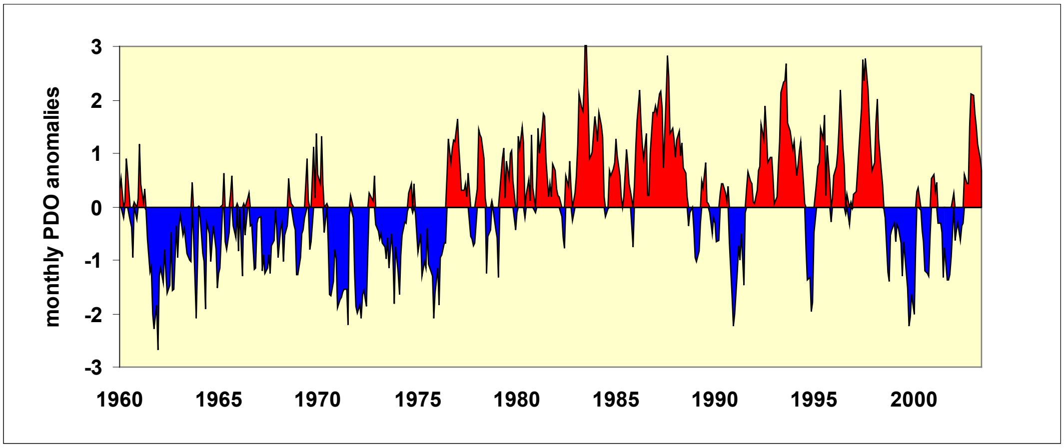


Figure 3.5: Top-down climate forcing mechanisms. Top, Averaged monthly southward transport indices between for 36 and 51 N (pink) with a standardized 13 month running mean (blue). Bottom, monthly values of the Pacific Decadal Oscillation (PDO).

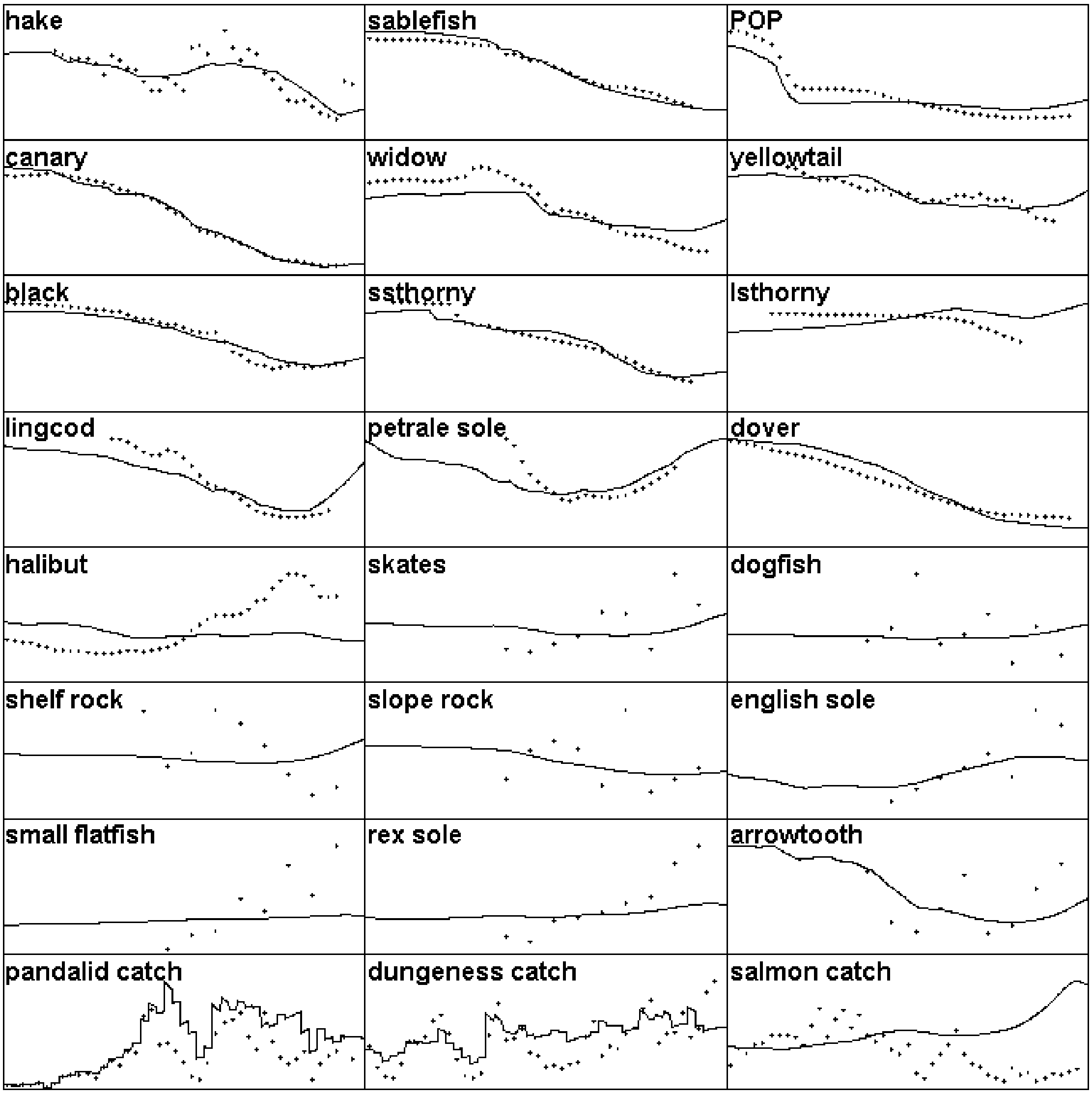


Figure 3.6: Model trajectories from 1960 to 2004 (solid lines, x-axis) fitted to stock assessment trends, survey indices, and landings (dotted lines, y-axis), with no environmental forcing.

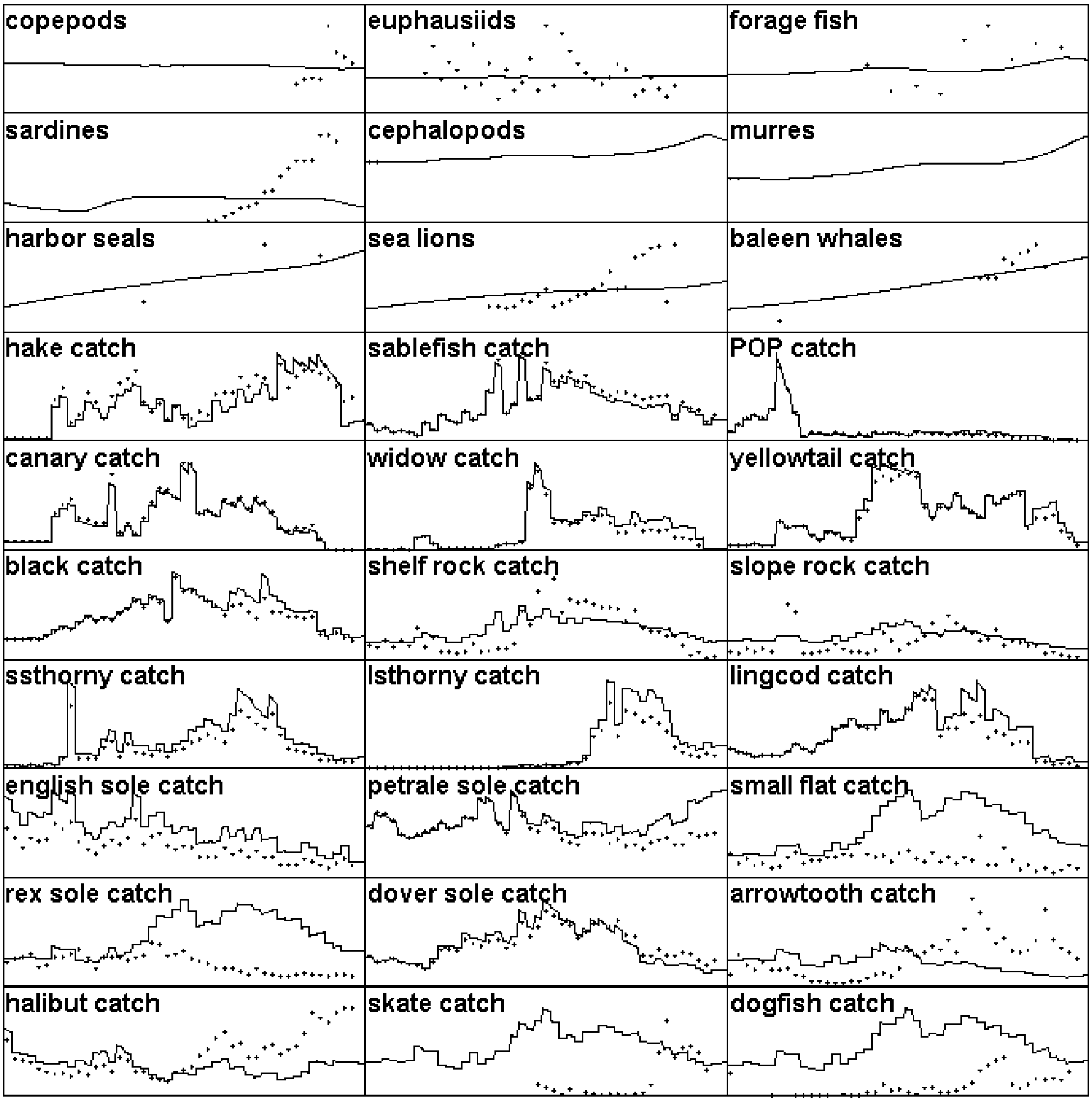


Figure 3.7: Top panels: model trajectories from the fishing only (no climate) run (as in figure 3.5) for select lower and higher trophic levels (solid lines, x-axis) with select indices (often from outside the NCC) shown for scale. Bottom panels, model estimated catches (solid line) and reported catches and landings (dotted lines) from key species in the NCC.

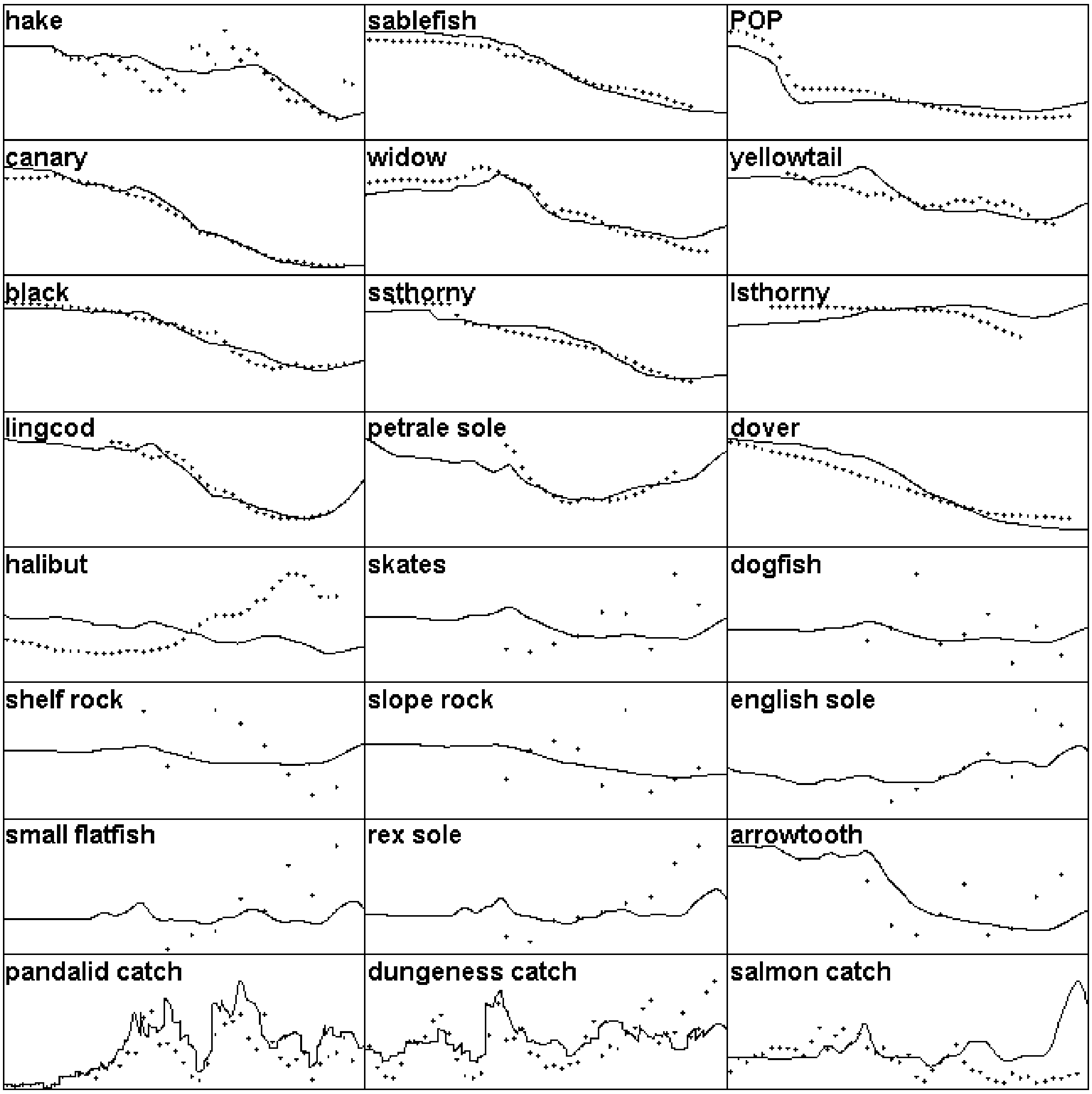


Figure 3.8: Ecosim trajectories (as in Figure 3.5) with “bottom-up” environmental forcing driven by the OPI coho survival predictive index developed by Logerwell et al. (2003).

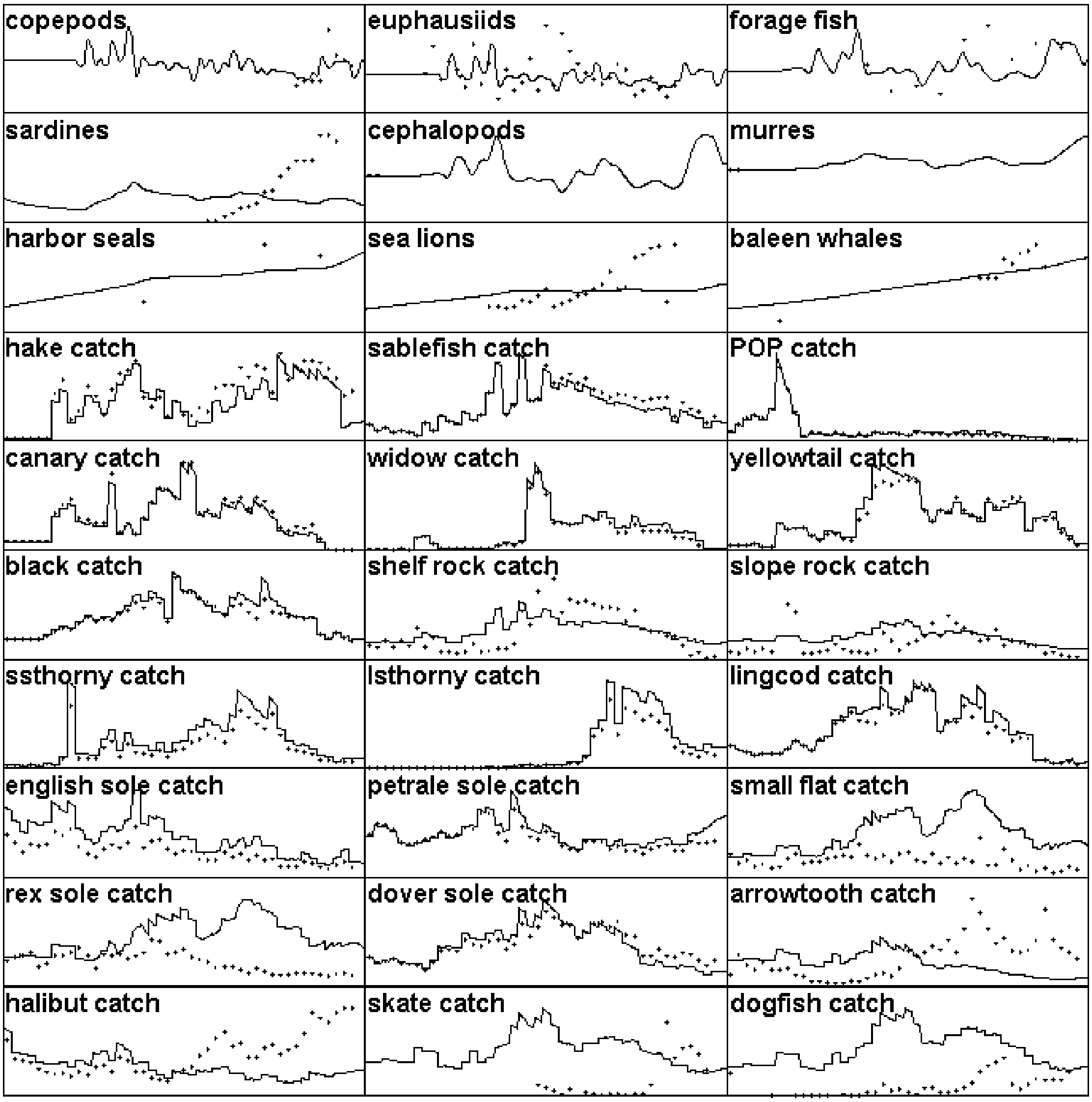


Figure 3.9: Model trajectories for lower and higher trophic levels, and catches of key species (as in Figure 3.6) for the bottom-up OPI coho survival run (as in Figure 3.7).

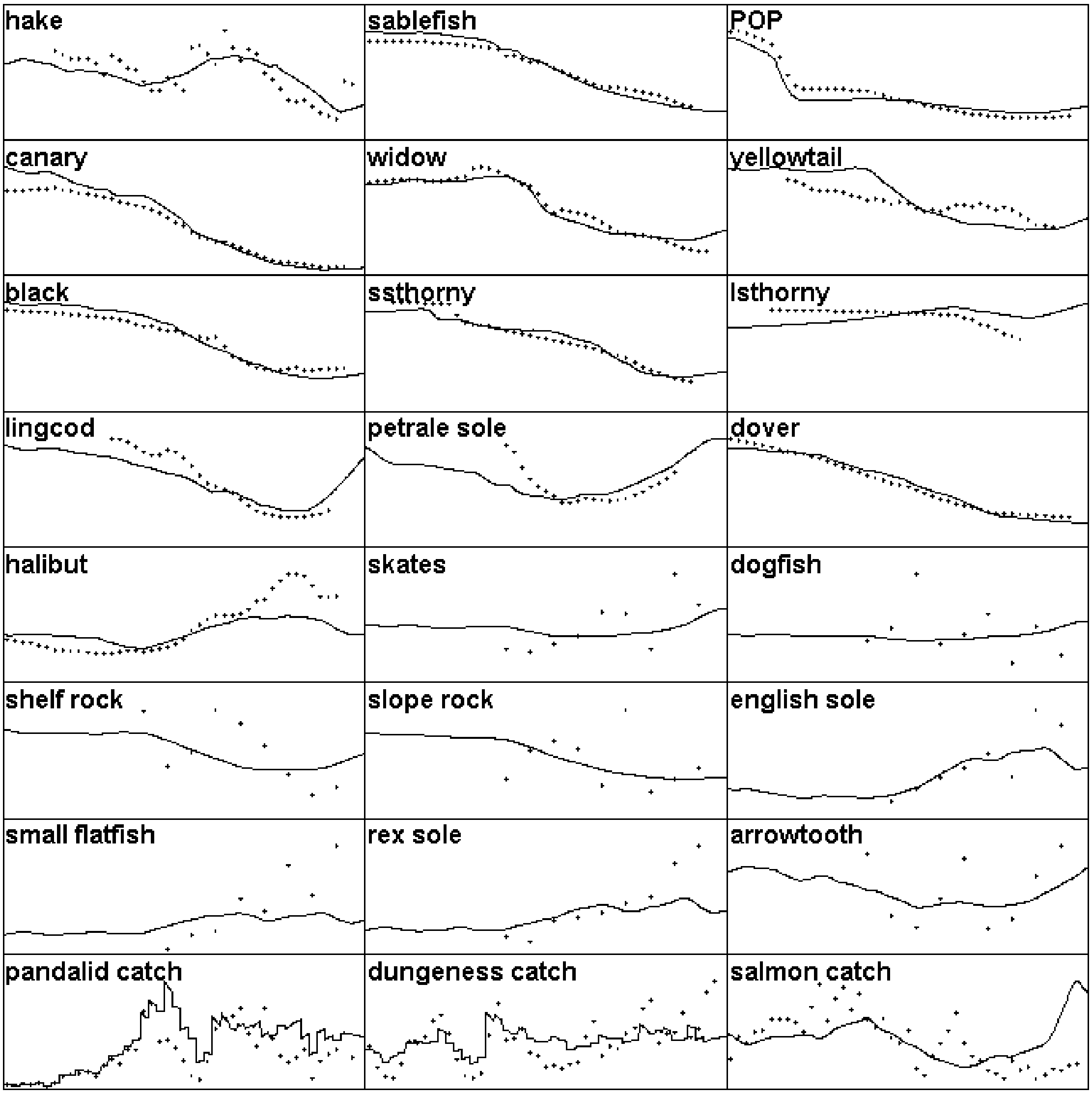


Figure 3.10: Model trajectories with "top-down" environmental forcing based on PDO mediation on the vulnerability of prey to key predators.

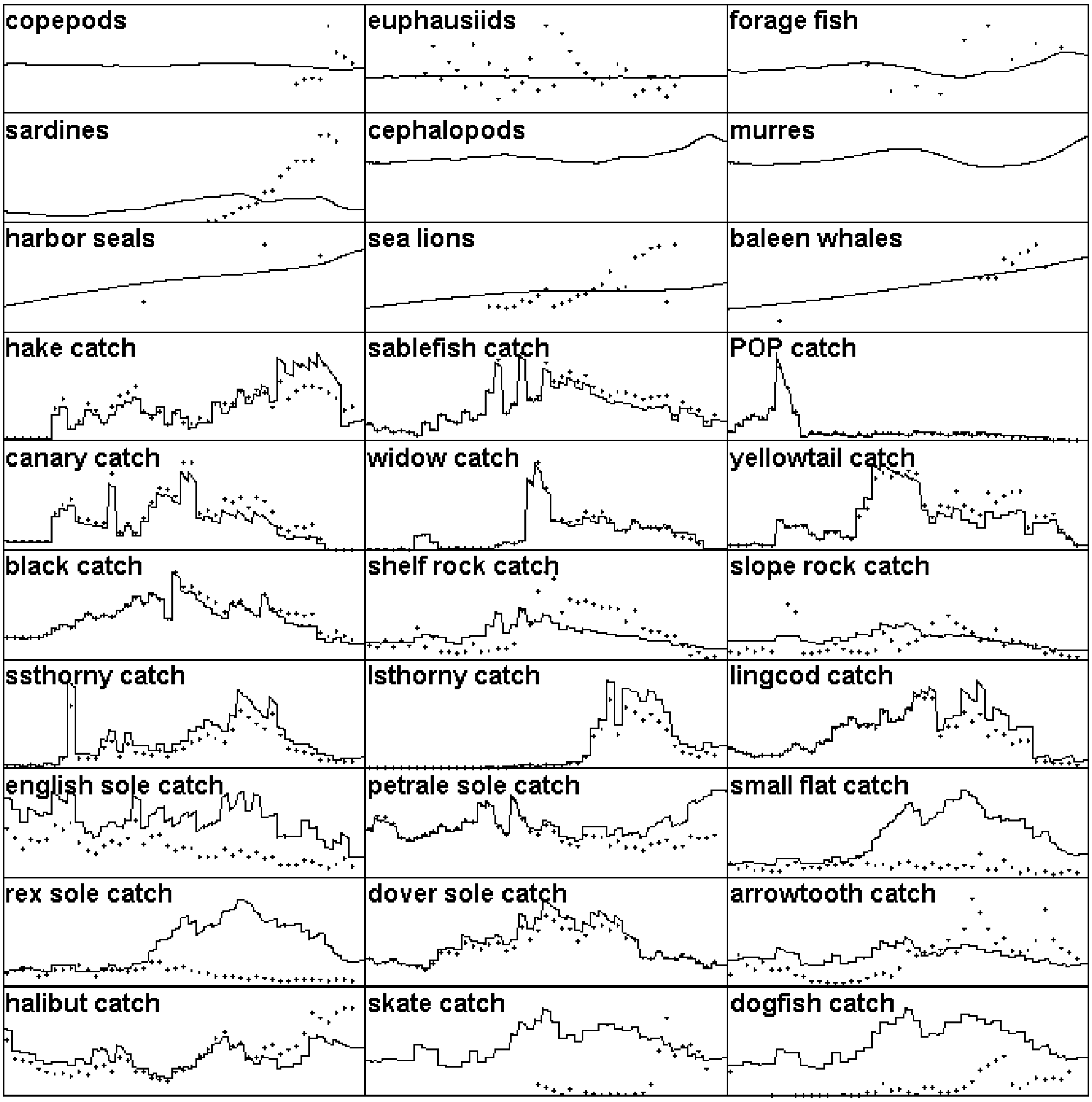


Figure 3.11: Model trajectories with “top-down” environmental forcing based on PDO mediation on the vulnerability of prey to key predators (as in Figure 3.9) for select lower and higher trophic levels and estimated catches.

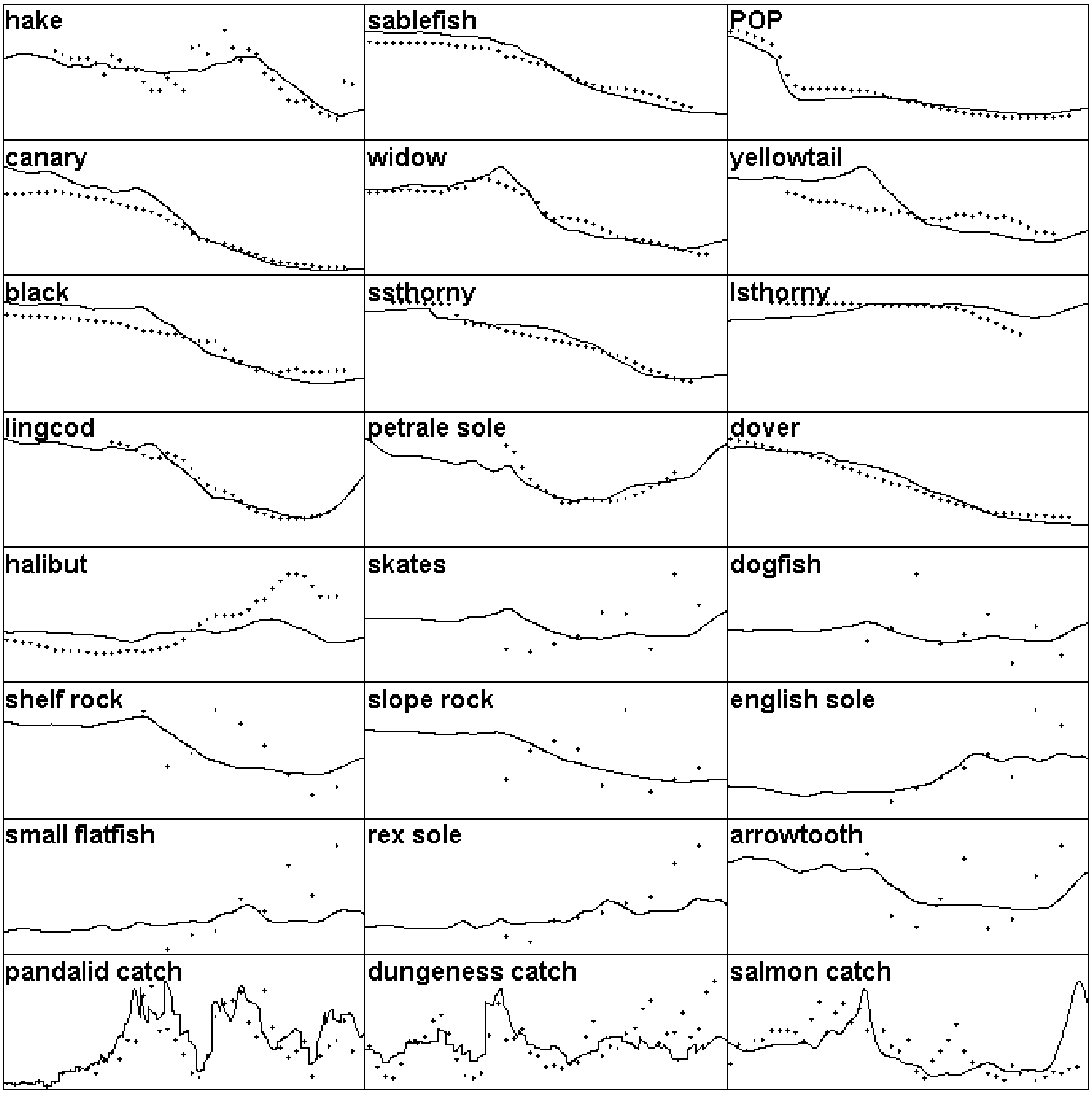


Figure 3.12: Model trajectories with a combination of "bottom-up" forcing from the OPI coho survival index and "top-down" forcing with PDO mediation on the vulnerability of prey to key predators.

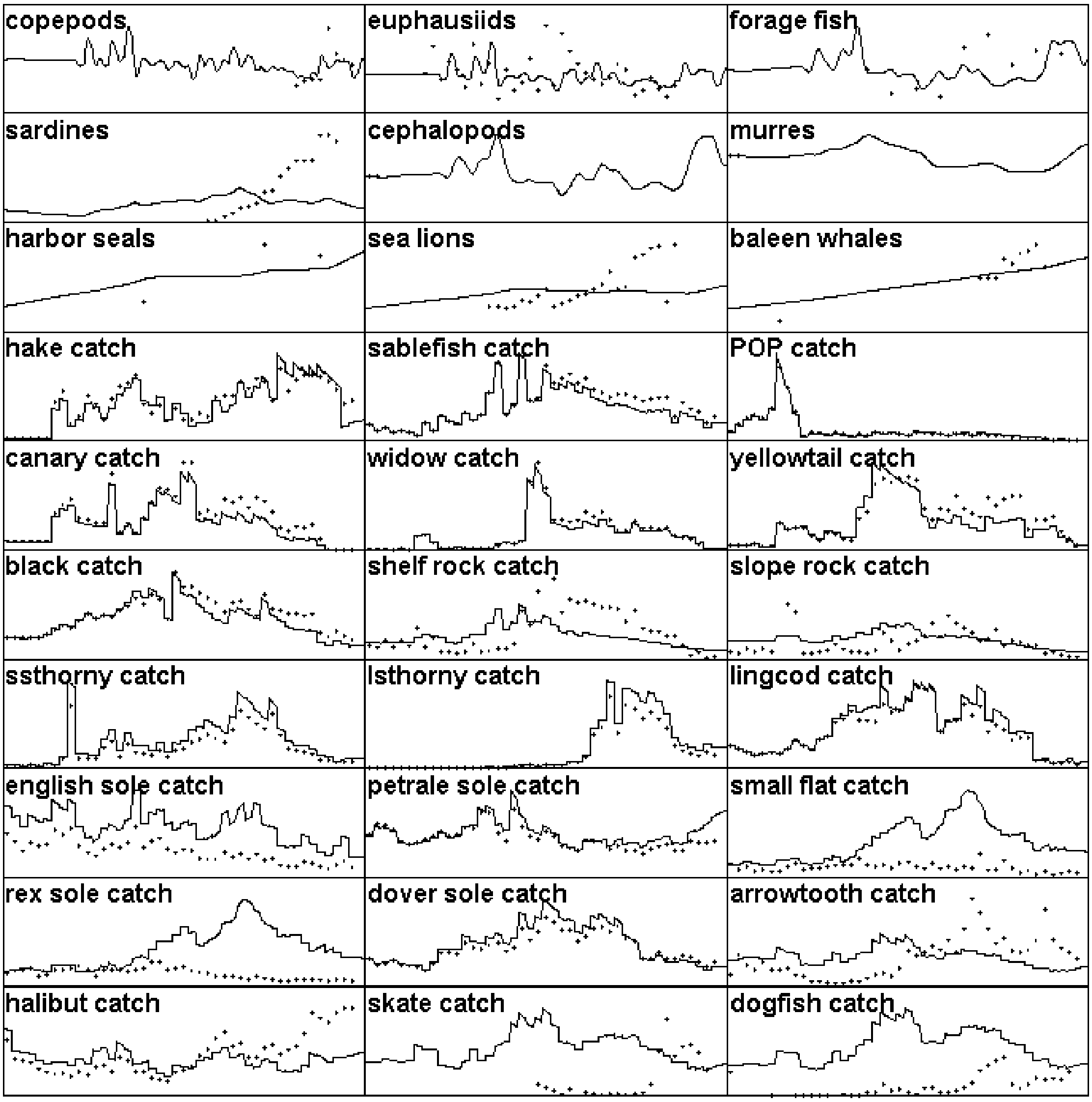


Figure 3.13: Model trajectories of lower and higher trophic level components and catches of key species with a combination of "bottom-up" forcing from the OPI coho survival index and "top-down" forcing with PDO mediation on the vulnerability of prey to key predators.

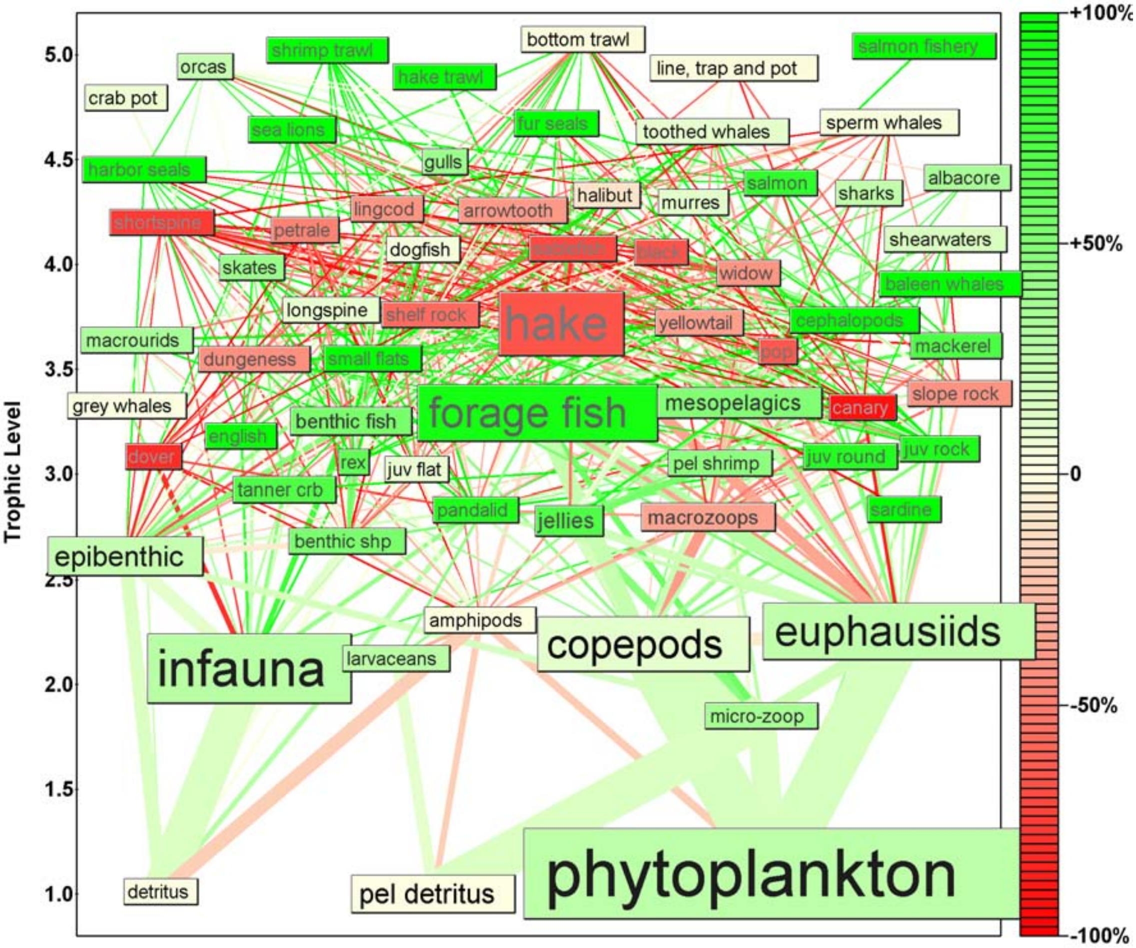


Figure 3.14: Model estimated changes in relative biomass, biomass flows and catches between 2002 (very high primary and secondary production) coded in color as % change from the baseline starting values (1960).

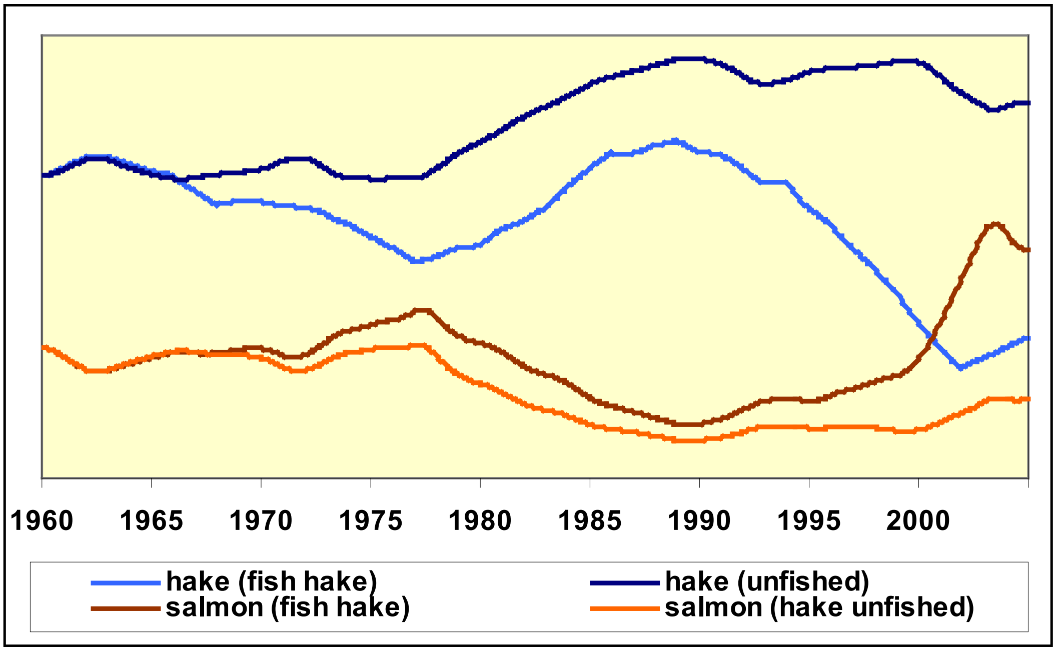


Figure 3.15: Example of simple indirect interaction between model components (salmon and hake) under alternative fishing scenarios (note that biomass is relative and not to scale between the two groups).

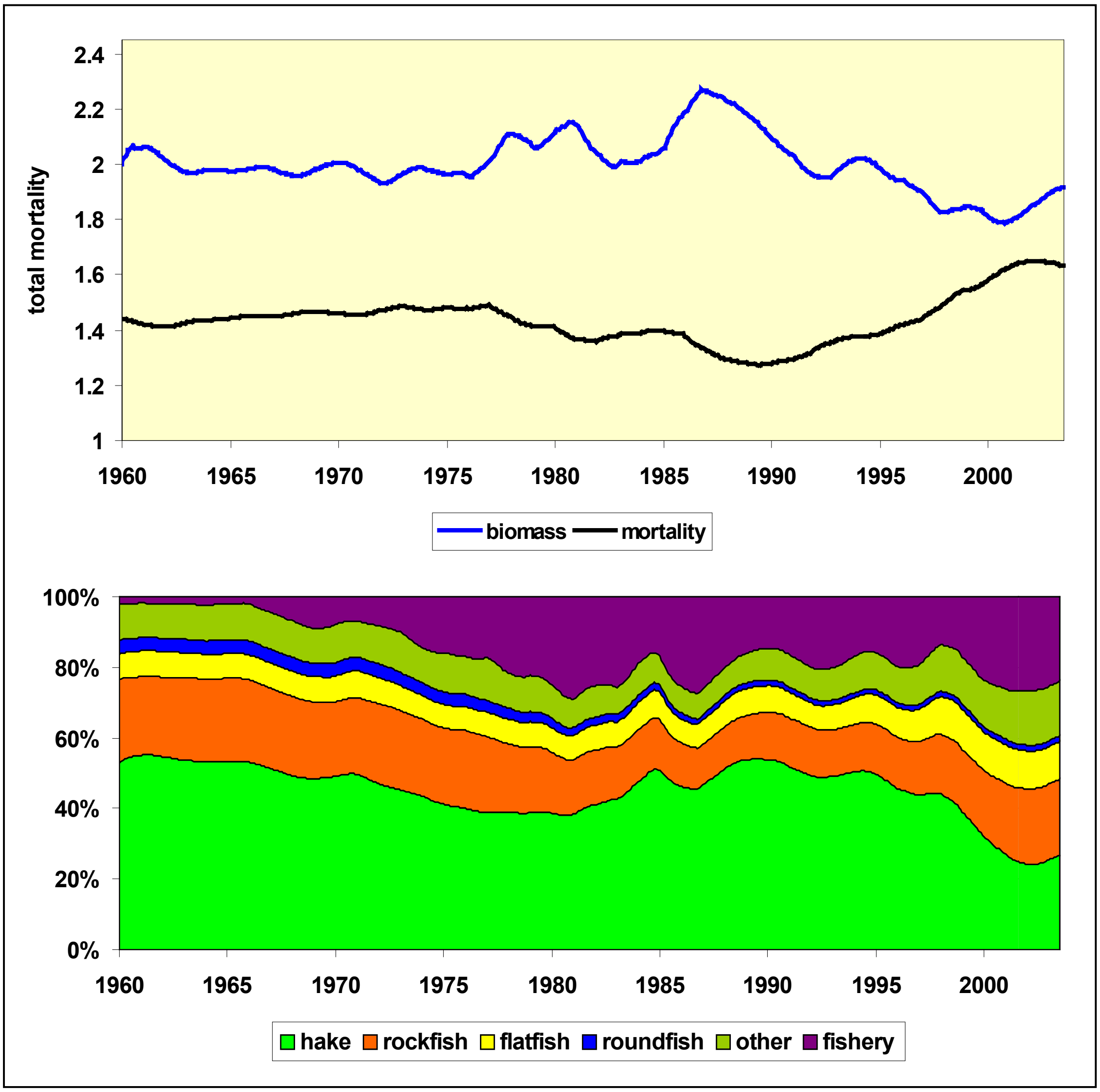


Figure 3.16: Model estimates of Ocean shrimp (*Pandalus jordanii*) total mortality and relative biomass (top panel) and relative sources of mortality (bottom panel) over time.

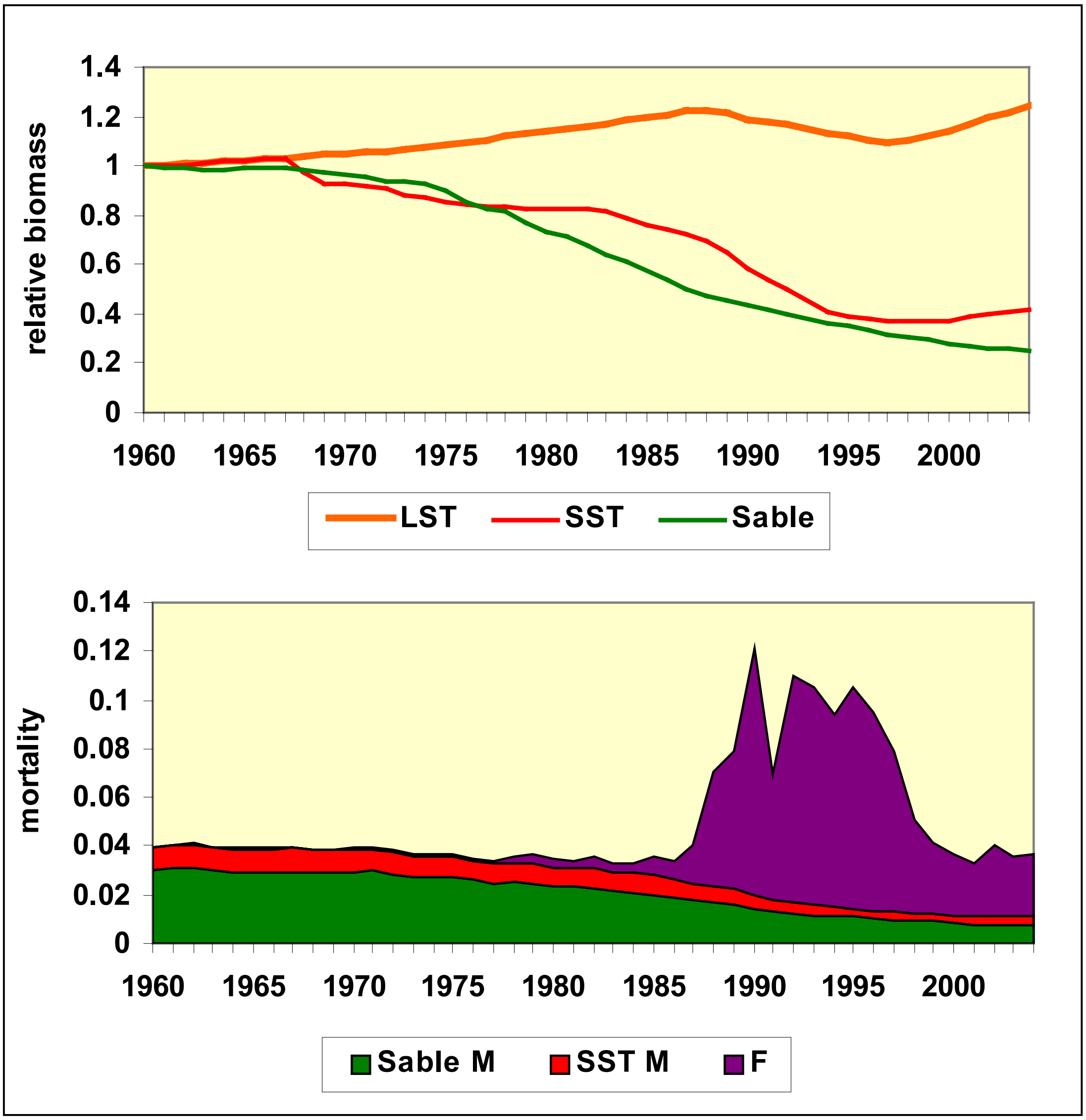


Figure 3.17: Example of changes in relative biomass of longspine thornyhead, shortspine thornyhead, and sablefish (top panel) and mortality rates (predation) on longspine thornyhead by shortspine thornyhead, sablefish, and fisheries (F) (bottom panel).

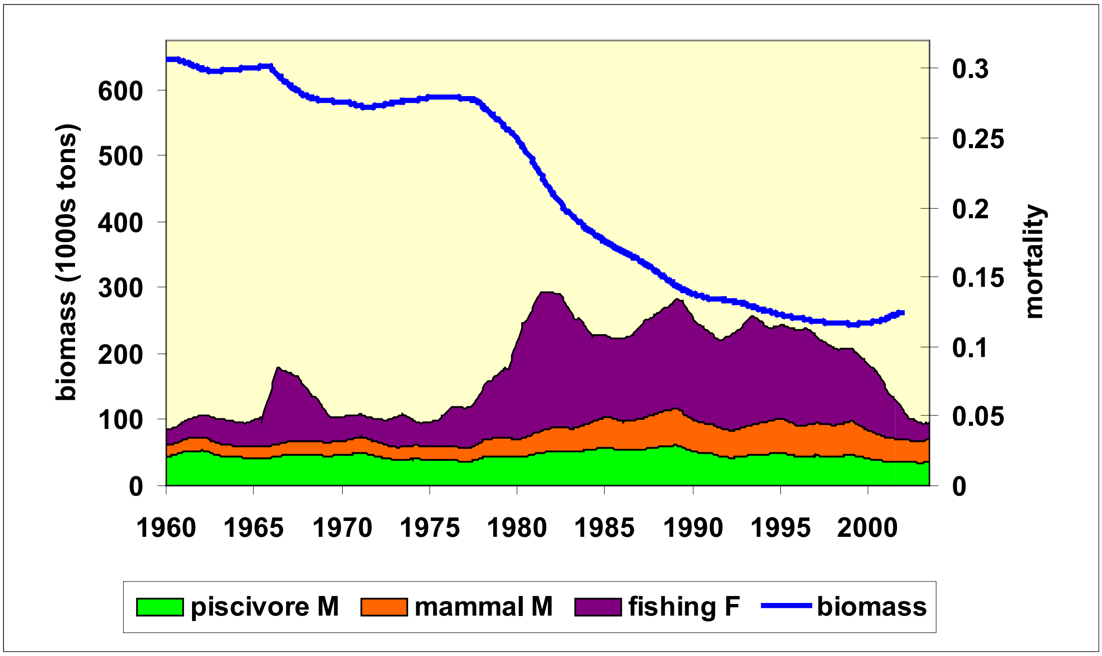


Figure 3.18: Example of changes in natural mortality (predation) rates relative to fishing mortality for all *Sebastes* rockfish stocks.

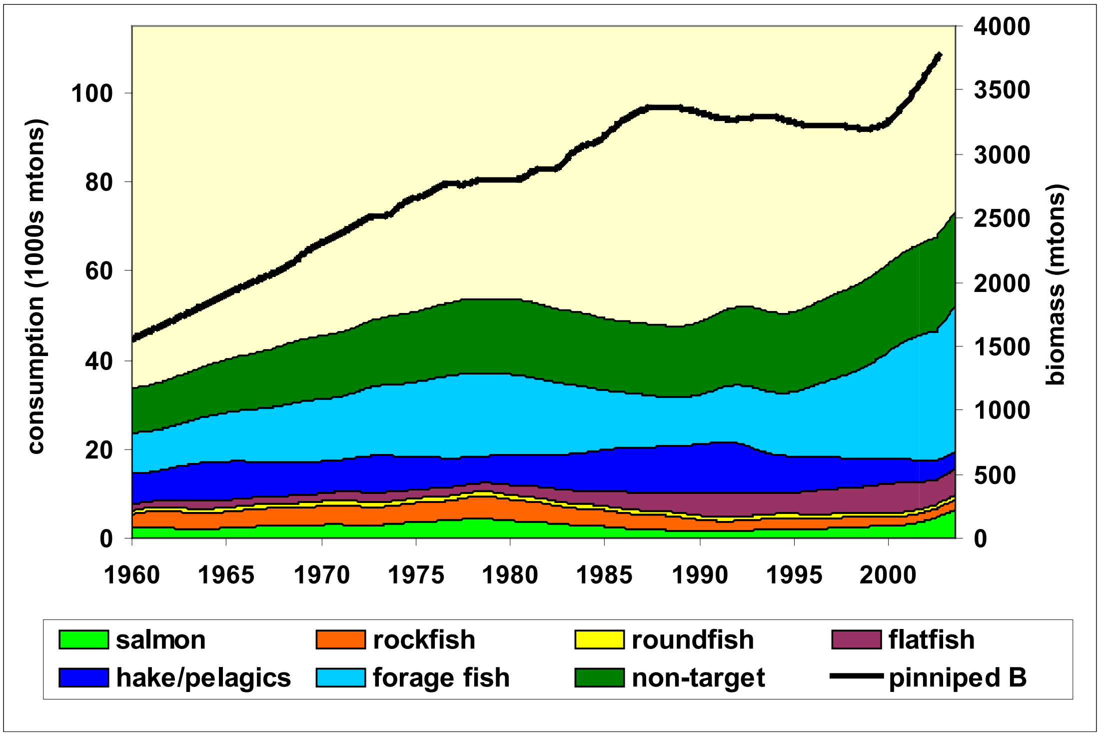


Figure 3.19: Model predicted changes in total pinniped biomass and corresponding estimates of changes in total consumption by pinnipeds on key forage guilds.

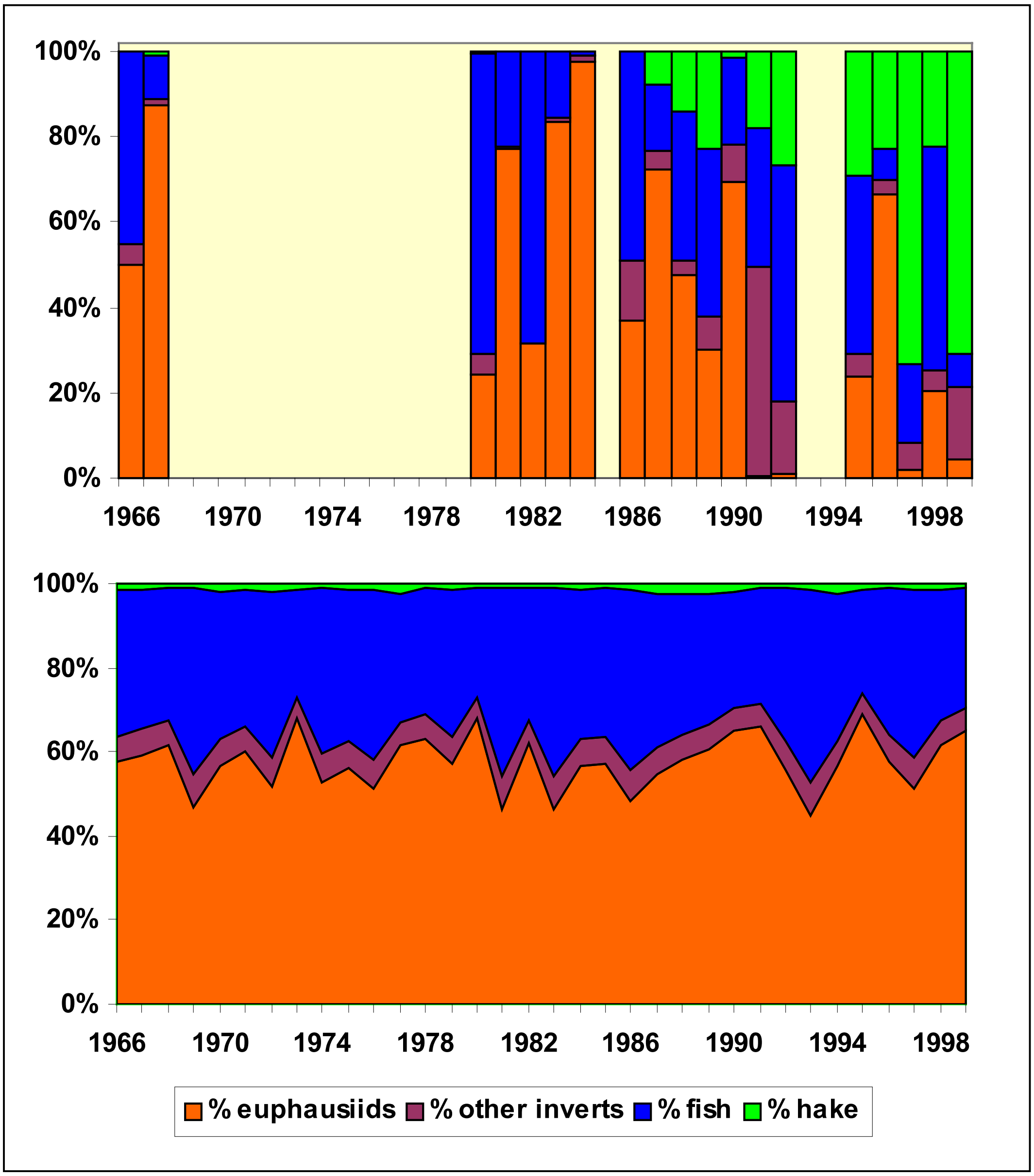


Figure 3.20: Observed (top) and model estimated (bottom) changes in generalized hake diet composition between 1966 and 1999.

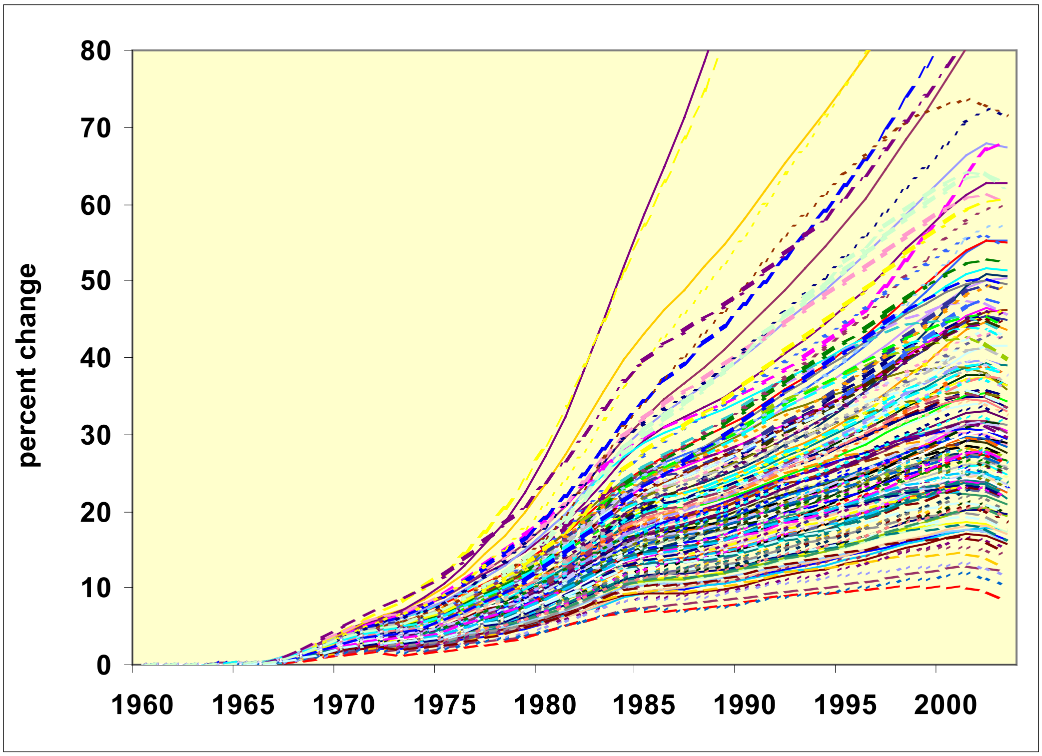


Figure 3.21: Model trajectory results for small flatfish from sensitivity tests in which the baseline response for each resampled model was removed from the perturbed model response.

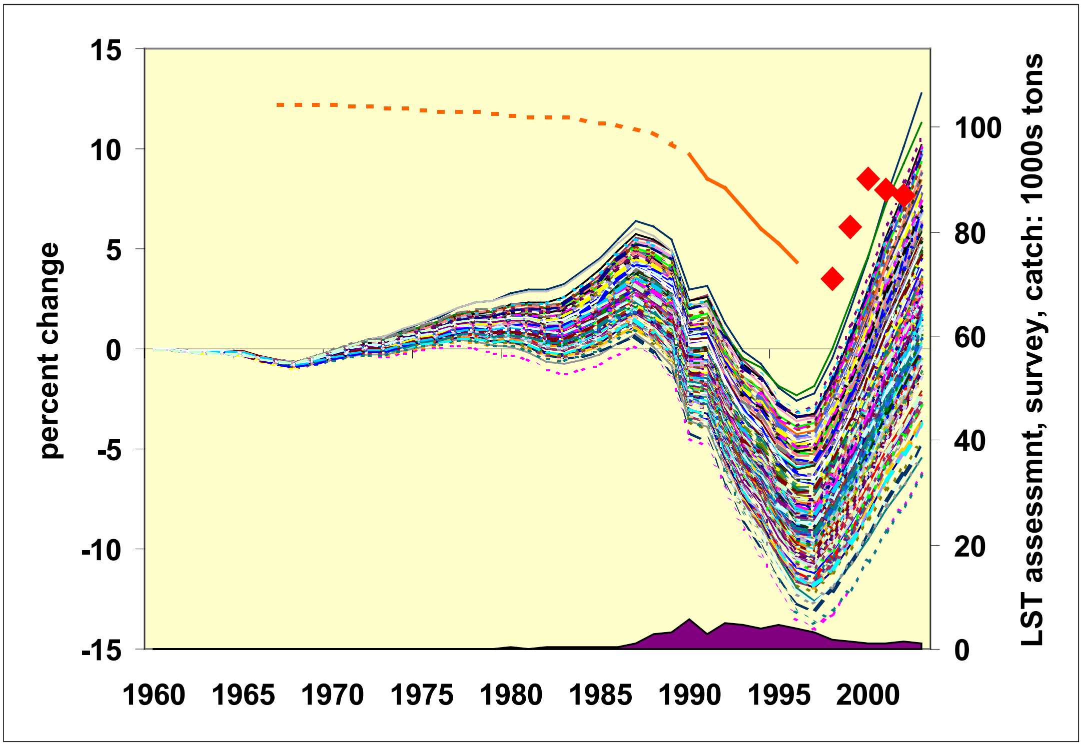


Figure 3.22: Model trajectory results for longspine thornyheads from sensitivity tests in which the baseline response for each resampled model was removed from the perturbed model response. Also shown are the most recent stock assessment trajectory from Rogers et al (1997), landings based on Pacfin, and biomass point estimates from the 1998-2002 NWFSC groundfish surveys.

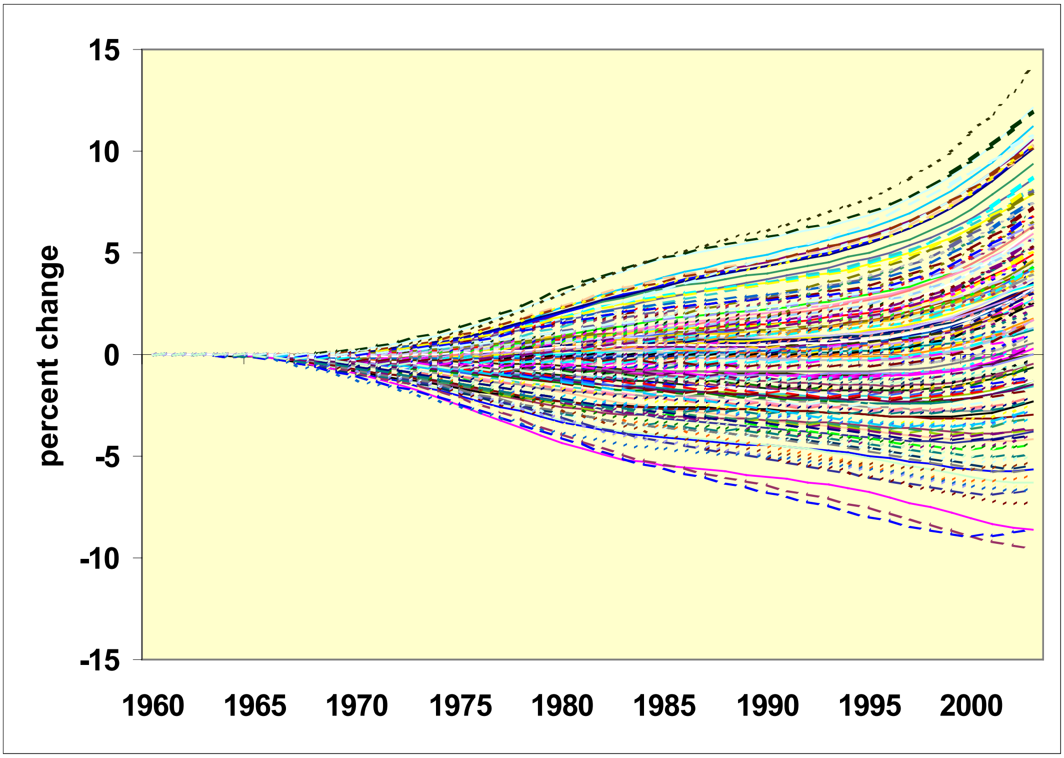


Figure 3.23: Model trajectory results for pinnipeds from sensitivity tests in which the baseline response for each resampled model was removed from the perturbed model response.

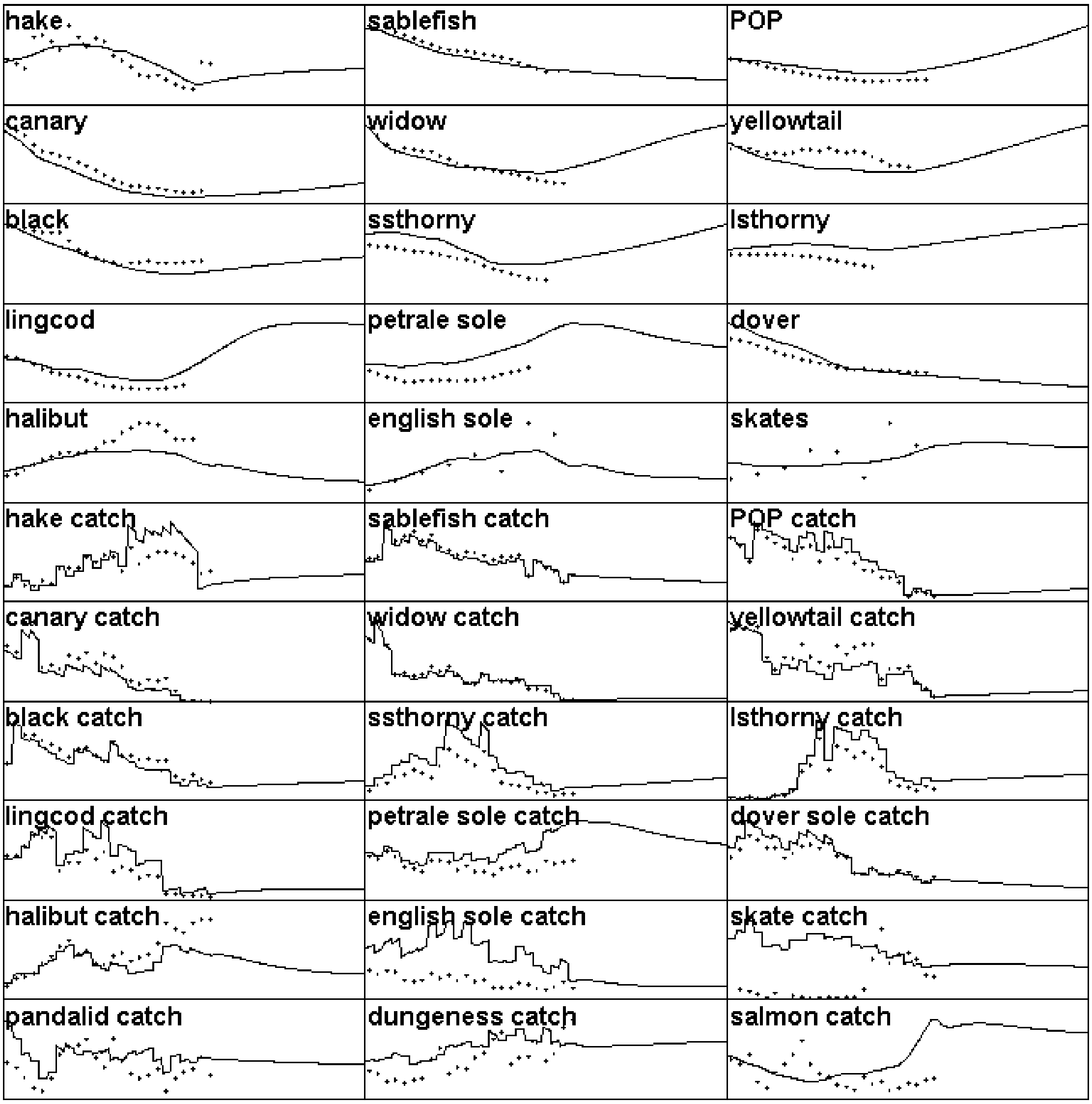


Figure 3.24: Model predicted biomass and catch trajectories between 1980 and 2020. Fishing mortality and effort are at 2003 levels, PDO forcing through 2003, no climate forcing post-2003.

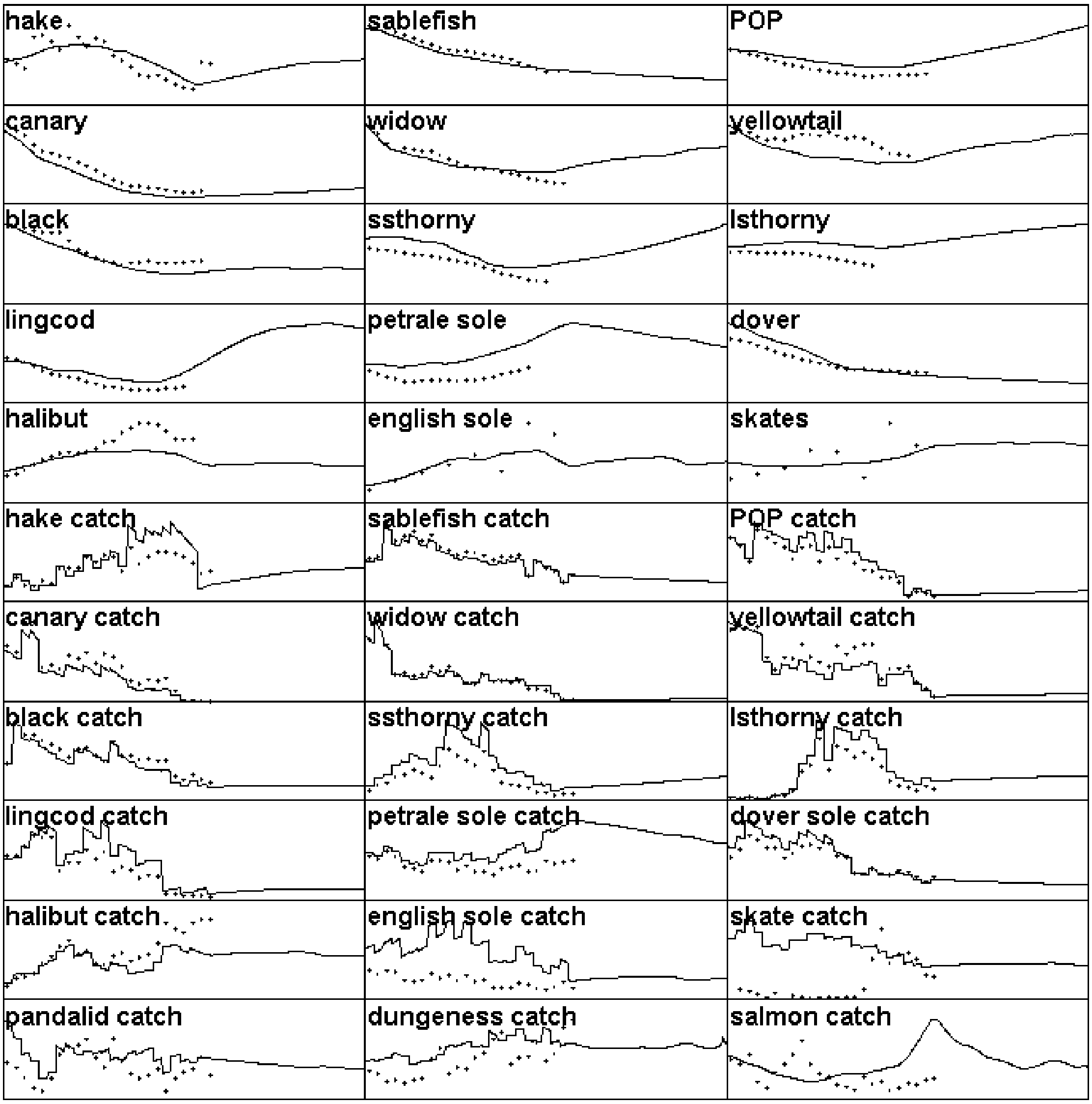


Figure 3.25: Model predicted biomass and catch trajectories between 1980 and 2020. Fishing mortality and effort are at 2003 levels, PDO is positive from 2004-2020.

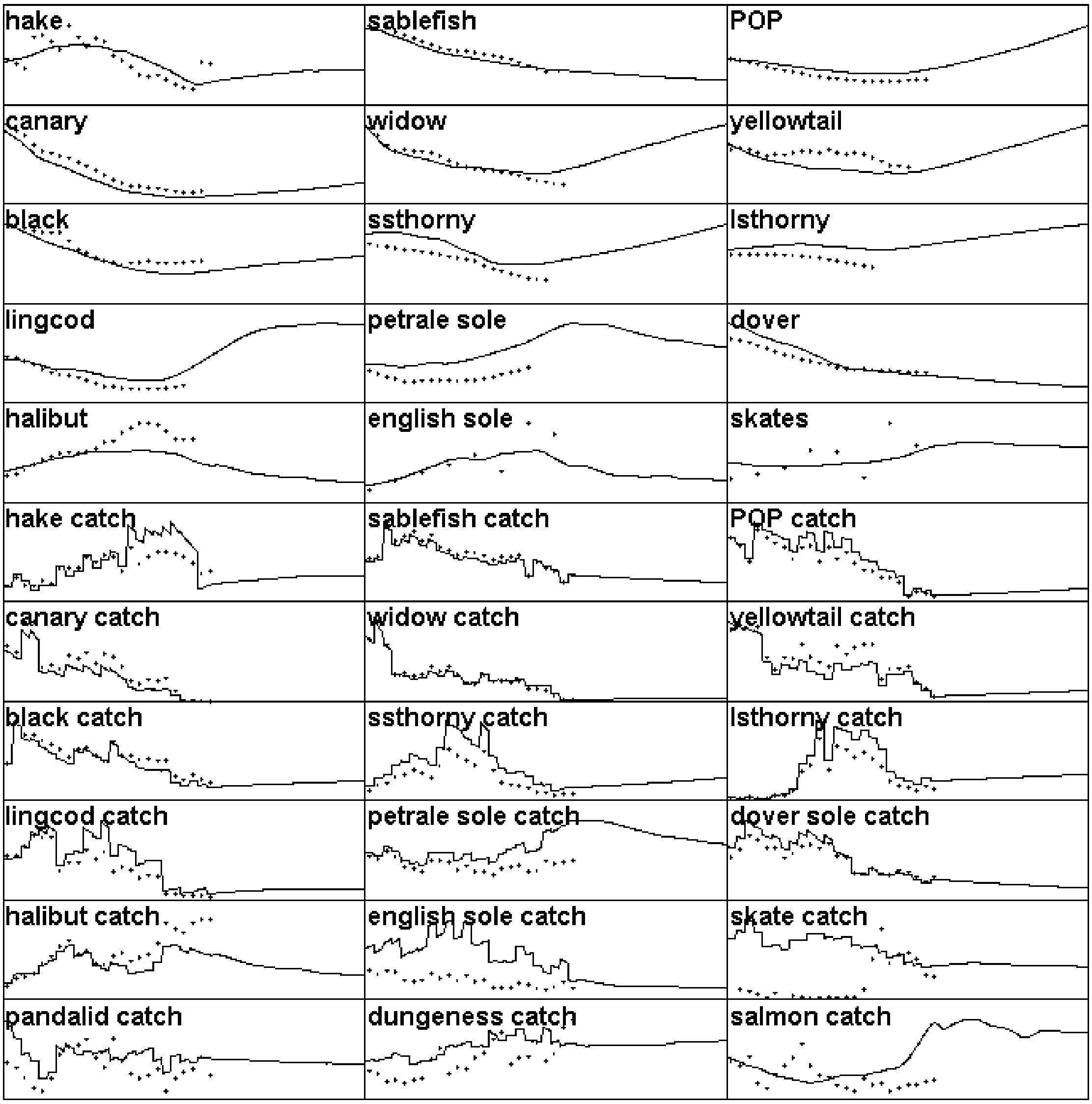


Figure 3.26: Model predicted biomass and catch trajectories between 1980 and 2020. Fishing mortality and effort are at 2003 levels, PDO is negative from 2004-2020.

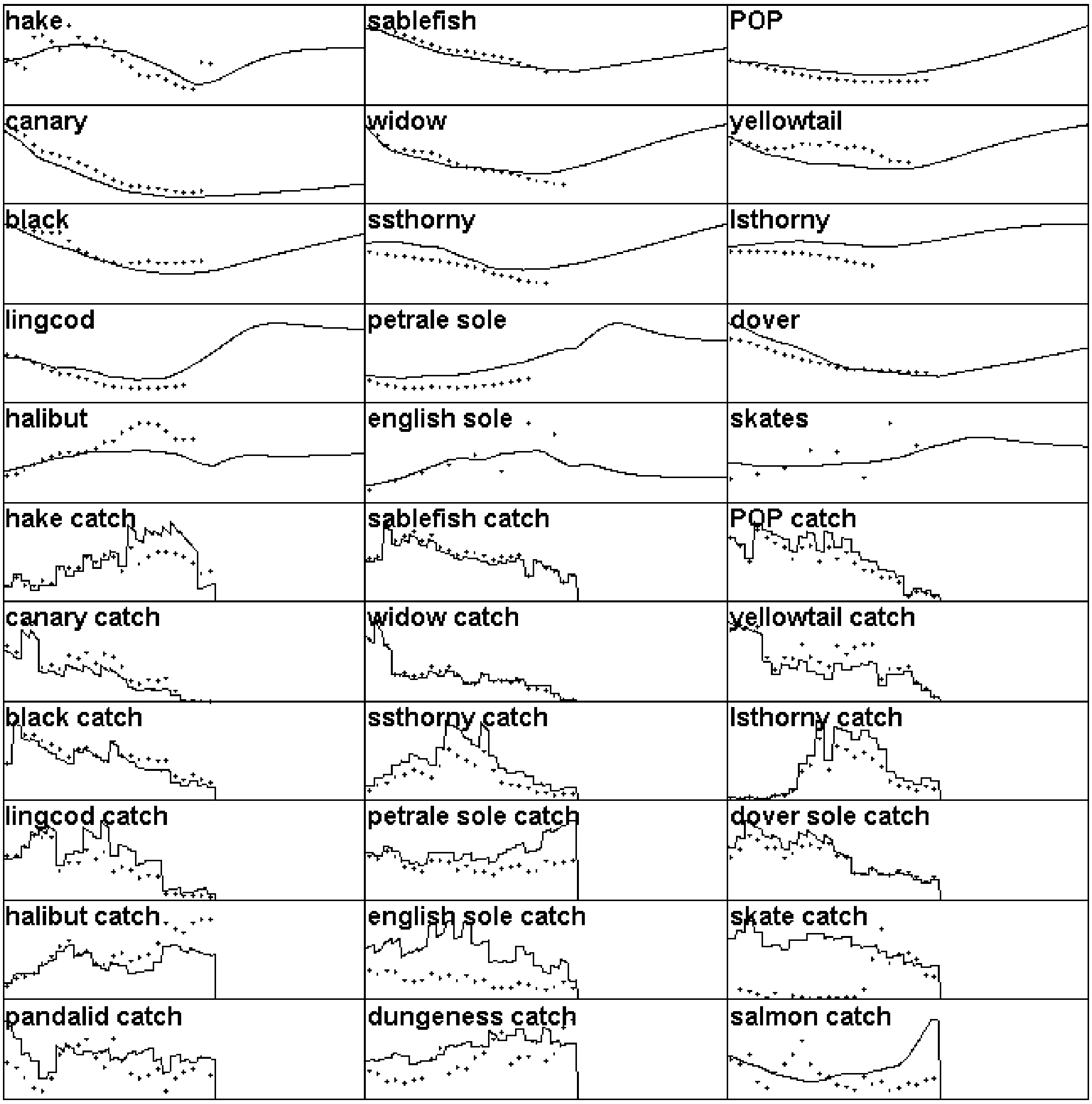


Figure 3.27: Model predicted biomass and catch trajectories between 1980 and 2020 with a total cessation of fishing in 2004. No climate forcing post-2003.

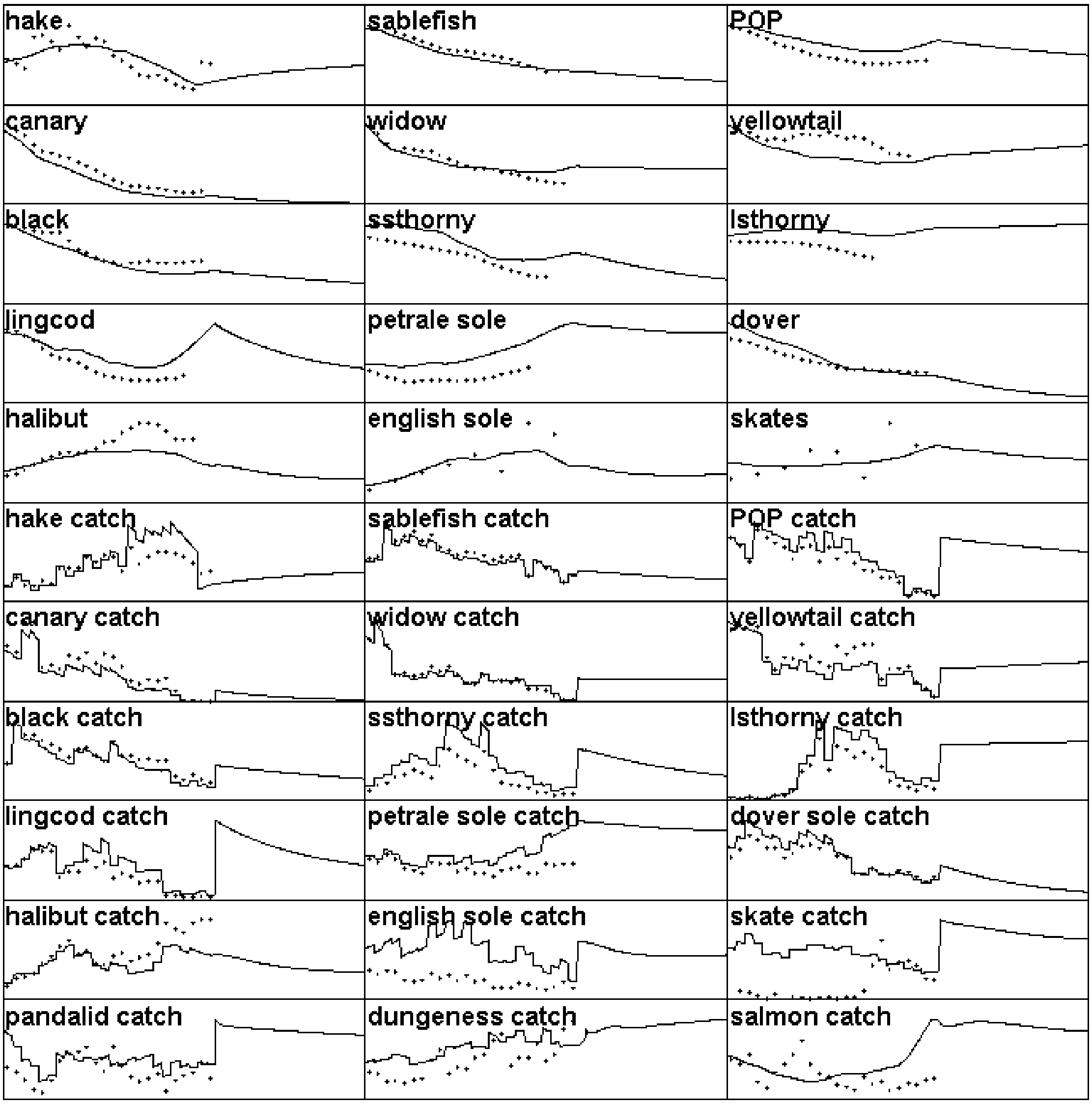


Figure 3.28: Simulated biomass and catch trajectories between 1980 and 2020 with fishing mortality rates in 2004 set equal to 1990 (average between 1988 and 1992) levels. No climate forcing post-2003.

CHAPTER 4

> *Ecosystems are devilishly complex and wonderfully idiosyncratic. No universal rules or principles exist to guide their deliberate manipulation or management (Callicott et al. 1999)*

4.1 Introduction

Until now the focus of this dissertation has been the development of models and model results relative to the biological and physical dimensions of the ecosystem. Chapter 4 departs from these themes, and focuses instead on the role of ecosystem insights, principles and models with regard to the governance sector of the fisheries system. Ecosystem information, models, and management approaches can integrate disparate data, insights and observations in generating a "big picture" view of fishery, climate and other impacts and changes on the entire ecosystem. Ideally, such considerations will encourage managers and decisionmakers to consider the past, present and future cumulative impacts on the system as a whole related to fishing, climate variability and other forcing factors. Realistically, to do so requires the proper context, and some form of mandate, to adopt or move towards an ecosystem-based approach to management. Although it is widely acknowledged that movement towards an ecosystem-based approach to managing fisheries and other marine resources will be incremental, it is equally acknowledged that such a transition is necessary for management in the future. Providing a framework for integrating and presenting such information to decisionmakers and managers in a useful manner remains much of the challenge of ecosystem-based fisheries management. A template for doing so with the NCC is the focus of this chapter. This template is based in part on existing management strategies elsewhere, in part on the scientific literature and technical reports, and in part on the insights and tools described in Chapters 1-3.

4.2 What is Ecosystem-based management?

As Larkin (1996) recognized, ecosystem-based management “means different things to different people, but the underlying concept is as old as the hills.” Larkin and many others have held that an ecosystem-based management approach in general involves a more holistic view of managing resources in the context of their environment than presently exists. Objectives of ecosystem-based fisheries management (EBFM) go beyond maintaining a sustainable yield of products for human consumption to generating (or maintain) employment and income, and include maintaining biological diversity, considering the needs of other predators and dependent species in the food web, and avoiding activities that may cause long term or irreversible impacts to ecosystem structure and function. For marine ecosystems, this must include greater consideration of climate dynamics and ocean conditions that drive recruitment and productivity, trophic interactions between fished and unfished populations in the ecosystem, the role of humans as both predators and competitors, and the impacts of fishing and other activities on habitat (Botsford et al. 1997, EPAP 1999, Mangel et al. 2000, Pauly et al. 2002, Pikitch et al. 2004). Recognizing that all management decisions have impacts on an ecosystem, an ecosystem-based approach to management seeks to better inform these decisions with knowledge and understanding of ecosystem dynamics, structure, and functions.

Ecosystem management, or ecosystem-based management, has had a longer history in terrestrial resource management, where two general philosophies have been developed. These have been described by Callicott et al. (1999) as the compositionalist and functionalist views, and by Stanley (1995) as the biocentric and anthropocentric views. The terminology of Callicott et al. is used here. While the authors acknowledge that the two views exemplify the extremes as a continuum, a comparison of the two is useful when considering the interactions between competing objectives, mandates and scientific perspectives (“ecologies”) in marine resource management. In general, the compositionalist view emphasizes the application of ecological science and knowledge, viewing the world "through the lens of evolutionary ecology," towards the goal of protecting diversity and integrity over the long term. From this perspective, humans are separate from nature, and anthropogenic needs are largely secondary. This is the view developed by Grumbine (1994) when he detailed five specific goals for sustaining ecological integrity:

- Maintain viable populations of all native species in situ.
- Represent, within protected areas, all native ecosystem types across their natural range of variation.
- Maintain evolutionary and ecological processes (disturbance regimes, hydrological processes, nutrient cycles, etc.).
- Manage over periods of time long enough to maintain the evolutionary potential of species and ecosystem.
- Accommodate human use and occupancy within these constraints.

Grumbine recognized that these goals were in striking contrast to traditional resource management objectives, which even when couched as ecosystem-based tend to be allied with the functionalist perspective. In reviewing the compositionalist view, Callicott et al. (1999) suggest that this view is obviously an appropriate approach for wildlife refuges, wilderness areas, national and state parks, and similarly managed lands, as well as areas of high biodiversity, endemism or unusual community assemblages.

A strict interpretation of the functionalist perspective is of an "essentially process-oriented, thermodynamical approach to ecology," with a foundation on the energy-transfer based view of ecological function (Callicott et al. 1999). Odum (1969) noted that terrestrial resource management has long been focused with obtaining as much production from landscapes as possible, such that "the goal of agriculture or intensive forestry, as now generally practiced, is to achieve high rates of production of readily harvestable products with little standing crop left to accumulate on the landscape- in other words, a high P/B (production to biomass) efficiency." This view is clearly more consistent with the concepts and science behind estimating maximum sustainable yields, and the current paradigm of contemporary fisheries management, which is based on the premise that “the ultimate causation of population productivity is energy flow, which determines the carrying capacity of the environment in terms of biomass” (Conover 2000). Clearly, the ecosystem theory and models discussed and developed in Chapters 2 and 3 are equally biased towards a functionalist (and equilibrium-based) perspective, albeit one that helps to identify some of the plausible consequences to the structure and composition of marine communities as a result of selective harvest of desired ecosystem components.

In fisheries management, conflicts have inevitably arisen when laws that might be considered compositionalist by virtue of their focus on restoring and maintaining biological diversity (including population diversity) and monitoring the status of unexploited “indicator” populations (such as the Endangered Species Act and the Marine Mammal Protection Act) clash with the arguably functionalist objectives of the Magnuson-Stevens Act. For example, a National Research Council review of changes in the Bering Sea Ecosystem (NRC 1996b) commissioned by the U.S. Department of State concluded that “fundamental conflicts between the usual goals of maximizing yields in marine fisheries management and the goals of the ESA, MMPA, and National Environmental Policy Act (NEPA) remain unresolved even at the federal level.” This conclusion was in reference to the debate over plausible causes of Steller sea lion declines in the Bering Sea and western Gulf of Alaska. Such conflicts have persevered since that period, associated with growing research budgets, extensive litigation and legal discourse over the implementation of ESA, MSFCMA and NEPA, and additional NRC reviews requested by the North Pacific Fishery Management Council (NRC 2003).

The functionalist perspective is intrinsically biased towards equilibrium resilience, the idea that populations and ecosystems are capable of restoring themselves to (or close to) past states given the opportunity (vis-à-vis the cessation of a perturbation) to do so.

This is in direct contrast to what Holling and Meffe (1996) have dubbed the "golden rule" of ecosystem management, which is that "management should strive to retain critical types and ranges of natural variation in resource systems in order to maintain their resiliency." This is based on the observation that ecosystems have thresholds and can flip into alternative states of behavior when thresholds are breached. By contrast, the foundation of traditional fisheries management is the premise that management can control multiple, interacting population trajectories with enough precision to shift both populations (and implicitly, ecosystems) into a mode that is as maximally beneficial to society as possible. As Hanna (1997) puts it, the "differing needs of the two types of economies (natural and industrial) lead to conflicts when fishery management proceeds on an industrial, linear, full-production basis in a natural economy which is based on reproduction, renewal and interdependence." Hanna argues that sustainability requires that human economies and management institutions more closely approximate the underlying organization of the natural system, just as McEvoy (1996) contends that the most important target for achieving sustainability is the "long-term health of the interaction between nature, the economy, and the legal system."

Perhaps the greatest difference between compositionalist and functionalist views is the implicit assumption in the former that ecosystem function and integrity are generally incompatible with the human interactions within an ecosystem.[1] By contrast, the functionalist view recognizes the ideal of human economies as "embedded" in the larger economy of nature, such that the two economies are mutually sustaining (Callicott et al. 1999). In his review of ecosystem management definitions adopted by the Forest Service, the Bureau of Land Management, the Fish and Wildlife Service and other federal agencies, Stanley (1995) not surprisingly finds that the functionalist view of ecosystem-based management is the one most often applied in contemporary resource

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[1] Callicott et al. (1999) argue that compositionalists tend to view humans as a "destructive force of change external to the biota," principally as a result of the very fair recognition that culture and technology have allowed humans to adapt to changing conditions many orders of magnitude faster than other species.

management.[2] Callicott et al. (1999) close their discussion by stating that while the two views are clearly two ends of a continuum. Although different legal and societal objectives may shape the basic premises upon which conservation and management efforts are based (for example, differences between objectives for wildlife refuges and lands designated as national wilderness areas, as opposed to multiple use national forest lands), management efforts will be most effective if they draw upon both ecosystem (functionalist) and evolutionary (compositionalist) ecologies.

A functionalist definition of ecosystem-based fisheries management was made by the NRC Committee on Ecosystem Management for Sustainable Fisheries (NRC 1999a), who described the approach as one that would "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." Although the Committee acknowledged that adaptation of such an approach could cause short-term economic losses and impacts to communities, it suggested that the ultimate results would be rebuilt populations and increased sustainable yields. To claim that an ecosystem approach should ultimately lead to higher yields by fisheries as ecosystems are rebuilt sets a very high, and perhaps unrealistic, bar for future managers.[3] This may be true in limited instances, such as in coastal areas where impacts such as habitat alteration, eutrophication, water pollution or other large scale impacts have reduced the carrying capacity of the environment (Botsford et al. 1997). However, it is far more

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[2] For example, the ecosystem approach to forest management was defined as "the use of an ecological approach to achieve multiple-use management of the national forests and grasslands by blending the needs of the people and environmental values in such a way that the national forests and grasslands represent diverse, healthy, productive and sustainable ecosystems" (Robertson 1992, as in Stanley 1995).

[3] In all fairness, fisheries management policies have long included vague and incompatible goals and objectives. Larkin (1993) provides the most egregious example, in his critique of the Canadian government's official policy for commercial fisheries, which was to "maximize food production, preserve ecological balance, allocate access optimally, provide for economic viability and growth, optimize distribution and minimize instability in returns, ensure prior recognition of economic and social impact, minimize dependence on paternalistic industry and government, and protect national security and sovereignty." As Larkin saw it, the only thing missing was mention of Canada's national debt.

likely to be false in most scenarios, particularly where historical yields were far above those that might be sustainable under even a moderately precautionary single-species approach (particularly where such yields were associated with driving stocks down towards theoretical population levels of maximum productivity, at 40 to 50% of their unfished biomass). Moreover, it is already an obligation under the Sustainable Fisheries Act amendments to end overfishing and rebuild populations. As policy makers and resource managers struggle to consider what ecosystem management is in the future, perhaps it will be worthwhile to step back and realistically consider what it is not. Ecosystem-based fisheries management is not something that will maximize the objectives of all parties in a given fisheries management community.

Ecosystem management, or an ecosystem-based approach to fisheries management, has yet to be either mandated or embraced in managing marine resources, and by all expectations any eventual mandates would likely lean heavily towards the functionalist view. Currently, the North Pacific Fishery Management Council, the only Council to define and seek to develop an ecosystem perspective in managing their fisheries, has defined its objective as “a strategy to regulate human activity toward maintaining long-term system sustainability, within the range of natural variability as we understand it” (Witherell et al. 2000). Link (2002) proposes that fisheries management from an ecosystem perspective might be defined as a single species approach that is mindful of broader ecosystem considerations, such as the effects of fishing on non-target species, habitat, species interactions, and whole system processes. Mangel et al. (2000) add that perhaps even more important than these elements is that management “be cognizant of the levels of ignorance in which it is working.” There is also widespread agreement that successful adoption of an ecosystem-based approach to managing fisheries will be incremental, without discarding current management structures, criteria and objectives (NRC 1999a, EPAP 1999, Mangel et al. 2000, Goodman et al. 2002, Browman et al. 2004).

At a minimum, an ecosystem-based approach to fisheries management should include critical evaluations of the plausible consequences of alternative decisions to both the resource and the people and communities that depend (either directly or indirectly) on them over both short and long time scales. Fisheries management, from an ecosystem perspective or otherwise, is based on making tradeoffs among the multiple objectives of disparate user and interest groups. Walters and Martell (in press) explore the issue of tradeoffs in greater detail, and suggest that the nature of tradeoffs in fisheries management may be poorly suited towards meeting multiple objectives in such a context. They demonstrate that many tradeoffs have concave rather than convex relationships (or frontiers) with respect to maximizing objective functions. In other words, for many sets of objectives, small increases in one value measure (such as maintaining the abundance of an unproductive stock in a mixed stock fishery) require disproportionate reductions in the achievable value of another measure (such as maximizing the catch of a productive stock in a mixed stock fishery), such that alternatives that fulfill multiple objectives ("win-win" situations) are actually quite rare. If true, the actual implementation of ecosystem-based management approaches may be more difficult than we care to imagine.

4.3 Sustainable Fisheries, Fisheries Ecosystem Plans, and the Law

In the discussions leading up the passage of the 1996 Sustainable Fisheries Act, there was increasing recognition of the potential for an ecosystem-based approach to improve fisheries management. Although Congress ultimately passed a bill with conservation reforms that were generally lauded by conservationists and user groups, they chose not to explicitly adopt an ecosystem-based approach to management.[4] However, the Act

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[4] The SFA included no mention of ecosystem considerations in the National Standards or in fishery management plan (FMP) requirements, although some authority is inferred in the definitions section of the Act where optimum yield is defined as "the amount of fish which will provide the greatest overall benefit to the Nation, particularly with respect to food production and recreational opportunities, and

did require the National Marine Fisheries Service (NMFS) to convene a panel of experts to examine how best to amend or supplement current single species management approaches. The Panel's primary recommendation was that the eight regional Fishery Management Councils develop Fisheries Ecosystem Plans (FEPs) for the ecosystem or ecosystems under their jurisdiction (EPAP 1999). Although the current system of fisheries management plans (FMPs) would remain the basic management tool in the near term, they would be amended to ensure compatibility with the ecosystem principles, goals and policies of the FEP. The FEP would act as an "umbrella document" containing detailed information on the structure and function of the ecosystem under consideration, and increase the awareness of managers and stakeholders on the effects that their decisions have on the ecosystem. As such, FEPs would be the next major step in translating today's directed management efforts into more holistic approaches.

Although the Panel considered the preparations of specific guidelines as beyond their scope, they did identify actions to be taken by Councils in developing FEPs, including:

- Delineate the geographic extent of ecosystems that occur within Council authority, including characterization of the biological, chemical and physical dynamics of those ecosystems, and "zone" the area for alternative uses.
- Develop a conceptual model of the food web.
- Describe habitat needs of different life history stages for all plants and animals in the "significant food web" and how they are considered in conservation and management measures.
- Calculate total removals, including incidental mortality, and show how they relate to standing biomass, production, optimum yields, natural mortality, and trophic structure.
- Assess how uncertainty is characterized and what kind of buffers against uncertainty are included in conservation and management actions.

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taking into account the protection of marine ecosystems" (16 U.S.C. 1802). Yet there is little guidance on how to take the protection of marine ecosystems into account, or the extent to which this might be balanced against the economic considerations of coastal or fisheries dependent communities. Despite this, Macpherson (2001) argues that the SFA represents "a true paradigm shift away from viewing fish as a resource for extraction to fish as a component of a larger ecological system" and that current implementation provides "opportunities for use of an ecosystem-based approach to a certain extent."

- Develop indices of ecosystem health as targets for management.
- Describe available long-term monitoring data and how they are used.
- Assess the ecological, human, and institutional elements of the ecosystem which most significantly affect fisheries, and are outside Council/Department of Commerce authority.

In general, the Panel envisioned flexibility in the development and application of these products, for example recommending that each Council develop its own goals, objectives and metrics based on the characteristics of the ecosystem in question. The panel also recommended that one or more Councils be selected to develop demonstration FEPs, and that all Councils consider frameworks for future plans based on readily available information. Finally, the Panel concluded that further incorporation of ecosystem principles in fishery management would require a specific mandate, and recommended that Congress require full FEP implementation in the next reauthorization of the Magnuson Act.

Since the EPAP report, modest progress to develop guidance, framework and legislation for fisheries ecosystem plans has been made, and several bills to reauthorize the Magnuson Act have included FEP requirements or FEP demonstration projects.[5] In oversight hearings before Congress, the Administrator for Fisheries said that the agency approach has instead been to "conduct single species assessments and embed them in an ecosystem context."[6] The NMFS has continued to support ecosystem-based research and modeling efforts, including consideration of how biological reference points might

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[5] In the 107th Congress, H.R. 4749 to reauthorize the MSFCMA (sponsored by W. Gilchrest and reported to the House on July 10, 2000) included a process to begin the development of FEPs as envisioned by the EPAP Panel; a "staff draft" of reauthorization language developed by the Senate Subcommittee on Oceans, Atmosphere and Fisheries (majority) included similar language (E. Buck, Congressional Research Service, unpublished memorandum). However, recent administration proposals to Magnuson reauthorization have mentioned neither FEPs nor demonstration FEPs, as inferred by the administration's 2003 reauthorization recommendations posted online at http://www.nmfs.noaa.gov/docs/MSAFinal.pdf.

[6] W. Hogarth, testimony to the House Resources Committee, June 14, 2001. Hogarth added that while multi-species and ecosystem models were being developed in NOAA Fisheries Science Centers and academic institutions, they were difficult to validate and suffered from a lack of baseline data.

be altered to account for variable ocean conditions and production regimes,[7] efforts to develop technical guidance and potential guidelines for FEPs,[8] as well as demonstration FEP programs in the Chesapeake Bay (NOAA 2000). Thus, while the most recent National Oceanic and Atmospheric Administration (NOAA) Strategic Plan explicitly references one of four key objective of the NOAA as being to "protect, restore and manage the use of coastal and ocean resources through ecosystem-based management," the plan also recognizes that management in the near term will continue to be on a species and site-specific basis.[9] While the agency is unquestionably moving towards greater consideration of ecosystem-based management approaches, including broader consideration of the ecological consequences of fishing to habitat and other elements of the ecosystem, many of these impacts continue to be largely overlooked in the current management regime.

The extent to which existing legislation may or may not be interpreted as implementing ecosystem-based approaches to decision-making and management is unclear. For example, the National Environmental Policy Act (NEPA) of 1972 has the primary objective of "creation and maintenance of conditions under which man and nature can exist in productive harmony" (42 U.S.C. 4321). The Act requires a detailed statement (commonly known as an environmental impact statement, or EIS) on the potential impacts of every proposed federal action that might affect the environment. An EIS

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[7] In 2003 public comments were solicited with regard to the implementation of National Standard 1 of the Sustainable Fisheries Act, which required avoiding overfishing and rebuilding depleted stocks. Specifically, comments were solicited to consider such factors as the concept of minimum stock size thresholds (MSSTs), the difficulties in estimating MSSTs in data-poor situations, and how to calculate rebuilding targets appropriate to the prevailing environmental regime under variable ocean conditions.

[8] The Marine Fisheries Advisory Committee (MAFAC), an appointed, non-governmental advisory panel to the NMFS, drafted technical guidelines intended to aid in the development of FEPs in a 2003 report to the NMFS entitled "Technical guidance for implementing an ecosystem-based approach to fisheries management." However, this report did little to build on the momentum of the EPAP panel with tangible actions towards implementing FEPs. Internal discussions and guidelines relevant to the potential implementation of FEPs have also been circulating within the NMFS, potentially in anticipation of legislative mandates to develop additional demonstration FEPs.

[9] As a part of this new focus, the plan also suggests increasing the priority given to habitat protection and greater consideration of interactions target and nontarget species. This plan is entitled "New priorities for the 21st century: NOAA's strategic plan for FY 2003- FY 2008 and beyond," and is available online from the NOAA website at http://www.spo.noaa.gov/strplan.htm.

details not only adverse impacts that could not be avoided if the proposal was implemented, but "reasonable and prudent" alternatives to such actions. Although there is no requirement to select the most benign alternative with regard to environmental impact, there are obligations to mitigate likely or unavoidable impacts. NEPA requirements compel agencies to do analyses, with the intent being to inform both decisionmakers and the public of the likely or plausible consequences of proposed actions. NEPA is about analysis, disclosure, and transparency; one reason why it remains one of the most powerful environmental laws in the nation today.

Fishery Management Councils historically developed environmental impact statements, required for connected or closely related programmatic actions, such as the broad-scale management of multiple fisheries components included in fishery management plans. Councils also regularly develop separate EIS or environmental assessments (EAs) of plan amendments and annual harvest recommendations. There remains a lack of clarity regarding the longevity of programmatic documents. Although currently there is no clear regulatory requirement to revisit past Programmatic EIS, some interpretations of NEPA suggest that Programmatic EIS statements be revisited as both the availability of data and knowledge increase (CEQ 2003).[10] Until very recently, no Fishery Management Councils had developed such updates since the passage of FMPs, many as long as 25 years ago. Yet recent litigation regarding the impacts of fishing on marine ecosystems and endangered species may portend a new round of NEPA activity for Fisheries Management Councils (Walsh et al. 2002).[11] As a result of litigation, the NMFS and the North Pacific Fishery Management Council (NPFMC) were engaged in

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[10] There remains considerable confusion regarding the exact roles and responsibilities for programmatic analysis under NEPA, with most agencies and stakeholders having the opinion that such analysis are not being fully used for their intended purposes. There is widespread agreement that better guidance is needed by agencies to emphasize the need for interagency collaboration, explain relationships between current and future analysis (including where and when deferred issues will be addressed), and evaluate reasonable life expectancies for programmatic documents to determine when they may have become outdates (CEQ 2003).

[11] The Pacific Council recently initiated a Programmatic SEIS for the west coast groundfish fishery, but scaled the scope of the SEIS to evaluating solely the impact of bycatch due to a combination of factors including litigation and budgetary constraints.

a process of revisiting the PSEIS for their Eastern Bering Sea and Gulf of Alaska groundfish FMP over the past four years, and their ultimate results are relevant to the discussion here.[12]

The principal objective of the Alaska Center/NPFMC PSEIS is to serve as the central environmental document for the groundfish fishery, and provide a "big picture" environmental evaluation of the impacts of fisheries, as well as fisheries management objectives, for given fisheries throughout the region. The document includes consideration of alternative fisheries management policies, intended to illustrate a wide range of potential policy objectives. Although all alternatives must be crafted to be compatible with other existing laws (Magnuson Act, Endangered Species Act, Marine Mammal Protection Act), they are intended to "bookend" the extremes between harvest strategies and objectives. The alternatives ranged from fishing all stocks aggressively in order to maximize biological and economic yield from the resource, to adopting a highly precautionary approach in which the burden of proof is shifted to resource users to demonstrate negligible impacts of fisheries to the ecosystem.[13] The alternatives also included the status quo, described as adaptive to new information and reactive to environmental issues. The status quo is based on the assumption that while fishing does have adverse impacts on the environment, fishing at levels approaching, but not exceeding, MSY are compatible with ecosystem health and sustainability.

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[12] This process has taken over five years and several court orders to arrive at a final document. The discussion here was based on the draft form released for public comment in late 2003, entitled Alaska Groundfish Fisheries Draft Programmatic Supplemental Environmental Impact Statement, U.S. Department of Commerce, NOAA/NMFS September 2003. Time constraints prevented revisiting this discussion based on the recently released (June 2004) final PSEIS.

[13] In their comments on the North Pacific Council's most recent draft SEIS, a consortium of environmental groups suggested that the FMP SEIS provided an opportunity for NMFS to take the lead in the shift to ecosystem-based fisheries management, and offered an alternative that would implement such a shift. Key to their proposal was the recommendation to implement FEPs in order to provide "clearly stated goals, objectives, and guidance at the policy level requiring formal consideration and protection of the ecosystem as a binding, non-discretionary management obligation." Their document, entitled "The Oceans Alternative," is included in the Comment Analysis Report for the 2003 Draft Programmatic SEIS, online at http://www.fakr.noaa.gov/sustainablefisheries/seis/draft0903/.

The alternatives are accompanied by a corresponding philosophy, a set of assumptions, a plan of action, and suite of likely or expected impacts associated with adopting each one. The likely or potential impacts evaluated with respect to each of the alternatives considered in the most recent SEIS overlap considerably with the elements of fisheries ecosystem plans listed above, and as such are worth repeating here. They include:

- Sustainability of target stocks (prevention of overfishing).
- Sustainability of fisheries and communities.
- Stability of the food web and (ecological) community structure.
- Bycatch (discards) and incidental catches.
- Seabird and marine mammal interactions.
- Marine habitat, including benthic essential fish habitat.
- Value of marine resources (both commercial and non-commercial).
- Alaska native participation in fishery management and traditional ways of life.
- Data quality, monitoring, research and enforcement requirements.

Additionally, the assessment included qualitative (color-coded) estimates of the uncertainty believed to surround the likely impact under each alternative. Clearly there is substantial overlap between the impacts on the ecosystem that are evaluated in this contemporary implementation of NEPA in fisheries management, and the framework of proposed fisheries ecosystem plans as envisioned by the Ecosystem Principles Advisory Panel.

However it is equally clear that there are tremendous differences between the two approaches. The EPAP Panel recommendations included looking broadly beyond NEPA requirements as related to individual FMPs, to evaluate the cumulative impacts of all fisheries and other relevant activities, in delineating their proposed terms of reference for developing FEPs. Additionally, the framework for FEPs is generally oriented towards physical and biological impacts and consequences, while the Programmatic SEIS alternatives for FMPs delve more narrowly into specific resource assemblages, and more deeply consider the social and economic impacts and interactions with the fishing industry and fishing communities. Thus while NEPA might arguably be interpreted broadly enough to accommodate an ecosystem view, it seems clear that neither NEPA nor the MSFCMA explicitly mandates such a view.

Even without a clear mandate, the language in both of these laws infers that ecosystem-based assessments of the impacts of fishing should be an integral part of efforts to evaluate alternatives in making policy decisions within the context of the current fishery management system. This suggests that the ecosystem-based models, principles and considerations discussed throughout this dissertation, and indeed within a growing community of researchers worldwide, are ready to be integrated into the current fisheries management framework from a strategic perspective. At the very least, they could help NMFS and the Councils meet future Programmatic EIS requirements from a more holistic perspective, embed ecosystem considerations formally within the management arena, and contribute to better planning documents and research strategies. Although it will likely take a mandate from Congress to give ecosystem considerations the same weight as the national standards in making management decisions, the time is certainly ripe to consider ecosystem impacts formally with the best methods available.

4.4 Objectives for Ecosystem Based Management in the NCC

The Sustainable Fisheries Act amendments to the MSFCMA in 1996 clearly changed the nature of fisheries management in the United States, and resulted in dramatic changes in the way that both the NMFS and the Fisheries Management Councils operated. For the Pacific Council, the environmental conditions through the 1990s had already contributed to a sequential series of fisheries crises related to declines in salmon productivity and groundfish recruitment (reviewed in greater detail in Chapter 1). These, in association with growing recognition of the low productivity of many groundfish stocks, brought about wave after wave of reductions in total allowable catches and trip limits. Together with the clearly defined mandate in the SFA amendments to stop overfishing, rebuild depleted stocks, and protect habitat, the management measures necessary to meet the SFA requirements in recent years have included reductions in allowable landings to bycatch levels, massive closures of continental shelf and slope habitat to most fishing gears, and cooperatively (government and industry) funded buybacks of nearly one-third of the west coast trawl fleet.[14] Both the NMFS science centers and the Pacific Council staff have increased their budgets and personnel substantially to cope with additional legislative requirements, the growing complexity of the regulatory rulemaking regime, and ongoing legal challenges to their decisions and actions.

The Council currently has 14 permanent or quasi-permanent advisory bodies charged principally with implementing or guiding implementation of the fishery management plans, plus an additional 15 ad-hoc advisory bodies which deal with specific and emerging issues that (currently) almost exclusively relate to the groundfish fishery.[15] Although commercial and (particularly in recent years) recreational fishing industry representatives have continued to act as the primary participants in the Council process (and have remained the exclusive stakeholder participants on the Council itself),

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[14] In December of 2003 a $46 million dollar federally-sponsored buyout program permanently removed fishing rights from 92 of the roughly 270 limited-entry groundfish trawlers from west coast fisheries ($36 million is to be repaid by remaining fishermen over the next 30 years). Although this was a move widely recognized as necessary to reduce a substantially overcapitalized fishing fleet, some lamented the results as devastating for those fishing communities that lost most or all of their commercial fleet (see Rojas-Burke 2003, McDonald 2003, and Henion 2003).

[15] As of June 2004, the 14 standing or long-term advisory bodies include both an advisory subpanel (made up of industry and stakeholder representatives) and a management team (made up chiefly of state, tribal, and federal scientists and managers) for each of the four FMPs (salmon, groundfish, highly migratory species and coastal pelagic species), as well as an Enforcement Body, a Habitat Committee, a Model Evaluation Workgroup and a Scientific and Statistical Committee charged with vetting the scientific merits or shortcomings of the information that is the basis of Council decisions. The 15 Ad Hoc committees and workgroups include a (catch) Allocation Committee, a Channel Islands Marine Reserve Committee, a Full Retention Committee (dealing with regulatory bycatch), a Groundfish EIS Committee, a Groundfish Habitat Committee, a Groundfish Policy Committee, a Groundfish Multi-Year Management Committee, a Groundfish Strategic Plan Implementation Oversight Committee, a Groundfish Strategic Plan Implementation Oversight Committee- Open Access Conversion Subcommittee, a Groundfish Trawl Individual Quota Committee, a Groundfish Trawl Individual Quota Analytical Team, a Groundfish Trawl Individual Quota Enforcement Group, a Groundfish Trawl Individual Quota Independent Experts Panel, an Observer Program Implementation Committee, and a Vessel Monitoring System Committee.

increasing participation and influence by environmental groups and other non-industry interests increased throughout the 1990s (Hanna 2000, Eagle et al. 2003). Much of the Council's activities are currently related to crisis management approaches, and there are clearly substantial limitations on both the Council and the NMFS's abilities to develop and implement new initiatives. Furthermore, it is widely accepted that a prerequisite to implementing an ecosystem-based approach to managing fisheries is meeting the obligations of sustainable single-species management under the current MSFCMA.

Despite these limitations, it is clear that the fisheries system on the west coast is clearly going through a period of major upheaval, and the opportunity to change the fundamental nature of how fisheries resources are managed, with the goal of sustaining both the resources and the interactions between the resources and the resource users, is tremendous. An FEP could provide the Council with a vehicle for engaging issues that range widely across both individual FMPs (and state-managed fisheries not covered by FMPs) and across various user and stakeholder groups, such as climate, trophic interactions and ecological factors such as biodiversity and life history complexity. Given the opportunity, it is worth considering how the Council might implement a general movement towards an ecosystem-based approach to managing fisheries, above and beyond the plethora of other activities (stock rebuilding, fleet restructuring, habitat protection and crisis-driven spatially-based management), given what we know now about the structure and dynamics of the NCC. If we were to embrace an ecosystem based approach in principle, but were limited in the rate at which we could prescribe such an approach as policy, where would we start? Three elements would be key to such an approach, these being:

- Increasing exposure to the management community of short and long term climate and ocean status, trends and scenarios for the California Current
- Consideration of trophic interactions among fished and unfished species as associated with fishing impacts on ecosystem structure and dynamics

- The increasing application of new management approaches, including spatial management measures to protect life history characteristics and biodiversity, within the context of the current regulatory regime.

These, obviously, would complement rather than replace existing management efforts and improvements relative to single species conservation objectives. As such, they are intended to complement the plethora of ongoing activities and developments currently being undertaken by the NMFS and the Council, and in all fairness are likely to be of a lower priority in the immediate term. However, they should rightly be considered critical elements of any future success at meeting NOAA and NMFS' most recently outlined objectives, as outlined in the most recent NOAA strategic plan, which explicitly references the need to protect, restore and manage coastal and ocean resources through ecosystem-based management approaches.

4.5 Climate Considerations

Climate forcing is unmistakably a key factor in understanding the nature and dynamics of production across all trophic levels in this system. Highly detailed, descriptive and meaningful climate information and forecasts are now widely available in status reports and on the internet to researchers and managers alike. As discussed in Chapters 1 and 3, examples include upwelling indices, sea surface temperatures, relative sea level (as an indicator of transport) and short-term ENSO forecasts. Abundant biological indices exist as well, such as the CalCOFI zooplankton time series, Oregon and British Columbia zooplankton time series (Peterson and Schwing 2003), estimates of rockfish year class strength (Ralston and Howard 1995, Brodeur et al. 2003), and predictive models of salmonid survival based on physical ocean indices (Logerwell et al. 2003). Clearly, the impacts of climate are complex, affecting not only primary productivity, but the distribution, species composition, reproductive success and (perhaps) transfer efficiency of primary and secondary consumers as well as top level predators. Yet the growing recognition of the role of climate in shaping marine ecosystems and their dynamics suggests that the time is overdue for their inclusion into the management framework.

Over the last decade, numerous ecosystem "status reports" have evolved that summarize trends in climate, oceanographic conditions, biological productivity and trends in the abundance of sensitive species. Such status reports include:

- The State of the California Current: included in the annual publication of CalCOFI Reports since 1994, includes trends in physical forcing and biological productivity taken from a wide range of monitoring and research efforts (although with a focus on CalCOFI data collection activities and results).
- The NPFMC Ecosystem Considerations Chapter: included in the annual Stock Assessment and Fishery Evaluation (SAFE) reports since 1995, summarizing available information on climate trends, climate and fishery interactions and potential ecological consequences of fishing.
- State of the Ocean Report: annual report by the Canadian Department of Fisheries and Oceans (DFO) providing an overview on the physical, chemical and biological state of the marine environment, and the impacts of the same on both potential yield and the operations of the fishing industry itself.
- North Pacific Ecosystem Status Report: in development by the North Pacific Marine Science Organization (PICES) intended to review and summarize the status and trends of the marine ecosystems in the North Pacific, and consider the processes that are causing or expected to cause change in the near future.

All of these documents summarize and integrate physical and biological observations and indices to develop a contemporary picture of the ecosystems or regions in question.[16] Although the format tends to be oriented toward scientists, all either are, or could be repackaged, in a format suitable for decisionmakers and stakeholders. The North Pacific Council's Ecosystem Considerations Chapter began with this objective in mind, and elements of this chapter are regularly presented to NPFMC advisory bodies (principally the Plan Teams the Scientific and Statistical Committee) as well as made available to the Council community as an element of the Stock Assessment and Fishery

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[16] There are also annual workshops and meeting reports produced by the GLOBEC science programs that could be sources of conditions, trends and physical observations. This is an important role, given that a primary objective of the California Current program was to "provide managers and policy makers with better information on the role of environmental variability and climate change" (U.S. GLOBEC 1994)

Evaluation reports.[17] Similarly, the NPFMC's Ecosystem Committee has held meetings and seminars intended to both digest and disseminate ecosystem information across the Council Community. The time is long overdue for documentation and briefings of this nature to other Councils and their advisory bodies on climate and ecosystem status, trends, and research that is relevant to the management of their particular resources.

Indeed, even simple exposure to climate trends, forecasts, scenarios and other information through briefings and summaries is essential in acclimating the management community to the vocabulary, nature and potential utility of such information. Thus, a key recommendation for moving towards an ecosystem-based approach to managing fisheries would be to ***periodically brief the PFMC and the Council community with summary reports on climate and ocean observations, forecasts and scenarios for the California Current***. Such briefings could be as simple as integrating already existing documents and information, from the reports listed previously as well as global observations and (where possible) short term predictions regarding the likelihood (and northerly manifestation of) patterns such as ENSO or the PDO. A complementary review document detailing climate and ecosystem status, trends, and observations could also be integrated into the Stock Assessment and Fishery Evaluation Reports, or made otherwise available to the Council community, with references and links to the increasing number of such reports available elsewhere.

In addition to generating such a document, it would greatly benefit the Council and the management community to ***consider appointing a regional fisheries oceanographer***, whose primary responsibility would be to synthesize climate information into usable and understandable formats, orchestrate the development of a climate and ecosystem status and trends document, and act as a conduit between the climate research

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[17] Over time the size of the Ecosystem Considerations chapter has grown considerably, from 56 pages in 1997 to over 350 pages in 2003. However, there remains no formal mechanism for considering "how" the observations, indices and insights in that document should be interpreted, although Plan Teams have been asked to formally consider and respond to the Ecosystem Considerations chapter itself. Yet there remains a widely accepted need to consider in greater detail how the findings could be interpreted by managers.

community and the fisheries management community. A blueprint for defining the role of regional fisheries oceanographers could be taken from the existing framework for the role of state climatologists. As defined by the American Association of State Climatologists (AASC),[18] their own role includes summarizing and disseminating weather and climate information to user communities, demonstrating the value of climate information to the user communities, performing climate impact assessments and evaluations, and conducting climate research, diagnosis and projections. The users of climate information include a wide and growing range of business, planners and local government workers, including those involved with water management, agriculture, forest, public utilities, and emergency response, for which short-term (seasonal to annual) forecasts have the potential to reduce expenses or increase revenues by millions to billions of dollars (Hamlet et al. 2002, AASC 2003).

Given widespread recognition of the broad and large-scale impacts of climate on fish and fisheries, it would seem only rational that the inclusion of climate information and considerations by the Council community could significantly improve the context in which management decisions are made. For example, an improved understanding of the relationship between salmon success and climate might suggest that greater precaution is taken under the expectation of an El Niño event, or a particular phase of the PDO (Mote et al. 1999). The position would also offer a venue for transmitting climate information and forecasts to fishermen and fisheries-dependent communities. This too is an important role, given that Dalton (2001) found substantial direct impacts of climate on fishing effort, catch prices and future expectations of production and availability in fisheries for salmon, squid, albacore and sablefish in Monterey Bay fisheries. His results also implied that regulations that allowed fishermen to allocate

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[18] According to the AASC website (http://lwf.ncdc.noaa.gov/oa/climate/aasc.html#ABOUT), state climatologists are individuals who are usually employees of either state agencies or state-supported universities. Their work is done in concert with the National Climate Data Center (NCDC) and the NCDC's six regional climate centers. The NCDC is a component of the National Environmental Satellite, Data, and Information Service (NESDIS), which is a line office of the National Oceanographic and Atmospheric Administration (NOAA).

their effort freely in response to climate and price variability would maximize the value of future climate information, and emphasized the importance of improving the understanding of complex physical, biological and economic feedbacks between fisheries and the ecosystem. Consideration of how managers might facilitate such effort reallocations, without increasing the jeopardy of resources, would be one way to attempt to operationalize McEvoy's (1996) key target for sustainability, "the long-term health of the interaction between nature, the economy and the legal system."

4.6 Ecosystem Models and Trophic Considerations

As discussed in greater detail in Chapter 1 and above, we have seen that energetic and highly variable oceanographic processes shape the physical environment and drive the production at the base of the food web. Over the past two hundred years, massive and pulsed removals of whales, pinnipeds, salmon, coastal pelagics, groundfish, invertebrates and hake have taken place throughout the California Current, and it would be irrational to presume that such removals have not fundamentally disturbed these energy pathways and altered the basic structure and function of the ecological community. Despite a lack of adequate data with which to compare past ecosystem structure and function with the present, the only way in which to gain insights (recognizing that full understanding will remain elusive) is to document and model both the removals and the plausible impacts to structure and function that have resulted. We know now that many of these resources are not capable of providing a steady and predictable surplus to humans year after year, and we know too that we have exceeded, often dramatically, the productive capacity of many such stocks. Yet we also know that many elements of the system are resilient, as populations of whales, pinnipeds, sardines and many salmon runs have rebounded from past impacts over recent decades (recent years for the latter), providing us with opportunities to better appreciate the resilience of stocks, species and communities in this dynamic ecosystem.

Almost by definition, ***the continued development, improvement and discussion of quantitative ecosystem models is an essential element in the adoption of any ecosystem approach to management***. Although most of the current generation of models, including those discussed in Chapters 2 and 3, are unavoidably biased in aggregating the considerably diversity of lower, and often higher, trophic levels, the spatial and temporal scale of most such models matches those of greatest significance to stock assessment and management. Most current multi-species and ecosystem models are consequently built on the same foundation as single species assessment models, and provide a pragmatic template for using available data, albeit with considerably less detail in population structure. Although climate and trophic interactions with fishing are among the most challenging of ecosystem-scale challenges to improving marine resource management, they allow a means to evaluate the compatibility of multiple sources of information on interspecific interactions and variability. As such, they force us to confront issues that are widely recognized to be important, yet complex, and provide managers and decisionmakers with a tangible product to respond to.

The quantification of energy pathways and trophic interactions in the Northern California Current (NCC) discussed in Chapter 2 has expanded on existing insights regarding the tremendous significance of hake as both a predator and competitor to other elements of the ecosystem, uncovered potential bias in food habits sampling that overemphasizes the tight coupling of sablefish to longspine thornyheads, and contrasted the relative roles of fisheries and top-predators as sources of mortality for long-lived and slow-growing groundfish. Particular emphasis was made on presenting insightful visual representations of ecosystem trophic structure and energy flow, and on using comparative evaluations of model outputs to scale the impacts of fishing on ecosystem structure and productivity. The comparison of flows among various components of the ecosystem, and a concurrent analysis of the ecological “system-wide” cost of fishing are important visual and quantitative tools that allow managers and stakeholders to increasingly envision the role of fisheries in altering energy flow through marine ecosystems. Pikitch et al. (2004) have reiterated the often-made point that there remains a need to derive and develop community and system-wide standards, reference points, and control rules analogous to single species criteria, including evaluations of ecosystem productivity relative to the requirements of other ecosystem components and removals by fisheries.[19] Quantitative ecosystem models offer a valuable vehicle for doing so. As such they should be key elements of future efforts to complement single-species information when informing managers and decisionmakers of ecosystem condition and status.

The insights gained in static modeling of the NCC were emphasized further in the dynamic simulations, particularly as much of the variability from landings and from single species assessments could generally be replicated over recent decades. That climate forcing could often improve the fit of the model to data significantly was a finding that bodes at least moderately well for the potential of dynamic ecosystem models to include climate forcing in meaningful ways. The one-way trips of many groundfish stocks notwithstanding, it is clear that to even roughly replicate ecosystem dynamics over recent decades it is necessary to include climate as a key forcing factor from both the bottom-up and the top-down. The results also suggest that the stronger interactions in the NCC were observed in groups such as shrimp, salmon, hake and small flatfish, where high turnover rates and predation mortality is coupled with substantial changes in many of their key predators (hake, sablefish, marine mammals) over the last forty years. This makes sense in a community dominated in part by long-lived rockfish, roundfish and flatfish, where low mortality rates are indicative of low predation rates and potentially weaker trophic interactions. Interestingly however, one

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[19] Although a review of literature related to ecosystem metrics was included in Chapter 2, it is worth citing Mangel et al. (2000), who argue that ecosystem-based objectives should be made in direct relation to the fishery-ecosystem interaction (such as the mean trophic level of the catch, or the percentage of new production removed by fishing), rather than the ecosystem as a whole. Most ecosystem models, including those discussed in Chapters 2 and 3, offer some insights with regard to both system-level and fisheries-level metrics.

of the strongest potential interactions was among some of the slowest growing species; sablefish, shortspine thornyhead and longspine thornyhead. As the fauna and environmental conditions along the continental slope differ tremendously from those on the shelf and near the shelf break, evaluating these interactions more carefully is likely to require finer resolution modeling efforts, coupled with more appropriate consideration of age and/or size based bioenergetic requirements and predation vulnerabilities.

Where trophic interactions between exploited species seem clear, dynamic modeling can obviously offer valuable information regarding the likely or potential trade-offs between harvest strategies, and provide a template to evaluate both the magnitude and some measure of reasonable consequences of removals of either predators or prey in the NCC. Although quantitative modeling of significant trophic interactions in the NCC may not lead to substantive changes in harvest or management strategies in the near term, it may aid in the understanding of variations in population trends, and will contribute to a more holistic understanding of ecological connections and interactions. [20] Conveying to decisionmakers the significance of such variability may be just as important as monitoring and conducting process-oriented research into the causes and consequences of the same. Both quantitative and conceptual models of climate driven changes in productivity, indices of zooplankton abundance and productivity, and dynamic simulations of food webs over time may all be useful tools in conveying the importance of such variability, particularly when periods of low production are either occurring or are anticipated.

Ecosystem models provide an increasingly accepted means of evaluating the consequences of trophic interactions and large-scale shifts in community structure

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[20] These considerations also demonstrate that an important element of monitoring in the NCC and throughout the CCS is continued investigations of food habits and trophic considerations, particularly of key predators such as increasing pinniped and marine mammals populations, Pacific hake and sablefish, as well as key forage species such as copepods, euphausiids and forage fishes.

associated with both climate and human impacts on marine ecosystems (Aydin et al. 2003, Christensen and Walters 1994, Plagányi and Butterworth 2004). Many criticisms of ecosystem modeling approaches are based less on the model structure, but on the misuse and misunderstanding of the model limitations (Hollowed et al. 2000, Plagányi and Butterworth 2004), a characteristic shared with single-species models (Schnute and Richards 2001). Their far more important feature however, is that if based on reasonable knowledge, and presented with appropriate skepticism, these models serve as a stimulus and focus for initiating dialogues and discussions with regard to both past ecosystem dynamics and plausible ecosystem futures. Perhaps their greatest asset is that they can complement the insights gained from single species models through a more strategic consideration of past and current abundance and productivity, and offer a means to evaluate plausible expectations of future system trade-offs between management decisions.

4.7 The Importance of Demographics, Life History and Biocomplexity

As discussed in Chapter 3, and in the beginning of this chapter, even a robust combination of single and multi-species data, models, reference points and thresholds would be insufficient to fully adopt an ecosystem perspective. The often vague but critically important definitions of diversity, biocomplexity, ecological integrity and other “compositionalist” concepts are just as important to managing from an ecosystem perspective as more “functionalist” single species and ecosystem model metrics and objectives. Models have a critical role to play by allowing the management community to relate to the consequences of their decisions. However, neither single species nor ecosystem models alone should be the sole determinant of management strategies and alternatives. Although this dissertation has not delved deeply into more compositionalist disciplines, some discussion of their significance is appropriate to a blueprint for implementing ecosystem-based management approach.

In considering the key differences between compositionalist and functionalist philosophies earlier in this chapter, it was clear that the latter, a thermodynamically-based view of ecosystems, represents the dominant worldview behind most applied fisheries science. Methods of estimating surplus production, stock-recruit relationships and maximum sustainable yields disregard the impacts of fishing as either a selective or evolutionary force, and discount (if not ignore entirely) the significance of demographic variability in populations. Most contemporary fisheries management is based on the assumption that fish populations are healthy if they are being exploited at levels that double (or more) their total mortality rate. Consequently, fishing often impacts severely alters demographic and life history characteristics, even when implemented successfully within the context of the current application of fisheries populations models, which may be contrary to perspectives of sustainability based on evolutionary ecology. Although the current National Standard guidelines recognize the significance of demographic and evolutionary impacts of fishing on both populations and ecosystems, there has been very little movement towards incorporating such considerations into harvest rate or policy decisions.[21]

As early as 1912 it was noticed that fish caught in the early or developing years of a fishery tended to be larger at age than those caught in more recent years, and fishing pressure is widely accepted to be a form of artificial selection towards smaller size or younger age at reproduction (Mangel and Stamps 2001, Conover and Munch 2002). That the potential consequences of such selection are important not only for

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[21] The National Standard guidelines state that Councils should build into status determination criteria an "appropriate consideration of risk, taking into account uncertainties in estimating harvest, stock conditions, life history parameters, or the effects of environmental factors." The guidelines also state that the benefits of protecting marine ecosystems (with regard to the consideration of the protection of marine ecosystems in defining optimal yield) include "maintaining viable populations (including those of unexploited species), maintaining evolutionary and ecological processes (e.g., disturbance regimes, hydrological processes, nutrient cycles), maintaining the evolutionary potential of species and ecosystems, and accommodating human use" (50 C.F.R. 600.310). However, as Macpherson (2001) points out, the SFA does not require the gathering of new data to address life history uncertainties or the protection of marine ecosystems, despite the observation that "true ecosystem management might very well require the gathering of new data, as recommended by the Ecosystem Principles Advisory Panel."

conservation reasons, but for economic reason as well is evident in Conover's (2000) observation that:

> Yield… is not a currency that is crucial to fitness. From the fishes' point of view, the goal is maximizing the relative contribution of genes (not biomass) to succeeding generations. Fisheries management plans, and the stock assessments on which they are based, are, therefore, non-Darwinian: they ignore the prey's co-evolutionary response to the effects of harvest.

Quite simply, these evolutionary consequences can reduce the sustainable yield of a population by decreasing the age at maturity and consequently reducing the relative amount of somatic growth in a population relative to reproductive effort. Consequently, intensive size selective fishing may ultimately prove even more detrimental to the humans and communities dependent upon such resources; particularly where larger fish are significantly more valuable than smaller ones. Although Heino and Godø (2002) point out that such adaptations do enable fish to sustain higher fishing pressure in the short term, and all else being equal (i.e., exclusive of the extremely adaptive behavior of most fishermen), might reduce the risk of total stock collapse or extinction.[22]

As it is clear that species across all trophic levels have adapted a wide range of complex life history strategies for coping with their environment, particularly in highly dynamic environments, it is increasingly obvious that consideration of demographic and life history strategies is long overdue in developing management approaches. McEvoy (1996) argues that successful fisheries management requires that "managers and policy makers cooperate with each stock's strategy for responding to the environment," while

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[22] Although examples in which factors other than fisheries have been linked to such changes are rare, Mangel et al. (1993) cite early work in Quebec, Canada in which lakes supporting landlocked harbor seals had brook trout populations which matured at considerably smaller sizes than lakes without harbor seals. Obviously, selection could work in the opposite direction as well. Heino and Godø (2002) found that for some Northeast Atlantic cod populations, delayed maturation was a result of historical fishing effort being focused on spawning grounds. By delaying maturation cod postponed exposure to fishing, and were consequently more fecund (larger size at maturity) when they were ultimately exposed to fishing mortality.

King and McFarlane (2003) emphasize that "consideration of life history strategies for coping with the environment should be fundamental to fisheries management." Longhurst (1998) argues that life history traits should not be forced to depart very far from the values that evolved for each stock prior to human exploitation, and that the maintenance of a diverse age structure is critical to the sustainability of most, if not all, groundfish stocks, given the expectation of episodic recruitment failure typical of coastal temperate and subarctic environments. For example, Murawski et al. (2001) demonstrates that first and second time spawning Atlantic cod breed for shorter periods of time, produce fewer egg batches, and produce smaller size eggs with lower fertilization and hatching rates. When such considerations were incorporated into stock assessments, overfishing thresholds were considerably lower. Berkeley et al. (2004) have similarly found that older female black rockfish produce larvae with faster growth rates and greater larval survival than younger fish, with age being a more significant predictor than size alone. Hilborn et al. (2003) demonstrate that the "biocomplexity" of stock structure in western Alaskan sockeye salmon has played a critical role in providing both stability and sustainability to fisheries, findings that echo those of Bisbal and Mcconnaha (1998) and Nickelson and Lawson (1998). All of these examples reveal that long-term sustainability of many fisheries is based on complementary patterns of production from different stock components under varying environmental conditions.

In the NCC, Field and Francis (2002) established that most commercially important stocks are dependent upon some form of population insurance as a buffer against environmental variability and change. In summary, they found that for:

- Coho and chinook salmon: population insurance is a combination of quality freshwater habitat and complex metapopulation structure for coping with ocean variability. Protection and restoration of freshwater habitat, hatchery reforms, and greater consideration of ocean conditions in setting harvest rates.
- Rockfish and many other groundfish: insurance is in the form of low turnover rates, remarkable longevity and diverse age structure. Sustaining these

populations requires a diverse age structure, spatial management measures will almost certainly be an integral part of future management strategies.

- Pacific sardine, Pacific hake and other coastal pelagics: populations respond to environment with enormous population expansions and contractions. Current sardine management includes threshold biomass levels and environmental control rules, similar strategies might be plausible for Pacific hake and mackerel.
- Pandalid shrimp and Dungeness crab: dynamic populations with high turnover rates known to be very sensitive to climate conditions. Continued facilitation of feedback between the resource and the fishery should reduce the vulnerability of the resource to overexploitation.

We can envision that a range of strategies might be applied towards providing population insurance within the context of current management efforts. In particular, future management efforts should capitalize on the opportunity (currently enabled by the regulatory flexibility) to operationalize measures of life history characteristics that contribute to resilience. For example, management plans might supplement current quantitative operational objectives such as target spawning biomass levels, with more qualitative measures that are widely recognized as important to the sustainability of the resource. This is not to say that single species models and reference points should be replaced, but rather that measures of bio-complexity, such as the diversity of age structure in long-lived groundfish, or the range of salmon life histories in a watershed, could augment traditional reference points with more ecological (although empirical) measures of stock status and resilience as best we understand it.

The application of marine protected areas (MPAs) and other spatially-based management efforts (such as rotating closures and ocean zoning) have been increasingly accepted as critical tools to be applied in future marine resource management (Botsford et al. 1997, EPAP 1999, Murray et al. 1999, Murawski et al. 2000, Roberts et al. 2001, Pikitch et al. 2004). Similarly, an NRC panel charged with investigating the potential use of MPAs in meeting biodiversity, conservation, and fisheries management goals concluded that MPAs found “compelling empirical evidence and strong theoretical arguments” for the use of MPAs and reserves as tools for managing fisheries, protecting habitat and biodiversity, and enhancing the anthropogenic value (esthetic and otherwise) of marine habitat (NRC 2001). As management tools, MPAs offer a form of insurance for the future against overexploitation and recruitment overfishing, the truncation of age distribution, the protection of non-target species and biodiversity, and the protection of habitat from fishing (and other) impacts. As the literature describing both the merits and the uncertainties associated with implementing MPAs is substantial, and growing, the issue will not be discussed in depth here. Importantly, the more thoughtful proponents of MPAs, as well as many of the critics, point out that MPAs are not a panacea for fisheries management problems, that while their potential impact on yields might be negligible or even beneficial in some instances, it could be detrimental in others,[23] and that the immediate consequences of area closures could include increased effort and fishing mortality on sedentary stocks that remain outside MPA boundaries (Hilborn et al. in press). As discussed earlier, closed areas have already become a necessity in crisis-based management efforts throughout the California Current, where huge swaths of the continental shelf have been closed to most fishing as an emergency measure to protect depleted rockfish. Clearly, the increased use of spatially based management measures, including ocean zoning and marine protected areas (MPAs), are appropriate tools for achieving conservation needs related to life history characteristics and biocomplexity that are rarely achieved under the current management approaches.

For species that are not formally assessed, qualitative measures of life history characteristics may be the only factors available in considering the impacts of fishing, particularly those that are the targets of developing fisheries. For example, even prior to the closure of massive areas of shelf habitat to trawling in 2003, the combined landings

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[23] While the potential for actual fisheries enhancement is controversial, there is some evidence for enhancement under certain circumstances (Roberts et al. 2001). Perhaps more significantly, the prospect of increasing profitability through rotating harvest areas is substantial in the scallop fisheries off of New England (Murowski et al. 2000). Botsford et al. (2003) provide one of the most comprehensive reviews of general principles for designing MPAs, with a focus on evaluating the outcome of reserves relative to conventional management, and how the nature of movement of the species being protected (at all life stages) could, or should, affect the design of marine reserves.

of spiny dogfish, skates and grenadiers in the NCC had nearly surpassed landings of the most important rockfish species in the groundfish trawl fishery.[24] Since 2003, the total landings of these species have exceeded those of all rockfish combined, as total *Sebastes* landings have been at their lowest level since World War II. Yet none of these newly targeted species have had even a cursory evaluation of population status or abundance, despite the fact that elasmobranchs have often been characterized as highly vulnerable to overexploitation given their life history characteristics (Musick et al. 2000, Frisk et al. 2001, Benson et al. 2001). Even a minimal evaluation of abundance, life history information, and historical landings could provide the Council and the NMFS with guidance regarding the potential limits of newly developing fisheries.[25] Consideration of the vulnerability of life history types known to be vulnerable to overexploitation would merit proactive controls on expanding fisheries and improved monitoring and data collection based on existing surveys and observer programs. All of these observations support the conclusion that ***maintaining life history traits and otherwise facilitating each population's insurance strategy for coping with the environment is a critical element of an ecosystem-based approach to management.***

4.8 Moving towards an Ecosystem-Based Approach

In general, moving towards an ecosystem-based approach is bound to be a protracted process, regardless of whether the process is mandated or voluntary. As Jennings (2004) suggests, to avoid paralyzing the decision-making process there should be an emphasis on an evolutionary, rather than revolutionary, move towards an ecosystem

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[24] In 2000, combined landings of Pacific Ocean perch, canary, widow, and yellowtail rockfish in the NCC were over 6900 tons, but 2002 landings were only 1945 tons. By contrast, in 2000, landings of dogfish, skates and macrourids were 2244 tons, dropping slightly to 1710 tons in 2002. In 2003, the total commercial landings of dogfish, skates and grenadiers was greater than the total landings of all *Sebastes*, both in the NCC (1710 to 1411 tons respectively) and coastwide (2015 to 2013 tons respectively).

[25] For example, based on the standards of the NPFMC tier system for managing data-poor species (which are themselves based on natural mortality rates, survey biomass estimates, and other information), and the estimation of skate biomass and bycatch in the NCC, skates might already be considered fully exploited in the NCC.

approach. Progress is certainly ongoing in the NCC and elsewhere, in a large part in response to the requirements of the SFA amendments to the MSFCMA. As discussed earlier, there have been major, largely crisis driven changes in NCC fisheries, major efforts to evaluate and protect habitat (the current EFH EIS), bycatch evaluation and reduction measures (initiation of an observer program, the bycatch EIS), the use of environmental indicators in setting harvest rates (sardine fishery), successful capacity reduction programs (groundfish trawl fishery), and the recently initiated consideration of rights-based fishing regimes (IQ scooping committees). The North Pacific Council has made progress in addressing these and other issues as well, including (in addition to issues similar to those listed above) an increasing appreciation for trophic interactions between harvested species in some recent stock assessments (Dorn et al. 2003) and the previously mentioned efforts to consider system-wide impacts of fishing under NEPA. Obviously all of these developments have occurred in the context of the current management regime, which in turn suggests that moving towards an ecosystem-based approach can be consistent with the current structure and objectives of fisheries.

Certainly an adequately funded mandate to develop FEPs would be desirable from the perspective of truly developing an ecosystem perspective in west coast fisheries. However, from a more pragmatic perspective, the limited resources available for management and the need to focus resources and expertise on implementing mandates such as habitat protection, bycatch reduction and fleet rationalization may prevent the full engagement of both the management and the scientific communities that would be necessary to fulfill such overarching assessments effectively. This should not be interpreted by the PFMC or NMFS as license to avoid existing legal obligations to better consider the ecosystem effects of fishing. Instead, it should be recognized with regard to developing a strategy for the gradual movement to a greater ecosystem perspective in managing fisheries in the context of current, and likely future, legal mandates. ***Strictly speaking, the proper scale for such an FEP is likely to be the California Current Ecosystem as a whole***, including recognition of the cross-border nature of many ecosystem processes and commercially important stocks in the northern and southern reaches of the California Current.

Successful implementation of such a plan could have tremendous value in addressing and facilitating actions to new and emerging issues that cross over multiple fisheries and jurisdictions. For example, several National Marine Sanctuaries have recently requested that the Pacific Council consider a ban on harvesting krill (euphausiids) in the exclusive economic zone waters under Council jurisdiction, similar to bans on harvesting and landing krill in California state waters.[26] An FEP would have previously detailed the importance of krill to the ecosystem, and could provide a framework for quantitatively evaluating the potential consequences of a krill fishery on other elements of the ecosystem, particularly other commercially important resources, and subsequently provide a vehicle for either managing or prohibiting the development of a krill fishery in the context of the such consequences.

Although the development and implementation of an FEP is a major undertaking, particularly in the absence of either a mandate or the financial resources to do so, the Pacific Council should consider a road map towards reaching a long-term strategy for adopting an ecosystem-based approach to management, while integrating ecosystem considerations into the current management regime to the greatest extent possible. Goodman et al. (2002) presented such a framework for formally phasing in ecosystem considerations from a management perspective. Here their framework is used to consider how the PFMC might move through phases that gradually shift from implicit to explicit consideration of ecosystem considerations in management procedures. The discussion and figures are based largely on the figures in Goodman et al. (2002). These have been modified and reorganized to be consistent with McEvoy's (1996) conceptual

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[26] From Exhibit G.4 Situation Summary document dated June 2004 as an element of the PFMC briefing book for the June 2004 Council meeting. The exhibit included a letter to the PFMC from Managers of the Monterey Bay, Gulf of the Farallones, and Cordell Bank National Marine Sanctuaries requesting that the PFMC prohibit the harvesting of krill in the west coast EEZ or, at a minimum, the boundaries of those National Marine Sanctuaries.

model of fisheries systems (as discussed in Chapter 1), and have been abbreviated into three stages and figures, rather than the five developed in Goodman et al. (2002).[27]

Figure 4.1 shows what Goodman et al. (2002) describe as the conventional assessment world view, essentially the current fishery management regime. Here, the ecosystem is considered principally in the context of target populations, and there is both direct feedback between these populations and the fishing fleets (industry) and indirect feedback through the governance sector. This indirect feedback occurs through the evaluation of survey, effort and catch data, which is used to develop stock assessments and other evaluations of the status of resources. Where direct feedback between the resource and the fishery is strong, such as seems to be the case with pandalid shrimp and Dungeness crab in the NCC, the role of governance can be limited without substantial risk to the resource. Straightforward management measures, such as the harvest of only males, or the implementation of some form of limited entry, are likely to be effective in sustaining the resource. However, where the direct feedback between resources and fisheries is weak, as it is with many of the long-lived and slow growing groundfish in the NCC, sustainability is almost fully dependent on the indirect feedback of governance. If that feedback is too slow, or the messages too riddled with uncertainty to be clear, the resource is far more likely to be at substantial risk of overexploitation at the most base, single species level.

In the first stage of bringing ecosystem considerations explicitly into the management system (Figure 4.2), what Goodman et al. describe as the explicit ecosystem effects worldview, both the status of target stocks, and the status of their prey (forage, ecosystem productivity) and predators (competitors with fisheries) are formally considered by the governance sector.[28] In general, their consideration would be at

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[27] Goodman et al. (2002) credit the figures to B. de la Mare and A. Constable.

[28] Although considerations regarding the human elements of the fisheries system are not explicitly included by Goodman et al., they would be an essential element of an ecosystem based approach, consistent with McEvoy (1996), Sissenwine and Mace (2003) and others.

minimum a means of achieving transparency regarding likely or expected ecological consequences of management decisions. This is especially true for more tractable problems, such as the reduction of discards, the avoidance of incidental mortality, the impacts of fishing and other activities on habitat, and explicit consideration of the needs of top predators. Generally however, fishing activities would continue to be largely governed by estimates of target stock status and yield as in the conventional worldview, and the governance sector would remain heavily dependent upon the indirect feedback of stock and target species status from catches, surveys and effort data. This is the approach of the NPFMC, where tractable ecosystem problems are generally confronted as they arise, and the Ecosystem Considerations Chapter serves as a link between research and management regarding less tractable issues. Ecosystem considerations are certainly not at the top of the agenda, but at least they are on the agenda.

Figure 4.3 represents what might be considered an idealistic ecosystem management view (at least, from a compositionalist perspective), in which governance is provided with nearly complete knowledge regarding ocean conditions, productivity and the status of both target and non-target biota, as well as indicators of diversity and other measures of ecological health and integrity. In theory, this integrated ecosystem approach would make management decisions based on accurate indices of ecosystem productivity, the needs of other predators (such as marine mammals), and the consequences of fishing on habitat and ecological structure. Yet as illustrated by May (1999) and others, there are still far too many unanswered basic ecological questions to expect that such intimate knowledge of ecological processes or dynamics will soon be forthcoming.[29] Assuming that overall management goals and objectives were largely still functionalist, this would not infer that such considerations outweigh those of the social and economic

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[29] For example, May (1999) reminds us that even basic mechanisms responsible for density-dependent or density independent regulatory mechanisms continue to be unresolved for many populations, the role of biodiversity and the relative abundance of species is still poorly understood, spatial aspects of population dynamics and structure has barely begun to be appreciated, and concepts related to ecological stability and complexity are as contentious as they have ever been.

considerations of resource-dependent fisheries and communities, only that such factors are explicitly considered in making management decisions.

4.9 Summary and Recommendations

Management bodies and decisionmakers are making ecosystem management decisions every day, the relevant question is whether they can improve on such decisions. The answer almost certainly is yes. This is despite the fact that we are decades away, at best, from having the knowledge, data and insights to make management decisions that fully consider ecosystem processes, productivity, and integrity. Management decisions will continue to be made with incomplete information, yet they can be improved upon with greater appreciation and understanding for the complexity of systems, the importance of life history considerations and greater recognition of the uncertainties that inevitably shroud all management decisions. There is widespread agreement that successful adoption of an ecosystem-based approach will be done gradually, without abrupt displacement of current management objectives and practices. The following recommendations are made in this context, as means to move towards an ecosystem-based approach.

In the short term:

- Establish an ad-hoc ecosystem committee, charged with developing ecosystem considerations briefing materials and information. Focus on climate and ecosystem indices already identified as relevant to fisheries resources, draw largely from existing efforts, such as State of California Current Report.

- Use the document as a means to acclimate the Council community to ecosystem indices measures that may play a greater role in future management, and as an opportunity to engage the community with respect to existing data, knowledge, and potential directions for modeling or research efforts.

- Consider the appointment of a regional fisheries oceanographer, whose responsibilities would include synthesizing climate information, orchestrating the development of an Ecosystem Considerations Chapter, and acting as a conduit between the climate research community and the fisheries management community.

- Recognize that ecosystem and life history considerations should play a greater role in the current management regime. Encourage management strategies, harvest rules and plan amendments that provide population insurance, or facilitate the resilience, of resources; particularly those that augment, rather than replace, traditional reference points.

In the long term:

- Encourage and support the development, documentation and discussion of quantitative ecosystem models and indicators, as essential elements in the adoption of any ecosystem perspective for management. Consider both models and ecosystem indices and considerations over the scale of the entire U.S. portion of the California Current Systems at a minimum.

- Develop a road map for phasing in ecosystem considerations within the current management context. Track successes and accomplishments, work in progress, and major gaps in order to frame a clear understanding of what might practically be gained with further research. Recognize the difference between feasible and idealistic, long-term objectives.

- In the absence of a legal mandate for the development of FEPs, use existing NEPA framework to assemble the elements proposed by the Ecosystem Principles Panel, consider policy options and directions for future management, and evaluate likely ecosystem impacts that would be associated with each. Engage the industry and stakeholder communities to explore such visions, confront potential trade-offs, and consider the interactions of alternative policies with plausible future climate regimes.

Any or all of these recommendations should be pursued with the clear recognition that fisheries and marine science may produce glimpses of underlying ecosystem processes and mechanics, but not complete understanding (Ferrero and Fritz 2002). Funding commitments, both with regard to the science and the implementation of ecosystem based approaches, are also critical in achieving any effective movement in both the science and the implementation.

Despite the problems and challenges associated with today's fisheries crises, recognition of the important conservation role that MSY, reference points and stock rebuilding requirements have made is key. As Larkin (1977) said in his premature eulogy to the theory of maximum sustainable yield, "to appreciate what MSY has done, we need only ask what the world's fisheries would have looked like today if the concept had not been developed and advocated with such fervor. The fish, I'm sure, would shudder to think of it." However, waiting for a fully refined and globally accepted system to arise without making incremental improvements is like driving a five ton sports utility vehicle while waiting for the development of the hydrogen car. There are abundant and reasonable means to bring ecosystem considerations into the current management regime now. Doing so serves to increase the awareness of ecosystem structure and function (and the limitations of understanding with regard to both ecosystem and single-species dynamics), focus the nature of ecosystem science and research, and facilitate future legal implementation of ecosystem-based approaches to management.

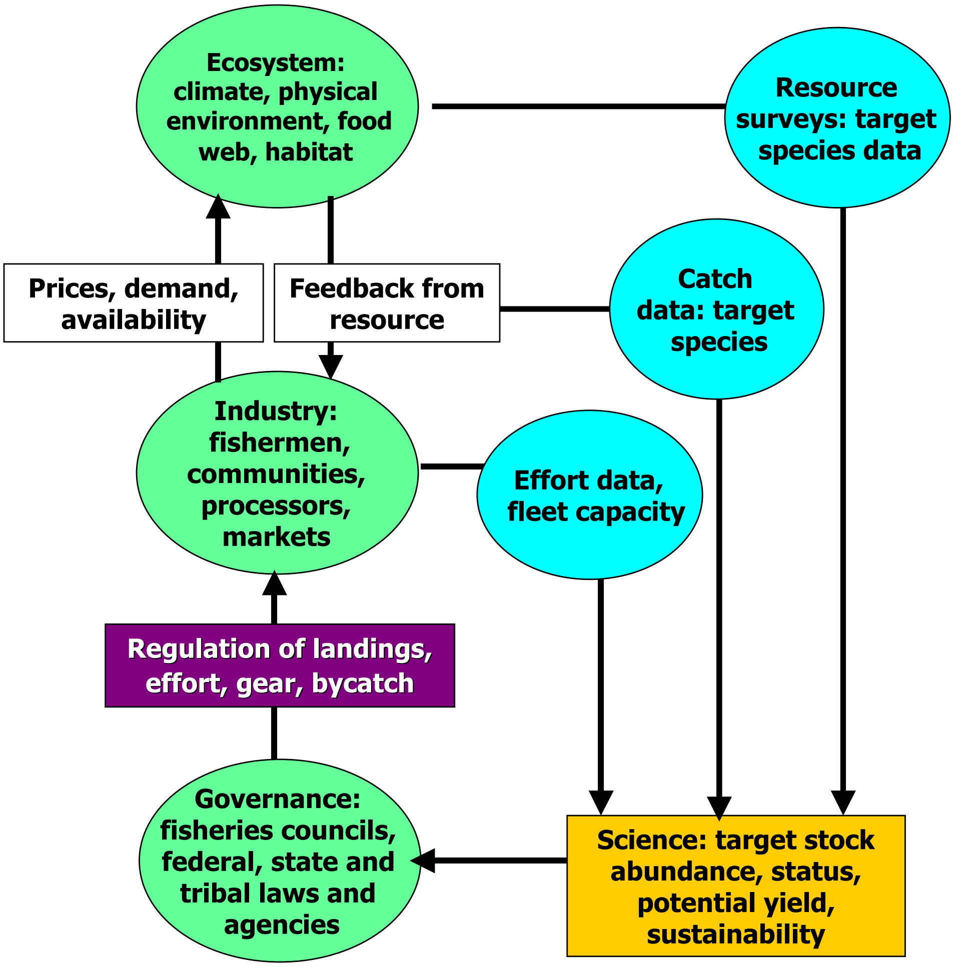

Figure 4.1: The conventional fisheries management world view

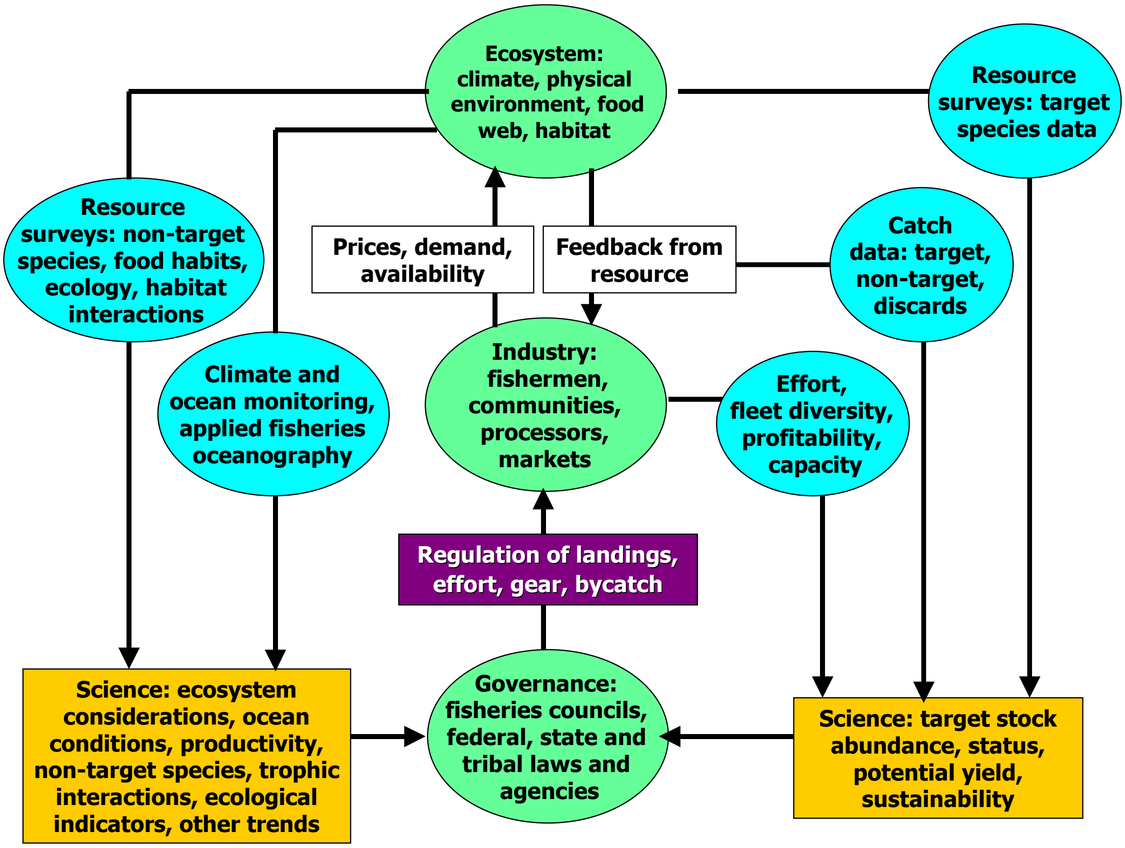

Figure 4.2: A transitory stage between the conventional fisheries management view and a wholly ecosystem-based management perspective. Tractable problems are addressed by the governance sector to the extent practicable, while climate, productivity, habitat, and the needs of predators are implicitly considered in the context of making decisions.

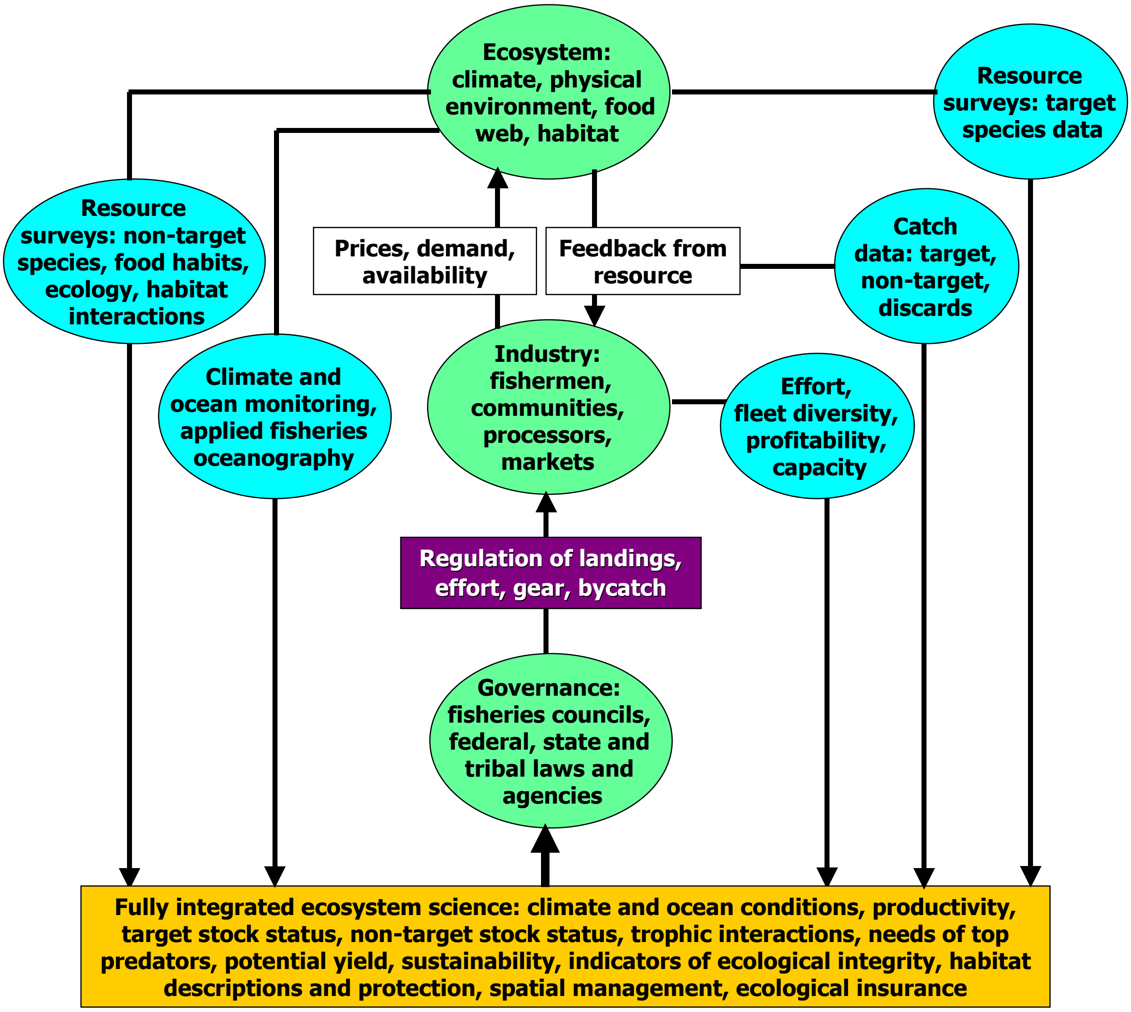

Figure 4.3: An idealistic ecosystem-based world view, in which all elements of the ecosystem, including predators, prey, target stocks, habitat, biodiversity and other measures of ecological integrity are explicitly considered in the context of making management decisions.

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Appendix A: NCC Model Documentation

A.1 Primary Producers and Detrital Pools

Phytoplankton and primary production

According to Thomas and Strub (2001) the California Current was one of the most frequently imaged regions of the global ocean by the Coastal Zone Color Scanner (CZCS), and they cite a long list of studies that use the CZCS data to examine various aspects of pigment pattern variability. However, the Washington and Oregon coasts present difficulties in measuring pigments by satellite, in a great part as a result of interference from the Columbia River Plume. Their summary of the CZCS data between 1979 and 1983 suggest that chlorophyll A concentrations above 3 mg/m^3 are present within ~40 kilometers of the coast (occasionally extending outward rarely as far as 100 km) between spring and fall, with peaks between April and June, and October. Concentrations drop to 1 to 2 mg/m^3 outside of 40 to 50 km and falling to the lowest concentrations more than 200 km offshore in mid-summer. This is consistent with many other earlier studies the region, including some of the same CZCS data. On a broader scale, Longhurst et al. (1995) used CZCS data in an attempt to estimate total ocean productivity in 57 biogeochemical provinces; their estimates for the entire California Current region were 388 grams C m^2/year[1], by contrast their estimates for all coastal domains was 385 grams C/m^2/year[1], and for upwelling provinces was only slightly higher, at 398 grams C/m^2/year[1].

As suggested earlier, any calibration of satellite estimates of productivity with total water column production is difficult, but earlier *in situ* data on primary production is available from Perry et al. (1989), who summarize data collected mainly off Washington shelf between 1974 and 1982.[1] They estimated that shelf waters typically ranged from 1 to 11 mg Chl-a/m^3, with slope waters ranging from 0.3 to 8.5 mg Chl-a/m^3 and offshore waters typically averaging around 0.3 mg Chl-a/m^3. Fig 3.6 in their document shows the average abundance throughout this period of phytoplankton carbon

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[1] Any attempt to convert Chl-A concentrations per cubic meter into biomass concentrations per square meter within any meaningful context is an extreme challenge, above and beyond the simple challenge of averaging Chl-a concentrations over space and time they must be integrated over depth and converted into biomass. Mixed layer depths are neither constant nor well monitored for the region, but the summer mixed layer tends to be shallower than the winter mixed layer (~20-30 meters versus 50 to 100 meters). If we assumed a 25 meter average MLD from spring to fall, with an average biomass of 3 mg Chl-a/m^3, we would estimate about 75 mg Chl-A/m^2. Using a Chl-A:carbon ratio of 1:50 from Robinson et al. (1993), and a C:wet weight of 1:15, we would then estimate a mean wet weight biomass on the order of 55 grams/m^2.

per square meter as a function of shelf, slope and oceanic area by season, pooled seasonally they suggest mean annual production of 646, 294 and 229 grams C/m^2/year[1] for each of these areas respectively (with coefficients of variation typically between 50% and 80%). Using the same conversion factors as above suggests annual production of 9690, 4410, and 3435 grams/m^2/year for shelf, slope and oceanic waters respectively. Thus the total production of phytoplankton in wet weight throughout the NCC for this time period might be estimated by multiplying the shelf and slope production by their respective areas in the NCC. This suggests to us a total production of 3.5*10^8 metric tons of phytoplankton throughout the region, or 6617 grams/m^2/year. If we assume a P/B ratio of 120/year (in order to approximate one turnover every two days between spring and fall, with little to no winter production) we get us a gross average standing biomass of 55 grams m^2. This value is very similar to mean spring-fall biomass crudely estimated from the Thomas and Strub (2001) Chlorophyll-a data above, and is of the same magnitude than those offered by Longhurst et al. (1995).[2] Finally, an additional source of information is Robinson et al. (1993) who modeled annual plankton production in the Juan de Fuca Eddy region just inside of the shelf break. These authors used a plankton biomass production dynamics model driven by seasonal variability in upwelling, light intensity and water temperature, and tuned to estimates of standing biomass and production from various DFO research cruises. Their results for phytoplankton production suggested a mean annual production of 345 grams C m^{-2} year^{-1}, with an estimated P/B ratio of 100 and a mean standing stock of about 51.1 grams wet weight m^2.

The problem, of course, is that most of these values are estimates for neither the 1960's nor the 1990's. Yet for lack of more appropriate data, we will use the above values to calibrate the 1960s model and use the estimated ecotrophic efficiency for that model to estimate the biomass of phytoplankton necessary to support the inferred production of higher trophic levels in the 1990's. Earlier studies are available, however due to the tremendous change in sampling techniques over time, with earlier methods in particular being often noted to underestimate productivity, they are not likely to be reliable. Table 3.2 in Perry (1989) summarizes seasonal primary production data before 1974, with their pre- 1974 values being considerably lower than post 1974 values (for example, spring and summer production estimates of 0.2 and 0.42 grams C m^{-2} day^{-1}, as opposed to see also Fig. 3.3 in their paper). Finally, while all of the above focus on the relative amount of primary production, there have been relatively few reports on the species

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[2] Limited data is available from the early 1960s, much of which might be suspect for underestimating total productivity. Laurs (1967) reported that standing stocks of Chlorophyll-a during spring, summer and fall periods of 1962 to 1964 off of southern Oregon ranged from less than 10 to 262 mg/m^2, with a mean of approximately 85 mg/ m^2 for inshore (within 40 miles) waters and ~60 mg/ m^2 for offshore waters. This corresponds to roughly 64 and 45 grams (wet weight)/ m^2 for inshore and offshore waters respectively, similar to the estimates above. Even earlier work in the Columbia River plume by Anderson (1963) suggested similar levels, on the order of 60 grams C/ m^2/year in oceanic and plume waters, up to 88 near the river mouth and 152 in upwelling areas. It is worth noting that Anderson thought these values to be surprisingly low, as they were on the order of estimates for ocean station P.

composition of primary producers in the northern part of the California Current (considerably more off in the CalCOFI region off of central and southern California). Those that have been done suggest that the phytoplankton species assemblage and biomass is dominated by large diatoms (which would be expected for upwelling-driven ecosystems), for example Postel (1975) reported that diatoms dominated the shelf biomass in terms of both numbers and biomass (by numbers >55% shelf, 30% subsurface Chl-a maxima, dropping to ~15% offshore of the shelf break). In the absence of better information, primary producers are considered to be a single functional group for the purposes of this model.

Detrital pools and the microbial loop

Pelagic and benthic detrital pools, and their associated bacteria, protozoa and other microbial recyclers, are as important as primary producers in accounting for energy flow through ecosystems. Protozoa and other benthic meiofauna may attain densities >20grams/m^2, and account for as much as 50% of the respiration of benthic communities, according to McLusky and McIntrye (1988). Benthic macro- and microscopic algae can also be important sources in littoral areas (up to 20 to 30 meters depth) but as such likely play a relatively minor role here, and are not considered explicitly. Most benthic production results from the decomposition of particulate organic matter into CO_2 by auto- and heterotrophic bacteria, although some microorganisms use other organic and inorganic compounds in anaerobic sediments. The source of the organic material is particulate organic matter, principally from dead phytoplankton and the fecal pellets of planktonic organisms. In the NCC, it is unclear whether the supply of organic matter to the benthos is primarily driven by primary production (sinking phytoplankton) or zooplankton production (primarily fecal pellets, appendicularian houses and molts). Steele (1974) suggested that the latter was a more important source of organic matter to the benthos in the North sea, similarly Chavez et al. (1991) suggest that most primary production off of California is advected offshore, rather than lost to the benthos over the shelf and slope.

As referenced in Chapter 2, the microbial loop is not explicitly included in the structure of this model, due to a lack of clear data or guidance regarding how one might do so. Instead, recycling is represented as predation on the detrital pool, and microbial processes are not explicitly considered in either model accounting or in the assignment of trophic levels. This is done to be consistent with the approach of Aydin et al. (2002) and others, as well as reflecting the lack of accurate knowledge regarding the relative role of recycling in this ecosystem. By contrast, models that explicitly include both sediment and water column bacteria as detritus feeders would assign them a trophic level of 2, and all other elements of the food web would be elevated accordingly (Bradford-Grieve et al. 2002). No estimates of their abundance or direct role is available for this region and the focus of these estimates are on standing biomass and production of macroinfauna which accounts for the production of prey for other components of the ecosystem. Two detritus pools were included in the NCC models, a benthic pool and a pelagic pool (both represent only particulate organic matter, or POM), with the pelagic pool representing both detritus that may be consumed by salps, larvaceans or other mucus web feeders, and detritus that may be recycled (for example, by bacteria that are then consumed by microzooplankton). The benthic pool is quite obviously the fuel for the benthic food web, and is consumed by most infauna, some epibenthic fauna (including shrimps), and consumption of carrion or discards by fish. The inclusion of a third and fourth detrital pool, to represent discards and carrion, might be a more appropriate means of addressing this issue in the future, and any future modeling efforts would benefit greatly from an increased focus on the importance of recycling.

A.2 Benthic Consumers

Amphipods

This group includes all amphipods, with gammaridae, caprellidea and hyperiidea being the most important suborders in the Pacific Northwest according to Grosse and Pauley (1986). For the moment this group does not differentiate between benthic and pelagic amphipods; although gammarids tend to be benthic, hyperiids are almost exclusively pelagic (and have been estimated as the third most abundant group of marine zooplankton, following copepods and euphausiids), and caprellids are a mix of the two. As amphipods do not make up more than a small percentage of any particular diet, this distinction should not have significant impacts on model behavior. Some estimates of production in estuaries is reported in Grosse and Pauley (1986), with April-October production as high as 3.6 to 10.7 grams/m^2 in Grays Harbor tidal flats (associated with a P/B ratio between 7.2 to 8.6). Local information on species is little, although Lie and Kisker (1970) cite the amphipod *Heterophxus oculatus* as the most abundant off the coast of Washington (depths of ~ 150 meters), with the amphipods *Ampelisca macrocephala* and *Paraphoxus obtusidens* as the most abundance in shallower waters (~35 meters). For pelagic amphipods, some information is available from Laurs (1967) who estimated pelagic amphipods biomass on the order of 0.19 tons/km^2. However as neither pelagic or benthic biomass estimates are well defined, the biomass is estimated based on consumption by top level predators. P/B will be estimated at 3.5 and Q/B at 22; as per the Bering Sea model; noting that these P/B estimates are consistent with reported studies of amphipod P/B values cited in McLusky and McIntrye (1988) and Postma and Zijlstra (1988) as well. Diet will be similar to Bering sea model (Aydin et al. 2002), with the addition of a small amount of pelagic detritus and zooplankton, to be 70% benthic detritus, 10% pelagic detritus, 15% phytoplankton and 5% zooplankton.

Benthic infauna

The majority of the organisms in this group are polychaetes, bivalves, small crustaceans (isopods, cumaceans, etc), echinoderms and others, which tend to feed either directly or indirectly (vis-à-vis the benthic microbial loop) on benthic organic matter. Most of the available information on infauna off the Washington shelf has been derived from the work done Jumars (1989), Lie (1969), Lie and Kisker (1970), and Lie and Kelley (1970). These authors reported mean values of infauna biomass for three different areas along the Washington shelf (between 20 and 350 meters depth) sampled with a 0.2 Veen grab and sieved through a 1 mm mesh screen. Values were given in ash-free dry weight (AFDW) along with a suggested conversion factor of 0.1 (Lie 1969). The areas are divided into three types of communities according to sediment and biotic characteristics; a deep-water (150-350 meters), mud bottom, shelf community dominated by echinoderms and polychaetes, an intermediate depth (50 to 164 meters), sand bottom community dominated by mollusks and polychaetes, and a shallow-water (15-83 meters) sand community dominated by crustaceans and bivalves. Jumars and Banse (1989) report that the mid and outer-shelf communities tend to be dominated by motile deposite feeders (echinoderms, mollusks and polychaetes). Their mean estimated biomass densities for these three areas were 26.1, 25.5 and 14 grams/m^2 respectively; weighting them by their respective estimated area as reported by Lie (1969) results in a mean density on the order of 23.3 grams/m^2. Greater resolution of benthic community structure would be one potential means of incorporating spatial considerations into the model, by more appropriately partitioning the prey of organisms segregated by depth to the community structure at depth.

For the Oregon shelf, Carey (1972) reported greater standing stocks of infaunal organisms, and Jumars and Banse (1989) suggest that Carey's use of improved sampling gear and finer-mesh sieves may be responsible for this difference. His work at stations approximately 10 km offshore and at 50 meters depth off of the central Oregon coast suggested standing stocks on the order of 31.8 grams/m^2 (wet weight); at 45 km offshore and 200meters depth the average biomass was considerably greater, at 45 grams/m^2. Molluscs and arthropods made up the majority of the biomass in the inshore depths, with arthropods, echinoderms and polychaetes constituting a larger proportion of the infaunal biomass in the offshore stations. If we make the gross presumption that the 50 meter station might be representative of the area between 0 and 183 meters, and the 200 meter station is representative of the area between 184 and 1280 meters (a flawed assumption, as Jumars and Banse suggest that standing biomass tends to be greatest near the shelf break), we arrive at a gross estimate of 37.64 grams/m^2 on the Oregon (and, as we extrapolate grossly, perhaps Northern California) shelf and slope. By combining these estimates with those above for the US Vancouver Region, we arrive at an estimate throughout the NCC of 35.7 grams/m^2 for benthic infauna.

Data on production and consumption rates is essentially non-existent for this region (particularly for a multitude of species within a large guild). Trites *et al* (1999) use values between 1.5 and 2 for polychaetes and infaunal mollusks in their model of the Bering Sea shelf. McLusky and McIntrye (1988) offer a summary of studies of benthic infauna rates which summarizes P, lifespan and P/B values for some 30-40 various species of benthic invertebrates. These include a dozen polychaete species with a range of P/B values from 0.5 to 4/year, with a mean of approximately 2.5 (and including *Pectinaria californiensis*, a Puget Sound species with a reported P/B of 4.32), nearly twenty mollusk species (primarily bivalves) with a range of P/B from 0.5 to 5 per year, and a mean of about 2.5; four crustaceans (benthic shrimps, amphipods and mysids) with P/B values averaging 3 per year, and three echinoderms with values ranging from 0.3 to 2.6 year. We will use an estimate of 2.5, as this seems to be a reasonable mid-range value for this guild, and we will use a Q/B of 12, as this is roughly equivalent to 20% transfer efficiency, and is consistent with the estimates by Trites et al. (1999) for the Bering Sea model. Jackson et al. (1981) describe the food web for English sole and other flatfish, suggesting clams, polychaetes and other benthic infauna feed principally on particulate organic matter (POM), bacteria and protozoa. Wakefield (1984) describes trophic relationships of nearshore benthic communities, and also suggests that polychaetes, nemerteans, and other infauna feed on POM, benthic bacteria or other microbenthic organisms that are represented by the benthic detrital pool, a generalization supported by Parsons et al. (1984). Consequently, diet is assumed to be 100% on benthic detrital pool.

Epibenthic fauna

Epibenthic macrofauna include a very wide range of larger benthic organisms that typically live above the sediments and are somewhat to highly motile; including holothuroids, asteroids, ophiuroids, crinoids, brachyurans (other than Dungeness or Tanner), anomurans, mysids, isopods, cumaceans, mollusks (primarily gastropods) and other organisms. We have considered (non-mysid) benthic shrimps (pandalids, crangon and others) seperately due to their significance to fisheries and as prey. As most epifauna are poorly sampled, as reported densities tend to come from trawl surveys where the sampling gear is specifically designed to ride over the bottom. Consequently a top-down balance (based on predation pressure) is used to estimate this biomass, and the resolution of this community, which consists of multiple phyla and a tremendous range of life history types (likely including predation between various members of this functional group) is poor. What little information does exist is yet nevertheless the information is worth summarizing briefly, and may provide sufficient basis in combination with diet studies to resolve the various key constituents of this group further, if it is desirable to do so in the future.

Carey (1972) estimated benthic epifauna at several sites off of the Oregon coast, his results suggested low abundance of epifauna at shallow sites (~0.5 grams/m^2 from 50 to

100 meters depth) and greater abundances near the shelf break (~2 grams/m^2 at 150 meters and ~1.5 g/m^2 at 200 meters). Another source of information for epibenthic fauna is from the same volume, by Pereyra and Alton (1972). They analyze data from sampling done between 1961-66 off of the Columbia River mouth and north Oregon shore, from approximately 100 to 1200 meters depth. They report densities of epibenthic fauna on the order of 0.74 grams/m^2, although these estimates include Tanner crabs which are actually modeled separately here.[3] This, of course, assumes that the gear is effectively sampling the bottom at all times, an assumption not likely to be met, but it provides us with some means to evaluate more recent sampling with similar gear by the west coast groundfish surveys.

It is not clear how quantitatively epibenthic invertebrates have been sampled in past triennial shelf surveys, as estimates of total abundance are extraordinarily low. The average biomass (over all areas in the NCC) between 55 and 183 meters since 1980 is 0.12, between 184 and 350 meters it is 0.31. However, estimates have been much greater in recent years, suggesting an increased focus on enumerating invertebrates. By contrast, AFSC slope surveys have estimated considerably more epibenthic fauna, even at overlapping depths. For instance, the average biomass estimated by the slope survey between 55 and 183 meters is 1.8 grams/m^2, roughly three times the highest estimated biomass in that depth strata over all triennial survey years (0.6 grams/ m^2 in 2001).

The results of all of these surveys clearly underestimate the likely standing biomass of benthic epifauna, as a top-down balance estimates standing biomass an order of magnitude greater than these estimates. Such higher estimates are far from unreasonable. Wakefield (1990) evaluated slope fish communities and abundances off of Central California using a camera sled, and estimated the abundance and standing biomass of dominant fish species as well as benthic invertebrates. For the latter in particular, he reported biomass estimates on the order of 10 to 30 tons/km^2 for stations between 400 and 800 meters, dropping to substantially lower levels (on the order of 3 to 4 tons/km^2) for slope habitat at 1000 meters depth and greater. Sources cited in Parsons et al. (1984) also suggest that epifaunal invertebrate densities along the northeast Pacific continental shelf can range between 20 and 200 grams/m^2. This suggests that top-down balances resulting in standing biomass estimates on the order of 10 to 15 grams/m^2 are reasonable, and the model estimate of epibenthic fauna, amphipods (both benthic and pelagic), benthic shrimps, pandalid shrimps, Dungeness and Tanner crabs is slightly less than this, at roughly 16 grams/m^2.

The Bering Sea model by Trites et al. (1999) and more recent models by Aydin et al. (2002) use P/B ratios of 1.578, and Q/B ratios of 5.78. Banse and Moser (1980)

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[3] They report the density of epibenthic fauna in lbs/hour trawled, but Pruter and Alverson (1972) provide a conversion factor from the same studies based on the average width of the gear used (40 feet) and a rate of 0.018nm^2/hour. The corresponding biomass in nm^2 is 100/0.018 = 5554 lb/nm^2 = 2520 kg/nm^2. Knowing that 1 nm = 1.852 km (and therefore 1nm^2=3.429km^2) we convert to an estimated abundance of 0.74 tons/ km^2.

summarize literature values of P/B for numerous invertebrates, of the epifaunal species included in their review, several gastropods had P/B values ranging from 2.6 to 5.8, several isopods had values ranging from 1.8 to 2.4, and an echinoid had a PB of 0.8 Postma and Zijlstra (1988) also review several P/B estimates for echinoderms, ranging from 0.3 to 2.6, and for many other benthic species. They also review a number of benthic food web studies that suggest using P/B ratios of 2 to 2.5. The NCC model will use very slightly higher estimates than those of the EBS, with a P/B of 2 and a Q/B of 10. For diet, both the Bering Sea models (Trites et al. 1999, Aydin et al. 2002) and the British Columbia shelf (Pauly and Christensen 1996) models assume that roughly half of the epifaunal diet is detritus, roughly half is infauna, and there is modest predation on other groups such as amphipods, crabs, shrimp and other epibenthic fauna. Jackson et al. (1981) describe the food web for English sole and other flatfish, suggesting that brittlestars (and presumably other echinoderms), clams, cumaceans, polychaetes and gamariid amphipods feed principally on detritus, bacteria and protozoa. Wakefield (1984) describes trophic relationships of nearshore benthic communities, and also suggests that the principal food of many mysids, gastropods, ophiuroides, cumaceans and isopods is POM, bacteria, microbenthic fauna, or benthic algae, although infauna can be important prey to crustaceans and other epifauna. Consequently, we use the following prey composition for the epifaunal group: 55% detritus, 42% infauna, 1% amphipods, 1% benthic shrimp, and 1% fisheries offal.

Pandalid shrimps

Pandalid shrimps (primarily the ocean shrimp, *Pandalus jordanii*, but including *P. platyceros, P. borealis* and several other less commonly encountered species) are both commercially important as well as key prey items in the diet of many fishes in the NCC. A fishery has existed for *Pandalus jordanii* since the mid 1960s, when the introduction of automatic peelers led to large increases in prices and production (Schafer 1981). Peak landings occurring in the mid 1970s and mid to late 1980s, reaching as much as 37,000 tons. The interactions between the shrimp fishery and shrimp predators (particularly hake and Arrowtooth flounder) has been the subject of several papers over time in the California Current (Gotshall 1969, Alton and Nelson 1970, Francis 1982, Hannah 1995), the latter found a significant correlation between shrimp natural mortality rates and the abundance of age 2+ hake (interestingly, the correlation was not significant with age 3+ hake). Hannah (pers. com.) has observed that hake tended to be more common in shrimping grounds during the 1990s than earlier years, an observation substantiated by an increase in hake bycatch in shrimp trawls between the mid-80s and 90s (based on Pikitch et al. 1988 and Hannah 1996). However as pandalid shrimp generally comprise a fairly small proportion of predator diets in the NCC, the interactions are difficult to quantify with a great degree of accuracy. Since 1978 the catch per unit effort in the shrimp fishery has also decreased substantially (while landings have remained high, albeit variable), despite considerable gear improvements, suggesting that either predation or the fishery have reduced the total biomass considerably (Hannah and Jones 1990). Between 1960 and 1967 landings averaged 2100 tons/year for the NCC, while between 1990 and 1996 average landings were on the order of 19,280 tons. As Hannah (1995) points out, fishing is unrestricted with respect to fishing area, catch quotas or trip limits; and consequently catch per unit effort data should to some extent reflect the abundance of shrimp available in the ecosystem. However a recruitment index has also been derived from Hannah (1999) for the years 1980 to 2000 based on a model of age1 abundance in August; this index suggests wide fluctuations in recruitment, which appears to be related both to spawning stock size and negatively correlated with spring relative sea-level height (and, presumably, transport). Although both catches and predation pressure is relatively high, abundance estimates are unavailable and thus come directly from estimates of their relative importance as both the target of fisheries and as prey, assuming an EE of 0.9.

Estimating other life history parameters for shrimp is difficult, however Hannah (1995) estimated monthly total mortality rates for pink shrimp between 1980 and 1990 under various assumptions of catchability for the trawl fishery. His estimates of annual M range from 2.5 (CV of 20%) under the low catchability assumption, to 0.97 (CV of 57%) under the high catchability assumption; with a midpoint of 1.82 (CV of 28%). This paper did not include estimates of fishing mortality, consequently this should underestimate total mortality by some degree (although we shall see that predation appears to be a considerably greater source of mortality for pink shrimp). The mid-point estimate consequently seems to be a rational starting point for estimating P/B. An alternative approach is inferred from McLusky and McIntyre (1988) suggest a relationship between potential lifespan and P/B ratios for benthic animals in which log (P/B)= 0.66-0.726 (log(lifespanyears)). *Pandalus jordanii* is a sequential hermaphrodite, with age 1 shrimp typically male and turning female at age 2 (usually fully mature at age 2½. Few, if any, shrimp live beyond age 3.

If we apply the method of McLusky and McIntyre to Pandalid shrimp, estimating a lifespan of 3 years, we arrive at an estimated P/B of 2.05; an estimate quite close to the middle estimate for M (of 1.82) suggested by Hannah. Consequently, we will use a P/B of 2 as the starting (1960s) value for this model. Hannah and Jones (1990) have also document an apparent change in shrimp population structure, which they believe is at least partially attributable to fishing; the number of age 3 shrimp in catches fell from an average of 20.4% between 1966-78 to 4.9% between 1979-1988, and the percentage of age 1 shrimp in landings has increased from 30.6% to 69.2% in the same period. These changes have been accompanied by an increase in the percentage of shrimp maturing directly into females at age 1, all of which might suggest a response to increased fishing mortality and/or predation. No reliable information exists for consumption rates; if we assume a (relatively high) growth efficiency of 0.2, we arrive at a Q/B of 10, which seems a reasonable starting point.

Food habits are even more troubling, for here some data exists that is somewhat conflicting. Dahlstrom (1970) suggested that *Pandalus jordanii* fed primarily upon detritus, based on stomach contents examined from shrimp caught off the northern California coast. Yet Pearcy (1970) described the vertical migrations of *Pandalus jordani* into the water column at night, at which point they fed heavily on euphausiids and copepods. Fish scales, chaetognath jaws, other shrimps, amphipods, eggs, and polychaete remains were also noted. However, not all shrimp did this vertical migration, and those found on the bottom at night also fed heavily on polychaetes, annelids and detritus (as would, presumably, animals feeding during daylight hours). Furthermore, the greatest numbers of shrimp caught in mid-water were between November and April; from May to June no shrimp were caught midwater. Alverson (1960) had earlier suggested that the vertical movements of shrimp were seasonal, and it might also be inferred that during the daytime shrimp remained in the benthos feeding on infauna, detritus or other prey. No other quantitative estimate of food habits or changes in prey preferences with age or size, are available for shrimps off of Oregon and Washington to our knowledge. Food habits of the pink shrimp *P. borealis* have been studied in the Northwest Atlantic, where Shumway et al. (1985) reviewed a greater volume of literature, all of which suggests that P. borealis is a highly opportunistic generalist in which food habits are determined by availability, time of day, and developmental stage of shrimp. They suggest that *P. borealis* is primiarily a benthic feeder, with occasional excursions into the water column, and dominant prey items tended to include gastropods, polychaetes, other crustaceans (particularly euphausiids, amphipods, decapods and copepods) and detritus. The B.C. shelf model (Pauly and Christensen 1996) estimates shrimp diets to be 30% infauna (polychaetes and annelids) and 70% (benthic) detritus, although no sources are provided for this estimate. In the face of all of this inconsistent information, and in the absence of better data, we will use the following as a starting point for diet composition; 35% benthic detritus, 25% infauna, 5% epifauna, 20% euphausiids, 10% copepods, 2% carnivorous zooplankton, 2% amphipods and 1% pelagic shrimps.

Benthic shrimps

This group includes a wide range of shrimp species which are key prey items in the diet of many fishes in the NCC (such as *Crangon* spp., *Eualus* spp., *Daridea* spp., *Calocaris* spp), although for our purposes we have excluded (perhaps unfairly) mysid shrimp and assigned Seregestid and other mid-water species to a separate category. Not surprisingly, estimates of P/B ratio are difficult to derive. For the British Columbia shelf model, Pauly and Christensen (1996) estimated an abundance of shrimps of 5g/m^2 , with a P/B of 1.2 and a Q/B of 8. McLusky and McIntyre (1988) cite one study of a cold water (Long Island Sound) Crangon spp. with an estimated P/B of 3.82; although this was a subtidal Crangonid. We will estimate a P/B similar to pandalid shrimps, of 2.5, with an associated Q/B of 10. No quantitative food habits studies of benthic shrimp in this region are available. Wakefield (1984) suggests that Crangon feed primarily on microfauna, amphipods, and polychaetes, with minor amounts of cumaceans and juvenile flatfish. Siegfried (1989) reported that juvenile and adult crangonid shrimp feed on a variety of crustaceans (amphipods, isopods and other shrimps), polychaetes, mollusks, foraminiferans and other material (based on studies of crangonids in San Francisco bay and other estuaries). Ghost and mud shrimp in the Pacific Northwest (which also tend to be subtidal) are thought to be primarily detritus and suspension feeders (Hornig et al. 1989). We will assume a primarily predaceous diet of 40% epibenthic fauna, 40% infauna, 15% detritus, 4% amphipods and 1% juvenile flatfish.

Dungeness crab

One of the earliest significant fisheries in the California Current, landing of Dungeness crab (*Cancer magister*) in the coastal waters of California, Oregon, and Washington have maintained a well described cyclic pattern for over half a century. Recent research suggests that Dungeness crab dynamics respond to both internal population feedback, as well as large scale environmental forcing (Higgins et al. 1997) although numerous hypotheses have been suggested over time, including density-dependent recruitment mechanisms (with cannibalism playing a key role), environmental forcing (principally temperature, upwelling and advection) and the role of egg predators and/or parasites (Pauley et al. 1989, see also Armstrong et al. 2003). Since 1950, harvests have cycled between 3,600 and 25,000 tons per year, and have peaked approximately every 10 years. The total value of the crab fishery has ranged between $17 million and $70 million/year over the last two decades. Landings are widely thought to reflect the abundance of mature (generally age 4+) adults, as the fishery targets mature males only (females and males below the size limit of 159mm carapace width are returned to the water). Fishing mortality rates on mature males are thought to be very high, perhaps varying with both abundance and fishing effort between the range of 60 to 90% of the standing biomass (Methot 1986).

The life cycle of Dungeness crab is fairly complex, and the reader is referred to Pauley et al. or other sources for a complete review, but all stages appear to play significant trophic roles in the coastal ecosystem. Eggs hatch between December and April in Oregon and Washington, and larvae progress through five zoea stages prior to molting into megalops (the last pelagic stage). All of these stages, and particularly megalops, may at times make up a substantial fraction of the diet of commercially important fishes, including herring and other forage fish, chinook and coho salmon, sablefish, and several species of rockfish. Megalopae molt into juveniles and settle into shallow coastal waters and estuaries, where they are prey for a wide number of species (particularly flatfish, linkcod, rockfish and cabezon) as well as highly vulnerable to cannibalism. Most gradually disperse to offshore waters as they enter adult phases, although some adults continue to inhabit nearshore waters and estuaries, and the fishery is generally prosecuted in waters shallower than 100 meters. Because of this complex life history the entire life cycle is not modeled in this version of the California Current model, and the zoea and megalopae are grouped with the carnivorous zooplankton group. The adult biomass is estimated based on landings as an index of abundance, under the assumption that the biomass of males and females is approximately equivalent, that fisheries catch approximately 75% of the adult males in any given year, the biomass of adult females is approximately equal to the number of adult males, and an equal biomass of sublegal crabs exists relative to “legal” adults. Consequently the estimated biomass for 1990 is twice the average landings in the NCC between 1988 and 1992, or 41,000 tons. The same type of assumption for the 1960s model would suggest a biomass on the order of 33,000 tons, and although fishing mortality rates may have been lower, the fishery was already quite well developed in the Washington and Oregon regions, and crab stocks along the Central Californian coast seem to have already collapsed.

With regard to consumption rates, Paul et al. (1994) conducted food usage rates of Tanner and Dungeness crabs following varying periods of starvation (to simulate entrapment in lost gear) and found that Dungeness crab typically consumed between 0.91 to 1.2% body weight per day (with no significant difference in rate between crabs starved over various periods). In recognition of the significance of temperature, all tests were done in non-stressful water temperatures ranging from 5.8 to 8°C (a plausible range for most waters of the Alaska or California Current). Taking a median value from this range of 1.05 would translate into an annual Q/B of 3.8. As we know F to be high (0.6 to 0.9) for males, and predation to be high for juveniles, a P/B of approximately 0.75, corresponding to a GE of 0.2, is likely to be a reasonable estimate, and is consistent with the McLusky and McIntyre method for estimating P/B for crustaceans with a maximum age of 5.

The diet of Dungeness crab is very much that of a generalist, including primarily fish, mollusks and other crustaceans with an apparent trend from mollusks and crustaceans to fish with increasing size. Because the crushing action of the mandibles and gastric mill makes identification to species (as well as volumetric assessment) difficult, most diet studies report frequency of occurrence rather than percentage weight for prey items. Food habits were reported by Gotshall (1977) in northern California (Humboldt bay area), who found some of the highest percent occurrences for polychaetes (10%), mollusks (snails from 2-5% for several species, clams up to 35%), cumaceans (8%), isopods and amphipods (~17% each), echinoderms (brittle stars and sand dollars at 8.2 and 1.4% respectively) and unidentified fish (24%). Other prey items were cephalopods(1%), euphausiids (2%), decapods (5%), other crabs (8%), Dungeness crab (3.4%), whitebait smelt (5.8%), other smelt (7.7%), northern anchovy (0.5%), tomcod (1%) and sanddab (0.5%). Stevens et al. (1982) examined 410 crabs taken from sub- and intertidal habitat in Grays Harbor, of which less than 1% had empty stomachs, and reported % frequency of occurrence as well as numerical and gravimentric composition to arrive at an index of relative abundance (IRI). Over several (highly variable) sites and time periods, the most important taxa tended to be bivalves, crangonid shrimps, barnacles, other Dungeness crab and teleost fish (including flatfish, lingcod, sandlance, tomcod and smelt). Canadian food habits studies cited in Stevens et al. (1982) suggested that crabs in Hecata Straight and the Queen Charlette Islands tended to have higher rates of bivalves and crustaceans in the diet. Other NCC studies include a unfound study by Tegelberg (1972, cited in Stevens et al. 1982) which suggested that bivalves, especially razor clams, were extremely important prey items for Washington coast crabs, with crustaceans and fish found in approximately 35% of stomachs examined. Cannibalism is certainly important, but seems to be more so for juveniles below 6 cm carapace width (Stevens et al. 1982). The diet was estimated as 40% infauna (presumably dominated by bivalves), 20% epibenthic fauna, 20% benthic shrimp, 2.5% amphipods, 10% forage fish, 2% small flatfish, 1% juvenile flatfish, 0.2% juvenile roundfish, 0.1% juvenile rockfish, 0.1% cephalopods, 0.1% rex sole, 1% benthic fishes and 2.5% fisheries offal.

Tanner crab

The true Tanner crab, *Chionoecetes tanneri*, is one of the most common epibenthic invertebrates found at depths greater than 550 meters in slope surveys in the NCC, with catch rates typically ranging from 1 to 2 tons/km^2. The estimated total biomass from slope survey data between 1989 and 2000 suggests an average biomass of 20,000 tons (almost exclusively deeper than 550 meters), which is likely to be an underestimate as the survey gear is not likely to sample all (or smaller) individuals. There is no suggestion of trends from these surveys, and the coefficient of variation in total biomass is relatively small (on the order of 12%). As this estimate is insufficient to balance the model, we will assume an EE of 0.9 and use a top-down balance, which gives an estimated standing biomass of 0.79 tons/ km^2, slightly more than double that of the slope survey estimates (which likely undersample juveniles). Although not currently landed due to the small size relative to *C. bairdi* and *C. opelio*, interest has been expressed in developing a pot fishery for the west coast stock, and the stock is likely being subjected to increasing bycatch mortality as the fishery for the deepwater complex moves into deeper depth strata.

Pereyra (1972) summarized the available ecological information for west coast tanner crabs, and since his work nearly all research has focused on more northern stocks and species. Paul et al. (1994) estimated consumption rates of *Chionecetes* and arrived at a range of 0.43% bwd for the control group, with slightly lower estimates for crab that had been starved to simulate capture in lost gear. We will use these rates, which translate into an estimated annual Q/B of 1.5, despite the fact that they are considerably more conservative than the EBS and GOA model estimates. Based on an estimated GE of 0.2 as assumed in the EBS model (Aydin et al. 2002) we will estimate P/B to be 0.3.[4]

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[4] In the Bering Sea, Aydin (pers. com.) found that most of the predation pressure for *Chionoecetes* species was on juveniles; which is likely to be the case on the west coast, especially given that *Sebastolobus* species are major sources of mortality. Juveniles in the Bering Sea were estimated to have a higher P/B, on the order of 1.5, with a corresponding Q/B of 3.8. However *Chionoecetes* species have a more shallow depth distribution in both the Bering Sea and the Gulf of Alaska, and thus may inhabit a more oxygen rich, and productive, environment.

Diet data are unavailable on the west coast, and consequently borrowed from the Bering Sea and Gulf of Alaska models, which estimate 79.2, 11.8 and 9% infauna, epibenthic fauna and benthic detritus respectively.

A.3 Planktonic Community

Microzooplankton

This group includes small protozoans, such as gymnodiniods, dinoflagellates, ciliates, and nanoflagellates. For our purposes, we will consider the entire group to be heterotrophic, presuming that autotrophs are included with other primary producers. Although this is a very poorly quantified and understood element of the ecosystem, it is a critical element for which biomass can be fairly high. Most of the information was derived from Landry and Lorenzen (1989) and Neuer and Cowles (1994). Landry and Lorenzen (1989) sampled the Washington shelf in August 1981, June 1982 and August 1983. An average of all numbers for all years and distance from shore (shown in Tab 5.9 of Landry and Lorenzen) suggests a mean biomass of 164 mg C/m^2. Assuming a C:dw ratio of 0.15 and a dw:wwt ratio of 0.4 would suggest a plausible wet weight estimate of 2.75g/m^2. Neuer and Cowles (1994) found that off of the Oregon coast, the relative biomass of microzooplankton grazers was smallest during phytoplankton blooms and the non-upwelling season, and greatest in late summer (August-September), and that grazing rates at times exceeded production rates of phytoplankton. Neuer and Cowles (1994) provide estimates of ug C/liter for several major groups of microzooplankton at different time periods, however the model estimated biomass is based on assuming an EE of 0.8.

It is well known that microzooplankton are capable of tremendous growth rates, with doubling times approaching (if not surpassing) those of their food when conditions are suitable (Verity 1985). Thus in the absence of better information, we will assign a P/B ratio of 100 to this group. The diet of this group is assumed to be mainly on phytoplankton, with a smaller percentage (we will estimate 25%) on pelagic detritus to represent bacterial recyclers in the water column.

Copepods

This group includes all developmental stages of copepods (such as furcilia, calyptosis, megalope, zoea, nauplii, trocophores). By far the greatest volume of work in the NCC is that from ongoing monitoring off of Newport, Oregon (Peterson and Miller 1975, Peterson and Miller 1977, Brodeur 1990, Peterson et al. 2002, Peterson and Keister 2003, Peterson and Schwing 2003). These data illustrate a substantial changes in the species composition of the copepod community over seasonal, interannual and interdecadal time scales. Early work in the 1970s had described the summer copepod community as a subarctic community similar to that found along the shelf of the Gulf of Alaska and the Bering Sea, including *Pseudocalanus* spp. *Calanus marshallae*, *Centropages abdominalis*, *Acartia longiremis*, and *A. hudsonica*. Although there was little monitoring at OSU during the 1980s, when substantial monitoring resumed in the late 1990s warm water coastal species were much more common. These included species that used to appear off Oregon only during winter, when they were transported north with the poleward Davidson Current, including *Paracalanus parvus*, *Ctenocalanus vanus* and *Calanus pacificus*. However, since 1999 it is again the cool-water species which have been observed as the dominant taxa in nearshore and shelf break waters (Peterson et al. 2002, Peterson and Schwing 2003).

Peterson and Schwing (2003) reported relative standing biomass and community species composition anomalies for 16 (discontinous) years of zooplankton sampling off of the central Oregon coast (1969-1973, 1983, 1990-1992, and 1996- 2003). Their average wet weight biomass over all years (based on extrapolation of grams C/m^3 to grams wet weight/m^2 by assuming a water column depth of 50 meters and conversion ratios as above), was on the order of 20 grams/m^2. However the total standing biomass when the cold-water (subarctic) species dominate the community (1969-1973 and post-1998) was nearly double the estimated biomass when the warm-water community dominated. For biomass estimates off of Washington, Landry and Lorenzen (1989) summarized work off of the Washington shelf, and suggest a standing stocks of these species were estimated at approximately 1.68 grams of carbon per meter squared for most regions of the shelf. Using a 0.4 C:dw ratio proposed by Landry and Lorenzen, and an estimate of 88.6% of water based on Davis (1993), this corresponds to a wet weight of about 36.8 grams/m^2. However, all of these estimates were over the continental shelf, and the average standing biomass of copepods tends to decline in slope and offshore waters. Average annual standing stock was estimated by the model, which suggested a mean biomass of 16.6 grams/m^2, well within the range of other estimates.

As with phytoplankton, the average standing stock is less important than the total (integrated) annual production that will determine higher trophic level productivity in the system. Landry and Lorenzen (1989) give a maximum consumption rate of about 50% of body weight/day for the indicated mix of copepods species, assuming an average rate of half of that during half of the calender year would suggest a a Q/B on the order of 45. Assuming that growth efficiency in copepods is about 25%, a fair estimate of P/B might be 10/year. Banse and Moser (1980) summarize published P/B estimates for several copepod species, which tend to range widely between 3.2 and 31 (although their estimates were based on the portion of the year when high biomass and production prevailed). Aydin et al. (2003) used estimates of P/B and Q/B ratios in the subarctic gyre models of 23.7 and 112.4 respectively, based on nutrient-phytoplankton-zooplankton model results. However Robinson et al. (1993) estimated a total annual production of copepods on the order of 287 grams/m^2 (wet weight) for this region, based on this and an average standing biomass of 20 would suggest a P/B of roughly 10. Diet has not been quantified in the NCC, but is generally assumed to be a mix of phytoplankton and microzooplankton (Parsons et al. 1984), the model assumes a diet of 80% phytoplankton and 20% microzooplankton.

Euphausiids

This group includes all life stages of euphausiids, principally *Euphasia pacifica*, *Thysanoessa spinifera* and *Nyctiphanes simplex*. Landry and Lorenzen estimated euphausiid biomass of the Washington shelf; and their results gave widely varying estimates of standing stocks ranged from nearly nothing in inshore waters (2 to 5 miles) to between 1 and 25 grams/m^2 at various offshore stations during summer months in 1981-83; the mean abundance for all stations beyond 10 miles over all three years was 6.2 grams/m^2. Day (1971) also sampled the abundance of euphausiids and small nekton along the Vancouver Island and Washington shelf; although his report did not provide estimates in units convertible to grams/m^2 his results did suggest (as have others) that by far the greatest concentration of euphausiids in the region occurred along and offshore of the shelf break. Smiles and Pearcy (1971) did extensive studies of *E. pacifica* off of Oregon, and came up with estimates of just over 3 grams/m^2 for this species (176 mgC/m^2), however they did not give estimates of *T. spinifera* biomass except to say that it may be as much as an order of magnitude greater. Pearcy (1972) sampled euphausiids (and other zooplankton) with midwater trawls taken from different depth strata at a station approximately 50 miles off of the Oregon coast between 1962 and 1964. He estimated a total euphausiid and shrimp biomass (wet weight) of 10.8 grams/m^2 at night, and 4.6 grams/m^2 in the daytime. Laurs (1967) measured macrozooplankton standing stocks in transects off of Brookings, CA, and estimated the total abundance of the euphausiids *E. pacifica, T. longipes,* and *T. spinifera* at 14.8 grams/m^2 (assuming 85% water content for his estimate of 22.2 grams dry weight/10m^2). A top-down balance of the 1960s mode suggests a total biomass of just over 27 grams/ m^2, slightly higher than most of these estimated. However, net and other gear avoidence is generally assumed to result in an underestimation of standing values. As with copepods, recent indications are that euphausiids in the NCC were at low levels during much of the 1990s, and have returned to substantially greater biomass levels since 1999 (Mackas et al. 2001, Feinberg and Peterson 2003), a trend consistent with that seen in the southern part of the California Current (Chavez et al. 2003).

As with other low-trophic level producers, we know that standing stock changes dramatically over short and long time scales. Brodeur and Pearcy (1992), by evaluating the food habits of fish assemblages, found that both species of euphausiids were more abundant (as prey) during high upwelling conditions in 1982 and 1984 as compared with the low upwelling conditions in 1981 and 1983 (the latter being a strong El Niño year). Biomass was also estimated to be very low through much of the 1990s, Tanasichuk (2002) estimated that the biomass of *T. spinifera* decreased by as much as

75% between 1991 and 1997 off of Vancouver Island, although he also cautioned that the major euphausiid species seem to respond differently to physical variability. More recent data suggests that abundance and productivity have increased since 1999. Swartzman and Hickey (2003) describe an increase in euphausiid biomass following the 1999 shift in parts of the California Current (generally south of Cape Blanco) based on hydroacoustic data from triennial cruises, and Feinberg and Peterson (2003) note a dramatic increase in the duration and intensity of euphausiid spawning off of Oregon between 1996 and 2001.

Estimates of P/B ratios are available from Tanasichuk (1998), who estimated P/B ratios for *T. spinifera* based on field research in Barkley Sound, British Columbia between 1991 and 1996. His results suggested that the population P/B ranged from 14 to 45 in any given year (including moults), with most of the variation accounted for by the proportion of larvae versus adults in the standing biomass. The lowest estimates occurred when larvae accounted for ~5% of the mean annual biomass and the highest estimates occurred when larvae were ~80% of the mean biomass. This illustrates first that population P/B is (obviously) highly dependent on age structure, also that major changes were occurring in this system as adult euphausiid abundance declined. He also noted that these rates were the highest reported rates for any euphausiid species to date, and he found substantially lower rates for *E. pacifica* which had an average P/B (over all life history stages) of 4.5 to 6.9. Siegel (2000) reviewed information on euphausiid life history parameters (maximum age, age at maturity, natural mortality and P/B ratios) taken from literature around the world, and echoed Tanasichuk's conclusion on the high rates of *T. spinifera* P/B. Estimates of P/B for other species obviously varied widely, with a typical ranged between 4 and 10/year. Taking these considerations into account, the estimate for P/B will be 8, assuming a 20% growth efficiency the estimated Q/B is therefore 40.

In general, it is widely recognized that euphausiids in the California Current feed primarily on phytoplankton (Ohman 1984, Mackas 1992, B. Marinovic pers. com., W. Peterson Pers. com). Ohman (1984) suggests that *E. pacifica* in Puget Sound preyed primarily upon phytoplankton, his work suggested that copepods were a suboptimal prey (although anchovy larvae were found to be more suitable). Brodeur and Pearcy (1992) suggest that the euphausiids *T. spinifera* and *E. pacifica* consume proportionally more microzooplankton than phytoplankton in their food web structures of the pelagic zone off Oregon and Washington throughout the early 1980's, however they do not cite data or sources for this estimation. Diet composition for the NCC is set at 90% phytoplankton, 5% microzooplankton and 5% copepods.

Macrozooplankton

Macrozooplankton include pasiphaid, seregestid and other pelagic shrimps, chaetognaths, pelagic polychaetes, and other various other (non-gelatinous) carnivorous zooplankton. As the challenges of linking different life histories together makes distinction of pelagic and benthic life history stages of some organisms difficult, this group will also include the pelagic stages of many benthic invertebrates, particularly crab megalopae. Midwater trawls by Pearcy and Forse (1966) suggest (and diet studies confirm) that the most frequently encountered species of pelagic shrimp are *Pasiphaea pacifica, P. tarda* and *Segestis similes*; although dozens of other species commonly occur in NCC waters. Peterson and Keister (2002) found that chaetognaths were one of the most important zooplankton groups off of Oregon in 1998 and 1999, making up roughly 5% of the total standing zooplankton biomass. Mackas (1992) also found that the chaetognaths *Saggitta elegans* and *Eukrohnia hamata* were the most important species of carnivorous zooplankton.

Laurs (1967) measured and reported on macrozooplankton standing stocks in transects off of Brookings, CA, and included estimated densities of chaetognaths, pelagic polychaetes and other carnivorous zooplankton. Taking the average values as a function of distance from shore, and assuming an 85% water content for his dry weight estimates, pelagic shrimp biomass are on the order of 0.56 grams/m^2, chaetognaths densities average 0.62 tons/km^2, and pelagic polychaetes (primarily *Tomopteris spp.*) average 0.07 tons/km^2. Pearcy (1972) also estimated day and night pelagic shrimp biomasses from midwater trawls off of Newport, OR as 0.57 grams/m^2 respectively (0.56 at night and 0.58 during the day). We will use a top-down biomass estimate in this model.

Although one of the most abundant species, *S. elegans*, was noted by Banse and Moser (1980) to have a PB as high as 5.6, we will use estimates of P/B and Q/B based on Aydin et al. (2003) estimates for chaetognaths and other carnivorous zooplankton (P/B 2.55 and Q/B 12.05). Butler (1973) described the diet of seregestid and pasiphaeid shrimps as being primarily mesozooplankton (copepods) and euphausiids, while Nishida et al. (1987) described diets for several midwater shrimp species off of the Oregon coast as consisting primarily of copepods, euphausiids, other decapods (and fragments of all of the same) and coelenterates. Fragments of radiolarians, dinoflagellates, tintinnids, centric diatoms, heteropods, chaetagnaths, and fish scales occurred infrequently. Based on this study, we will attribute their diet to be 40% copepods, 40% euphausiids, 5% gelatinous filter feeders, 2% gelatinous carnivores, 2% amphipods, 3% microzooplankton and 3% phytoplankton.

Gelatinous herbivores

This group includes essentially all filter-feeding urochordate herbivores; principally salps, doliolids and and larvaceans, as well as thecosome pteropods (principally the pelagic snail *Limacina helecina*, which is a mucous web feeder) which are an important (and often overlooked) element of coastal and pelagic ecosystsems (Lavaniegos and Ohman 2003, Arai et al. 2003). Hubbard and Pearcy (1971) evaluated the geographic distribution and relative abundance of salps off of the Oregon coast in the early 1960s, and found that the most abundante species were *Salpa fusiformis* and *Iasis zonaria*. Several other species were common, and there were no clear associations between abundance and either season or ocean conditions, although higher catches may have been be associated with high upwelling conditions in the summer, catches also tended to be extremely patchy over space and time. More recently however, Lavaniegos and Ohman (2003) have found that in the southern part of the California Current, many pelagic tunicates tend to have cool and warm water affiliations. They also present evidence that long term changes in the biomass of many cool water species may have been primarily responsible for the previously documented long-term declines in total California Current zooplankton, which seemed to have reversed in 1999 (McGowan et al. 1998). Suchman (pers. com) suggests that the abundance of salps off of Oregon since 1999 may also be greater than long-term average, and the food habits studies by Lee (2002), which suggest extremely high predation on salps (and several other gelatinous zooplankton species) in both 1998 and 1999 also support this. Peterson and Keister (2002) found high densities of salps off Oregon in April of 1999, when they comprised nearly 60% of the total zooplankton biomass For larvaceans, Landry and Lorenzen (1989) suggest that *Oikopleura* sp. may obtain high biomass levels as high as 30.6 mg C/m^2 off of the Washington shelf.

Salps and other gelatinous zooplankton are also capable of extremely high growth rates. Silver (1975) noted that salps may be food limited, but have the potential for extremely high growth rates and short generation times, and may form swarms when high concentrations of food are available. Salps may also impact other elements of the zooplankton community at such times. Silver (1975) noted that some studies found negative relationships between the abundance of salps and that of copepods and euphausiids, perhaps by clearing the water column of phytoplankton. Lavaniegos and Ohman (2003) also stressed that the high population growth rates can lead to high abundances over large areas, and reported that one swarm of *Thalacia democreatica* extended over 9000 km^2. Salps and other pelagic tunicates tend to be nonselective herbivourous filter feeders that feed primarily on diatoms (Silver 1975, Wrobel and Mills 1998) and can play an extremely important role in biogeochemical fluxes through the the production of appendicularian houses and rapidly sinking fecal pellets (Bruland and Silver 1981, Lavaniegos and Ohman 2003). Arai et al. (2003) suggest that due in part to their extremely high digestion rates, salps and other gelatinous zooplankton tend to be underappreciated with regard to their role as forage for fish and other predators.

In the absence of meaningful biomass estimates, gelatinous filter feeders will be top-down balanced. Estimates of P/B and Q/B are 9 and 30, based from Pauly and Christensen (1996) and Madin and Purcell (1992). Madin and Purcell (1992) also suggest that many salps have a lower assimilation efficiency, with as much as 40% of ingestion lost to defecation. While most salps are pelagic filter feeders, and presumably feed primarily on phytoplankton and microzooplankton, larvaceans and other suspension feeders also feed on molts, marine snow, and other organic carbon. Diets are assigned to be 50% phytoplankton, 25% microzooplankton, and 25% pelagic detritus (representing pelagic bacteria).

Gelatinous carnivores

This group includes essentially all gelatinous carnivores, principally cnidarians (hydrozoans and scyphozoans), ctenophores and heteropods. Shenker (1984) found that *Chrysaora fuscescens* was the dominant species collected off the Oregon coast between May and August, 1981, with *Aurelia aurtia*, *Cyanea capillata* and *Phacellophora camtschatica* also relatively abundant. Shenker reported that the densest swarms were reputed to contain some 80% as much carbon as the densest reported concentrations of copepods along the coast, and a crude estimate based on his results would suggest a standing wet weight biomass of approximately 10 grams/m^2.[5] Laurs (1967) estimated a biomass of 0.78 grams dry weight/10m^2 for small jellies off of Oregon (medusae, siphonophores and ctenophores). Assuming a 94% water content for these more watery species (Davis 1993), this suggests a total wet weight biomass on the order of 1.3 g/m^2. Both Shenker (1984) and Mackas (1992) found that gelatinous carnivores were particularly important over the continental shelf in late summer and fall, as early in the upwelling season distribution was often seaward of the shelf break, thus summertime biomass estimates would overestimate the average annual biomass. Hydromedusae such as *Aglantha* and *Phialidiu*, and the ctenophore *Pleurobranchia* tended to be the most important species in terms of biomass off the southwest Vancouver Island by Mackas (1992). The BC shelf model (Pauly and Christensen 1996) estimates a substantially greater abundance of these species; based on the work of Larson (1986) and Mackas (1992) they report an estimated wet weight of 6.19 g/m^2. However the NCC model uses a top-down balance for this assemblage, considered to be a minimum estimate based on poorly quantified consumption rates.

As with gelatinous filter feeders, many gelatinous predators can have extremely high rates of biomass increase; Larson (1986) found maximum daily P/B rates for gelatinous predators in Saanich Inlet (British Columbia) of 0.04 to 0.1, reflecting annual rates of 3 to 30. Literature values were similar (Larson 1986). However these reflect peak (summer) growth rates, and most species are either absent or at low levels of abundance and productivity throughout the year in the NCC. From the Bering Sea model (Trites et al. 1999) P/B and Q/B were estimated at 0.875 and 2 respectively, Pauly and Christensen (1996) estimated a P/B of 3 and a Q/B of 10 for carnivorous jellies in the Alaskan Gyre, estimates that were still used by Aydin et al. (2003) and are used here.

Food habits are sparse, but generally suggest that predation is greatest on zooplankton eggs and zooplankton. Mackas (1992) found that siphonophores, hydromedusae, and

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[5] Shenker (1984) found abundances ranging from 10 litres per 10^5 m^3 to >1000 litres per 10^5 m^3. If we assumed abundances on the order of 100L per per 10^5 m^3 throughout the nearshore, and assumed a 10m deep survey area, this would suggest a biomass of approximately 10 grams/m^2.

ctenophores off of southwest Vancouver Island are carnivorous, feeding primarily on small crustaceans. Raskoff (2001) found that the siphonophore *Nanomia bijuga*, which was most abundant 3 to 4 months after peak chlorophyll levels in Monterey Bay, fed primarily on euphausiids. Larson (1986) found that most gelatinous predators in Saanich Inlet were euphasuiid eggs, some also preyed on other hydromedusae as well as ctenophores, and Wrobel and Mills (1998) cite several species that predate heavily on other gelatinous species. Suchmann (pers. com.) reported that in 2002 and 2003 gelatinous predators (*Aequorea sp*., *A. labiata*, *C. fuscescens*, and *P. camtschatica*) off of northern California and Oregon were feeding primarily on (and were clearly selecting for) euphausiids eggs, and that predation pressure on the same may have been equivelent to 120 to 300% of the standing biomass. Other significant prey included early life stages of euphausiids and copepods, other gelatinous zooplankton, mollusks, cladocerans, polychaetes and small amounts of carnivorous zooplankton. We will estimate a diet of 60% euphausiids, 30% copepods, 5% gelatinous herbivores, 3% microzooplankton and 2% carnivorous zooplankton.

A.4 Forage species and coastal pelagics

Cephalopods

Although it would be advantageous to differentiate between smaller and larger cephalopod species, the sparse data for any species suggests including all as a single functional group. The market squid *Loligo opelescens* is among the most commonly described species in food habits data, as well as from triennial surveys. While major fisheries for *Loligo* exist in central and southern California, no major fisheries exist off of Oregon or Washington. However, Jefferts et al. (1987) estimated the abundance of *L. opalescens* off of the central Oregon coast acoustically in 1984, and found densities as high as 9.9 tons/ km^2 in known spawning areas, and 0.93 tons/km^2 in adjacent areas over the continental shelf (between 27 and 55 meters depth). Pearcy (1965) sampled the species composition and distribution of cephalopods using mid-water trawls along the Oregon shelf and slope (but primarily in slope and offshore waters), and found that *Gonatus, Abraliopsis* and *Chiroteuthis* species made up the majority of the squid vulnerable to their gear. Jefferts (1988) evaluated cephalopod zoogeography from a wide range of sampling programs, and found that the most important species in the California Current tended to be *Gonatus onyx*, *Chiroteuthis calyx*, *Abraliopsis felis* and *Japetella heathi*. These also occur in the NMFS slope surveys with some regularity, along with the robust clubhook squid (*Moroteuthis robusta*), Flying squid (*Ommastrephes bartrami*), Rhomboid squid (*Taningia danae*), Majestic armhook squid (*Berryteuthis magister*), and other less common or unidentified species. As such estimates clearly undersample cephalopods, the only reasonable approach is to have Ecopath estimate cephalopod abundance based on consumption estimates. For the time being, all octopus are included with the cephalopod group.

For their life history parameters, squid are somewhat unique. All squids have "live fast and die young" lifestyles (O'Dor and Webber 1986), with rapid turnover of population biomass in short time periods. Most squid die after spawning and generally spawn between the ages of 1 and 2, although Pacific giant octopus (*Octopus dofleini*) are the exception, with lifespans that may approach several decades. Cephalopods in general have high metabolic requirements, according to O'dor and Webber (1986) squid may use eight times as much energy to travel half as fast as a fish of comperable size. By some accounts, squid may eat as much as 14% of their body weight per day, which would correspond to a Q/B of ~50 per year, however they are much more efficient at transferring their consumption into biomass (higher GE). The Alaska Gyre model used an average P/B ratio of 2.55, and an average Q/B ratio of 7 for large squid (gonatid, clubhook and flying squid), and a P/B ratio of 3 with a Q/B ratio of 15 for smaller (micronektonic) squid. As the latter likely represent the bulk of the cephalopod life history types in the NCC, I will P/B estimates of 2.75 and Q/B estimates of 10 for this model.

For diet data in *L. opalescens*, there have been studies done by Fields (1965) and Karpov and Cailliet (1979). Karpov and Cailliet estimated roughly 30% forage fish, 10% juvenile fish, 40% euphausiids, 10% copepods and other mesozooplankton and 10% other cephalopods. Both of these studies suggested that the diet changes as size increases, with fish, other cephalopods, benthic gastropods and polychaetes becoming of greater importance. For larger squid species encountered frequently in continental slope surveys, diet data has been worked up by Buckley (pers. com.), whose results suggest that other cephalopods make up as much as 30%, with ~15% forage fish, 10% euphausiids, 10% pelagic shrimp and other macrozooplankton, and 35% other teleost fishes. Although differences in feeding habits alone should be enough to justify two squid boxes in the model, this group is already so poorly parameterized that we will stick with one, and assign prey to 20% forage fish, 10% juvenile fish, 10% mesopelagic fish, 38% euphausiids, 10% macrozooplankton, 15% copepods and trace amounts of pandalid shrimp, benthic shrimp, epibenthic fauna and other cephalopods (acknowledging that this underemphasizes both the role and the trophic level of larger cephalopods and their predators).

Forage fish

This category will by unfortunate necessity be a broad, functional group that includes northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea harengus pallasi*), sand lance (*Ammodytes hexapterus*), eulachon (*Thaleichthys pacificus*), American shad (*Alosa sapidissima*), surf smelt (*Hypomesus pretiosus*), whitebait smelt (*Allosmerus elongates*) and many other important clupeid, osmerid and other forage species. While these species all have highly varying life history characteristics, the abundance, even relative abundance, of most of these species is poorly quantified. Although food habits data could be used in an attempt to define relative abundance and productivity, the highly variable nature of food habits data combined with the patchiness of food habits studies over space and time would suggest that it would be difficult to paint a convincing picture that these groups could be defined as distinct species or assemblages; especially as the species composition seems to have changed considerably even over recent decades.

Emmett and Brodeur (2000) and Brodeur et al. (2003) describe changes in the relative abundance of forage fish as suggested by NMFS triennial groundfish surveys (which are not targeting, and certainly not reliably estimating, pelagic forage fishes), and OSU and NMFS salmon surveys (including surface trawls and purse seines) which suggest that northern anchovy and eulachon populations (as well as market squid and salmonids) have decreased over the last two decades while herring and shad (as well as hake, sardine and Pacific and jack mackerel) have increased. As Pacific herring and shad dominate the forage fish catch by volume (related no doubt to their larger size and greater vulnerability to the gear), Figure A.1 shows relative changes in abundance for four of the key forage fish groups in the NCC based on the triennial survey results (northern anchovy, Pacific herring, Pacific shad and a pooled group of osmerids including *T. pacificus*, *A. elongates*, *Hypoomesus pretiosus*, and *Spirinchuys starksi*). From this figure we see that the relative abundance of anchovy and osmerids was generally greater in 1977, that the early 1980s and mid 1990s were especially poor for these species, and that there have been recent increases in abundance in 2001. Herring were also low in the early 1980s, and were particularly high in the late 1980s and early 1990s (a period when the cool and more productive conditions seem to have prevailed for a short stretch). Shad seem simply to be quite variable, although they are considerably less abundant in food habits data and may be a less relevant indicator of actual forage fish availability. These trends are consistent with other changes in the relative abundance of forage fish in other surveys and research efforts, described in Brodeur et al. (2003).

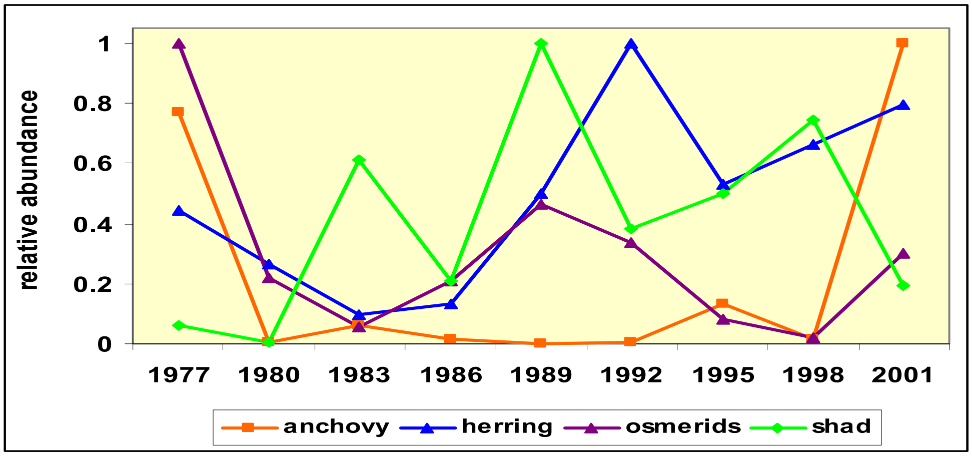

Figure A.1: Relative abundance of key forage fish groups in the NCC

Very few quantitative assessments of forage fish in the NCC have been done. Richardson (1981) estimated the spawning biomass (of 2+ year fish) for the northern anchovy subpopulation in the Columbia area in the mid 1970s using a variety of egg and larval production methods. Her estimates for spawning biomass were from 260,000 to 770,000 tons in 1975 and 145,000 to 1,005,000 tons in 1976, which were consistent with the results of a hydroacoustic survey done in 1977 that suggested a spawning biomass on the order of 800,000 tons (including only animals over 2 years old). For herring, Hay and McCarter (1997) used a comparison of continental shelf area to maximum herring biomass and estimated a biomass for Oregon and Washington outer coasts of 0.8 tons/km^2. They also estimated maximum average densities (over continental shelf areas) off of Southeast Alaska and British Columbia of 10 tons/km^2. Hay et al. (1997) estimated eulachon caught incidentally in shrimp trawl surveys off of Vancouver Island (between 1973 and 1996) to have a density of approximately 0.51 tons/km^2.

We can imagine that if we were to assume a total biomass on the order of one million metric tons (the maximum anchovy abundance estimated by Richardson, excluding juveniles), evenly distributed throughout the entire Columbia area from the nearshore to 1250 meters depth, this would suggest a standing biomass of approximately 25 tons/km^2. Spreading this biomass throughout the entire NCC would suggest a standing biomass of just over 14 tons/km^2. Thus while we know that the biomass of the northern anchovy subpopulation has declined significantly since the mid 1970s, we can also presume that estimates of standing biomass between 15 and 25 tons/km^2 are plausible estimates of forage fish abundance, particularly for the earlier years of the model. Yet as well defined estimates in appropriate time periods are not available, we use a top-down balance for this group, which gives us a starting value for standing biomass of 27.1 tons/km^2

For life history rates, Gunderson (1997) cited estimates of M for several important forage fishes, such as northern anchovy (0.9), sand lance (1.0), and Pacific herring (0.56), although these were adult mortality estimates. Butler et al. (1993) provide stage specific life history parameters for northern anchovy; for adults they suggest a best estimate of 0.77 (within a range of 0.4 to 1.3), for late juveniles and pre-recruits they estimate 1.6 and 1.13, and for late larvae and early juveniles they estimate 25 and 5 respectively. For Pacific sardine (which might be more likely to approximate Pacific herring in terms of growth and mortality rates) they suggest annual adult mortality on the order of 0.4 (within a range of 0.21 and 0.8); with five juvenile stages (early to pre-reccruit) ranging from 20 to 0.8 over the first 150 days of life. Because we include both juvenile and adult production in this functional group we will begin with a P/B estimate of 1.5. Assuming a 25% growth efficiency would suggest a corresponding Q/B estimate of 6, which is also consistent with Pauly (1989).

The best food habits information is from Brodeur et al. (1987), who describe food habits for Pacific herring, shad, anchovy, surf smelt and saury off of the central Oregon coast from 1981-1984. Herring, based on nearly 100 stomachs studied, fed primarily on euphausiids in 1981 and 1982 (88.1 and 91.2% of diet by weight), less so in 1983 (41.4%) and 1984 (0.5%). Copepods were the most significant prey in 1984 at 67.2% prey by weight, less so in other years (7.9, trace, and 11.6% in 81-83 respectively). Pagurid and other crab zoea and megalopae were present in trace amounts, and were important in 1984 (31.3%), and amphipods were present in significant amounts (3.8 to 6.7%) in all years except 1984. Pteropods were present in trace amounts in 1981, and anchovy, osmerids and unidentified fishes were present in small amounts (0.3 to 1.3) all years except 1982. Only 18 northern anchovy stomachs were examined (all in 1981), and these contained 18.5% pteropods (*Limacina helicina*), 0.2% cephalopods, 5.4% copepods, 0.3% amphipods, 13.6% euphausiids, 2.7% Dungeness crab megalopae and 0.4% fish eggs (the remainder was unidentified). A small number (28) of American shad stomachs taken in 1981 and 1984 suggested diets were composed of 51% euphausiids, 39.2% copepods, 0.7% amphipods, 0.6% cephalopods and 0.2% crab zoea. Surf smelt (17 stomachs in 1981 and 1983) food habits were poorly defined as nearly 70% of stomach contents were unidentified, but gastropods (*Limacina helicina*) made up 0.5%, copepods 3.8%, amphipods 5.7%, pagurids and other decapods 2.4%, larvaceans 4.2%, and fishes (sandlance and unidentified pleuronectids) 2%.[6] We will assign forage fish food habits to the following; 40% euphausiids, 45% copepods, 10% microzooplankton (presuming this to be critical for larval and juveniles stages), 3% carnivorous zooplankton, 1% amphipods, 1% gelatinous filter feeders and 0.5% cephalopods.

Mesopelagics

For our purposes this assemblage is an amalgam of all meso and bathypelagic species, including all myctophiform fishes as well as salmoniform families such as argentinids, gonostomatids, photichthyids, bathylagids and stomiatids. Pearcy and Laurs (1966) report on the abundance of mesopelagic species caught in midwater trawls at various depth strata in depths of some 2000 meters off of the Oregon shelf. They describe diel changes in distribution and include estimates of biomass that averaged 2.4 g/m^2 in daytime samples and 3.6 g/m^2 at night. They report four species as being the most common; the northern lampfish *Stenobranchius leucopsarus*, the California headlight fish *Diaphus theta*, the Blue lanternfish *Tarletonbeania crenularis* and the longfin dragonfish *Tactostoma macropus*. Other commonly caught species from slope surveys include California slickhead (*Alepocephalus tenebrosus*), Pacific viperfish (*Chauliodus*

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[6] Currently T. Miller and T. Wainwright (pers. com.) are evaluating food habits of these and other nektonic species collected in recent GLOBEC cruises, and using cluster analysis to assess similarities and differences in key species. Preliminary results from the year 2000 suggest that Surf smelt, whitebait smelt and herring consumed primarily copepods and larval decapods, with euphausiids being somewhat less important for these species (in this year).

macouni), and lancetfish (*Alepisaursus ferox*). Among the caveats to utilizing these estimates are that these abundance levels are only likely to be plausible at depths beyond the shelf break. Willis and Pearcy (1982) provide additional information on the abundance and depth distribution of these and other species of deepwater fishes off of the Oregon coast, but focus on quantifying vertical migrations rather than biomass or species composition. Beamish et al. (1999) suggests that biomass levels from 5 to 10 tons/km^2 are not uncommon throughout the northeast Pacific, and a top-down balance in this model produces an estimate of 7.6 tons/km^2.

Childress et al. (1980) reviewed growth, energy use and reproduction in meso and bathypelagic fishes off of California, and reported that most mesopelagic fishes are characterized by smaller size, slow growth, and early, repeated reproduction. They also estimated daily rations on the order of 0.87% body weight per day for mesopelagics (including *L. stilbius*, *S. leucopsaurus*, *T. mexicanus* and *L. ritteri*) and slightly less (0.68%) for bathypelagic species; corresponding to annual Q/B of 3.2 and 2.5 respectively. Finally, they estimated growth efficiencies for the four key mesopelagic species as ranging from 0.15 for *S. leucopsaurus* to 0.26 for *L. ritteri*. Assuming a growth efficiency of 20% and a consumption rate of 3 per year.would suggest a P/B of 0.6, which seems to be plausible for this assemblage. Aydin et al. (2003) use a slightly higher P/B, 0.9, with the same Q/B (3), which assumes a higher (0.3) growth efficiency.

For food habits, Tyler (1970) assessed the feeding habits of three of the most frequently encountered species of myctophids off central Oregon (*S. leucopsarus*, *D. theta* and *T. crenularis*); the results suggested that euphausiids were the most frequently targeted prey item (from 45 to 80% of prey by weight), followed by copepods (5 to 15%), amphipods (roughly 3 to 6%), larvaceans and other unidentified material. Euphausiids comprised between 40 and 75% of prey items for these species, and copepods generally comprised from 5 to 20%; with most of the remainder unidentified material. Cailliet and Ebeling (1990) reported on the feeding habits of the California smoothtongue (*Leuroglossus stilbius*, a bathylagid) and the northern lampfish (*S. leucopsarus*) off of Southern California (Santa Barbara and Santa Cruz basins). *L. stilbius* fed primarily on larvaceans and salps, with ostracods, copepods, euphausiids, amphipods, and pelagic shrimp also present. *S. leucopsarus* fed primarily on euphausiids, copepods, and ostracods, with minor amounts of fish eggs, fish larvae, chaetagnaths, amphipods, pelagic shrimp, salps and siphonophores. Beamish et al. (1999) review a wide range of food habits studies and conclude that myctophids are generalists that exhibit a preference for crustacean zooplankton, but will also feed on chaetognaths, coelenterates, siphonophores, cephalopods, ctenophores, larvaceans and other planktonic organisms. We will assume that euphausiids comprise 52% of the diet in this assemblage, with 32% copepods, 4% carnivorous zooplankton, 3% amphipods, 2% gelatinous carnivores, 5% gelatinous filter feeders, 2% cephalopods and 0.5% other mesopelagics.

Benthic fishes

This group must really be considered a “catch-all” of benthic species, and includes primarily the eelpouts (*Zoarcidae*) which are found in substantial quantities in the shelf and slope surveys, as well as snailfish (*Cyclopteridae*), poachers (*Agonidae*), sculpins (*Cottidae*), tomcod (*Microgadus proximus*), spotted ratfish (*Hydrolagus colliei*) and other species poorly enumerated and sampled benthic species. This group is significantly underestimated by surveys; the average shelf survey biomass between 1977 and 2001 for all these species is 3080 tons, most of which (62%) was from shallow strata and most of which consisted of tomcod, ratfish and various eelpouts. The average slope survey biomass was 13,700 tons, most of which consisted of eelpouts, poachers and sculpins. A top-down balance with an EE of 0.8 results in an estimate of 3.6 tons/km^2 for this functional group. We will also assume parameter estimates of 0.5 for P/B of and 2.5 for Q/B, as used in the Bering Sea model (Trites et al. 1999, Aydin et. al. 2002).

Diet data for species in this functional group is scarce, but some exists. No quantitative diet studies are known for zoarcids in the California Current, but Hart (1973) suggest that zoarcids (which appear to dominate this guild in terms of biomass) feed primarily on infauna (particularly polychaetes) and epibenthic fauna (amphipods, shrimp). Ferry (1997) reported on the food habits of the two-line eelpout (*Bothrocara brunneum*), which fed primarily on benthic shrimps and other zoarcids. However this species may have been anomalous, as Ferry also reported that most zoarcid species feed on bivalves, amphipods, ophiuroids and annelids. In the Eastern Bering Sea, stomachs collected by the Alaska center suggest a diet for zoarcids of primarily amphipods (~57%), infauna (~22%), crabs (~2%), pollock (~6.6%), other benthic fishes (perhaps 10%), some forage fishes (including herring), and trace amounts of mysids and other epifauna. In the NCC, Wakefield (1984) reports on some diet data for several nearshore benthic fishes, including tomcod (*Microgadus proximus*) and Cabezon (*Scorpaenichthys marmoratus*), and ratfish (*Hydrolgus colliei*) in nearshore areas off of central Oregon (samples all collected in May 1979). He found that tomcod preyed primarily on mysid shrimp (45 to 60%), amphipods (~23%), benthic shrimps (13%), Dungeness crabs (~5%), other crabs (~5%), and smaller amounts of infauna, gastropods and fishes. Cabezon (*Scorpaenichthys marmoratus*) fed heavily on crangonid shrimp (35%) and crabs (65%) with trace amounts of gastropods, mysids and sanddabs. Ratfish (*Hydrolagus colliei*) fed on infauna (38% bivalves and 4% polychaetes), benthic shrimps (7%), Dungeness and other crabs (30%) and small amounts of fish (6% tomcod, 4.6% sculpins and some unidentified), as well as small amounts of mysids and amphipods. These nearshore species do not necessarily reflect prey preferences of deeper shelf and slope species, however they are essentially all that is available. In the absence of better information, the diet composition used here was 30% infauna, 40% epibenthic fauna, 18% amphipods, 4% benthic shrimps, 1% pandalid shrimps, 1% Dungeness crab, 0.2% Tanner crab, 1% small flatfish, 2% juvenile flatfish, 0.3% juvenile rockfish, 0.2% juvenile roundfish, 0.5% small flatfish, 1% detritus and 0.2% fisheries offal.

California sardine

Well known to be seasonal migrants to the NCC during warm periods; a substantial fishery existed in Oregon, Washington and Vancouver Island in the 1930's and 40's when the population was estimated by Murphy (1966) to be as much as 3 to 5 million metric tons throughout the California current. Sardines were present at least sporatically since 1866 in Puget Sound and the outer coast, as well as in the late 1700's (Strom 2003). During the infamous collapse of the fishery in the late 1940s and 50s, it was clear that the sardine's range was contracting north to south, as evidenced by the sequential collapse of fisheries from British Columbia to San Pedro in the Southern California Bight (Murphy 1966). Similarly, as the sardines have recovered over the last two decades they have done so from south to north (Emmett and Brodeur 2000, Conser et al. 2002), reaching even far into the Gulf of Alaska during the anomalously strong El Niño event of 1997-98 (Wing et al. 2000). This is consistent with the notion that sardines tend to expand northward in both abundance and range during warm regimes (McFarlane et al. 2002), a characteristic shared with Pacific hake, Pacific mackerel and other pelagics. The most recent assessment estimates a coastwide biomass on the order of 1 million metric tons (Conser et al. 2002), most of which is presumably south of Cape Mendocino. Taking a perhaps optimistic 20% of the average ("unavailable" in southern area) stock from the assessment for the 1990s suggests a biomass of ~70,000 tons. A top-down balance (that includes heavy fishing mortality) is used in the 60s model to allow known sardine predators (including salmon, hake, sharks, albacore, fur seals, sea lions, whales). For P/B, both Murphy (1966) and MacCall (1979) estimated natural mortality rates of 0.4, although given modest fishing mortality we will raise this to 0.5. For consumption rates we will estimate a Q/B of 5.

Hand and Berner (1959) describe the diets of sardines in California waters as being upwards of 90% crustaceans, primarily small copepods but including larger copepods, euphausiids, amphipods and minor amounts of pteropods. Hart and Wailes (1931) evaluated food habits of sardines off of the British Columbia shelf, and found (by volume) 45% diatoms, 4% microzooplankton, 28% copepods, 7% euphausiids, trace macrozooplankton (chaetagnaths), and 15% unidentified or digested material. T. Miller (pers. com.) has been evaluating stomach contents of sardines taken off of Oregon in the 1990s, and suggests that the proportion of meso and macrozooplankton (and in particular, euphausiid and copepod eggs) comprise a greater proportion of the energetic content of sardine prey items. His results, when available, will likely be more appropriate for this effort. For the moment that sardines feed on 28% phytoplankton, 2% microzooplankton, 40% copepods, and 30% euphausiids.

Mackerels

For our purposes we will combine both jack mackerel (*Trachurus symetricus*) and Pacific mackerel (*Scomber japonicus*), as despite the fact that they represent different families, the undertainties in their abundance, life history characteristics and diet justify merging the two. The abundance of jack mackerel may be quite large throughout the northeastern Pacific, on the order of 1.2 to 2.6 million metric tons by some estimates (MacCall and Stauffer 1983). However this has been acknowledged to be extremely speculative, and there is no means of knowing what fraction of this might occur in the NCC. The triennial shelf trawl survey provides some measure (presumably an underestimate) of Pacific and jack mackerel abundance that suggest trends and minimum biomass levels. The most recent assessment of Pacific mackerel (Hill et al. 1999) suggests a biomass of over half a million (short) tons the early to mid 1990s, although the shelf survey data do not reflect as much, most of this biomass was presumably south of Cape Mendocino. The shelf survey estimates (Table A.2) suggests a mean abundance through the early 90s of perhaps 25,000 tons in the NCC. A doubling of this estimate for Pacific mackerel is barely 10% of the total stock biomass, which seems a reasonable minimum estimate. Doing so for both species suggests 50,000 tons of Pacific mackerel and 75,000 tons of jack mackerel for the 1990s, for a total of 1.78 tons/km^2. For the 1960's we know that Pacific mackerel abundance was extremely low (Hill et al. 1999), but we know very little about jack mackerel in the region during this period. Ermakov and Stepanenko (1996) reported 12,400 tons of jack mackerel in Russian exploratory surveys between 1965-66, but only trace (200-1400 tons) amounts in later years. There is virtually no mention of either species in other surveys from the 1960s and early 1970s, even where other pelagics (shad, herring and anchovy) were reported (Pereyra and Alton 1972, Demory et al. 1975, and Barse 1976). Based on these sporatic and unconvincing observatins, and the absence of better information, we will estimate a modest 20,000 tons (0.286 tons/km^{2}2) for the 1960s model.

Table A.1: Shelf survey biomass estimates for Pacific and jack mackerel

	All survey areas			NCC		
	scomber	trachurus	both	scomber	trachurus	both
1977		4145	4145		824	824
1980		117	117		51	51
1983	10	6231	6241		5944	5944
1986	29	1568	1597		1559	1559
1989	7588	40319	47907	7315	30502	37817
1992	27134	53890	81024	26850	53657	80507
1995	16348	25293	41641	15107	14484	29591
1998	6087	9522	15609	2533	916	3449
2001	2256	3791	6047	2225	3777	6002

While there is a significant (~40,000 tons) fishery off of California for both Pacific and jack mackerel, only incidental numbers of jack mackerel are caught in the NCC as bycatch in the whiting fishery (on the order of 400 tons per year). Jack mackerel reach ages of 35 or greater, and natural mortality has been estimated between 0.2 and 0.25 per year. Natural mortality for Pacific mackerel has been estimated by Yaremko et al

(1998) to be approximately 0.5. For the moment, we will use 0.4 for the group, and for Q/B we will use 6 as in the Alaskan gyre model (Aydin et al. 2003).

For food habits, early CalCOFI studies (1953) found that jack mackerel off of Southern California consumed (by volume) primarily euphausiids (~65%), pteropods (~15%) and large copepods (~15%), of the more important minor food items were amphipods, fish larvae, foraminiferans, decapod larvae, annelids and isopods. Brodeur et al. (1987) describe a highly opportunistic diet for both species; jack mackerel fed principally on euphausiids in 1983 and 1984 (~72% by volume both years, contrast to ~12% in 1982) and on forage fish in 1982 (70% anchovy in 1982, contrast to 13% herring in 1983 and small percentages of various forage fish in 1984). Other prey included varying amounts by year of pteropods (5.7% in 1983), and trace amounts of cephalopods, amphipods, copepods, decapods, chaetagnaths, and juvenile rockfish, flatfish and roundfish. Pacific mackerel fed principally on euphausiids (76% in 1983, 21% in 1984) and copepods (25% in 1983), other prey included thaliaceans (6.4% in 1983), cnidarians and ctenophores (3.1% in 1984), amphipods, decapods, crab larvae and various (mostly unidentified) fishes (including juvenile rockfish, roundfish and flatfish). Other diet data from northern waters includes studies by Grinnols and Gill (1968) found that jack mackerel consumed saury, myctophids and cephalopods when feeding at night off the Oregon coast, and Ashton et al. (1985) described jack mackerel diets off of Vancouver island as 75 to 100% herring, but with one instance of high predation on salmon smolts. Personal observations of jack mackerel off of northern California and Southern Oregon in 2001 suggested a diet of primarily euphausiids. We will use as a starting point the following breakdown; 60% euphausiids, 5% copepods, 6% macrozooplankton, 1% pelagic shrimps, 1% amphipods, 1% gelatinous zooplankton, 20% forage fishes, 1% myctophids, 3% juvenile fishes, 1% small flatfish, 0.4% benthic fishes, 0.1% juvenile salmon and 0.5% cephalopods.

A.5 Salmon and Pacific hake

Chinook and coho salmon

Salmon are a difficult group to address on many levels, most obviously as a result of their life cycle complexity. Consequently, we acknowledge that we will not be able to fully and accurately account for salmon dynamics in the NCC model, although we can make a reasonable effort to represent the role salmon play in coastal waters as both predators and prey. In doing so, we have chosen to group all salmon species, stocks and life history stages (smolts and adults) together, essentially reducing all to the level of a functional salmonid group. For estimating catches and biomass, we rely on data from PFMC reports on commercial and recreational troll fisheries in the NCC; we have chosen to exclude in-river landings and estimated interceptions for the purposes of this modeling effort. In general, parameters appropriate for Chinook salmon are utilized, as

Chinook make up a slight majority of the average landings and are more likely to be resident in the California Current for longer stages of their life cycle.

The distribution of salmon entering Pacific Northwest coastal waters is poorly understood. Some smolts and adults continuing to occupy the coastal waters of the NCC, others migrate to northern and offshore waters, and still others entering NCC waters from elsewhere. Generally, stream-type (subyearling) chinook are thought to move very quickly offshore into the central North Pacific, while ocean-type (yearling) tend to inhabit coastal waters for most of their lives (Myers et al. 1998). South of 55°N, most chinook stocks ten to be ocean-type, however detailed information regarding ocean migratory patterns (and variability in such patterns) is limited. Chinook tend to stay at sea from 2 to 4 years, with a range of 1 to 6 years. Marine recoveries by age and state (or province) suggest that while most coastal Washington and Oregon chinook are caught in Canadian or Alaskan waters (with a significant fraction of Oregon chinook caught in Washington and Oregon waters), California chinook are primarily caught in Oregon and Californian waters (Myers et al. 1998). By contrast, most (southern) coho salmon are 3 years of age upon their return to natal rivers and streams, after approximately 1.5 years in fresh and marine environments respectively. Upon entering the ocean, most coho between California and British Columbia tend to move northward along the coast, with some foraging in the coastal Gulf of Alaska and others migrating out into the Alaska Gyre. However some coho appear to remain in nearshore waters for the majority of their ocean phase (Groot and Margolis 1991). Coded wire tag studies show that coho which outmigrate (or are released) from south of Cape Blanco are almost exclusively recovered in California or Oregon waters (with most recovered in California), while those that outmigrate (or are released) from north of Blanco tend to be recovered principally in Washington, Oregon and (for WA coastal runs in particular) British Columbia (Weitkamp et al.1995). For juveniles, Brodeur, et al. (1992) estimated abundance from purse seine collections made during 1981-1984 off Washington and Oregon, which would suggest biomass levels on the order of 0.05 tons/km^2.[7]

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[7] We converted numbers by strata into biomass by multiplying by the weight of individual salmon, as presented in growth curves from the same paper, which were based on marine growth rates from recoveries of CWT coho (Fisher and Pearcy 1988) and chinook (W. Pearcy unpubl. data). We then summed the biomass estimates for each stratum in a given month and year and divided by the total area. Only the areas of two of the strata were reported, B and C, but stratum A appears to be almost exactly the same size as stratum B. We took the mean of the biomass estimates for each month surveyed to arrive at a single value, of 0.05tons/km^2, although we recognize that these estimates do not reflect the expected changes in smolt abundance over time. Another way to estimate gross biomass levels of smolts was done, based releases from all hatcheries in the NCC watersheds. Smolt releases by number, as well as the mean weights of smolts, increased steadily from the 1960s to the early 1980s, where it more or less leveled off. Combining data for all OR, WA and ID releases suggests that the total biomass of smolts released has been on the order of 5000 metric tons since the early 1980 (data from Magnuson 2001). Obviously habitat quality and wild smolt production have varied or declined substantially, but if we consider 5000 tons to be a minimum estimate of smolt biomass reaching the ocean we would end up with

As ocean commercial and recreational landings represent fish that were known to be in the NCC, and because we know fishing mortality to be fairly high (although quantifying fishing mortality in detail is challenging) we will assume that these fisheries catch (on average) 50% of the mean annual salmon biomass in the NCC (the other 50% representing escapement and/or in-river harvests, as well as fish that are remaining out at sea), and furthermore that salmon are present in the NCC an average of 50% of their ocean existence. This gives us a plausible estimate, likely to be an underestimate, of the role of salmon in the ecosystem within the context of other predators and prey. Figure A.2 shows the reported commercial and recreational troll landings for the NCC based on the most recent salmon SAFE document (PFMC 2003), as supplemented by numbers from a 1999 data synopsis (PFMC 1999). Based on these observed landings and the formentioned ratios of abundance, the starting biomass for the 1960s and 1990s models respectively are 0.37 and 0.270 respectively, and corresponding average annual fishing mortality is set at 0.5. Estimates of P/B and Q/B are based on Aydin et al. (2003), who used bioenergetics models of salmon in the North Pacific Gyre to arrive at an estimate for chinook P/B of 0.8, with a corresponding Q/B of 5.3.

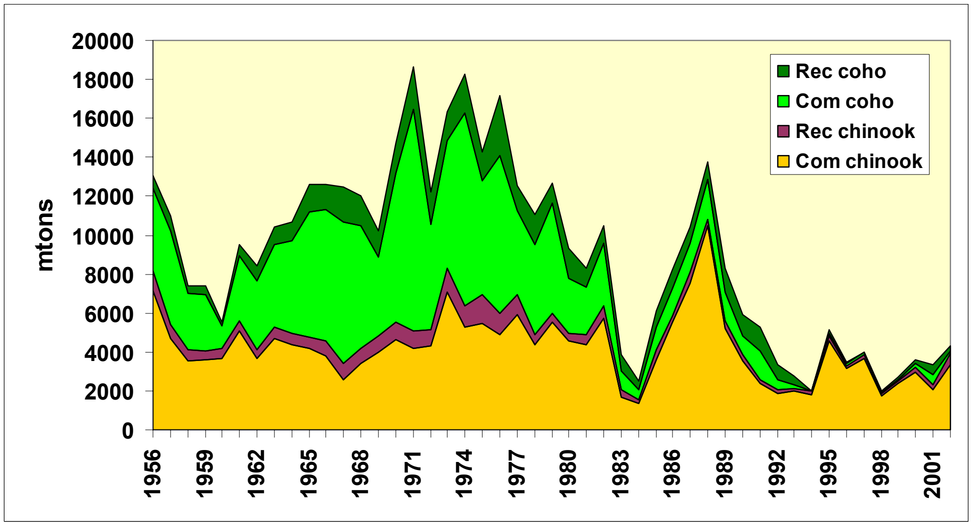

Figure A.2 At-sea salmon catches in the NCC

The diets of chinook and coho salmon in coastal waters tend to be very similar, although regional differences can be significant (Groot and Margolis 1991). Silliman (1941) evaluated chinook and coho stomach contents off of Washington in 1938 and found that dominant prey items were forage fish (included Pacific sardine,[8] herring,

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a total NCC biomass of 0.071 tons/km^2. That these two very uncertain estimates suggest numbers of a similar magnitude indicatess that these are plausible estimates of "mean" smolt biomass in the NCC.

[8] Pritchard and Tester (1940) found that sardines were heavily utilized by spring salmon off of the west coast of Vancouver Island and in the Straight of 1940, when they averaged approximately 25% of the observed stomach contents (although they were absent in stomach contents in 1939). Chapman (1936, as

smelt, anchovy and others) and euphausiids, with rockfish, sablefish (presumably juvenile), small flatfish, crab larvae, cephalopods, copepods and amphipods also present. Merkel (1957) found that chinook off of central California fed primarily on anchovy (29.1%), rockfish (22.5%), euphausiids (14.9%), herring (12.7%), squid (9.3%), other fishes (7.3%) and crab megalopae (4%). He also documented seasonal patterns in food habits, with herring and anchovy more important in fall and winter (August-March for anchovy, January- April for herring), euphausiids, squid and crab megalopae more important in spring and early summer (March-June), and rockfish more important through the summer (May-August). Other species noted included sanddabs and lingcod.

Brodeur et al (1987) took stomach samples of adult coho and chinook salmon between Cape Blanco and Cape Flattery between 1981 and 1985, and found that for both fish made up the greatest fraction of diets in the coastal zone (particularly herring and anchovy), with squid (mostly *loligo opalescens*) and euphausiids comprising the majority of remaining prey items by volume. Minor prey items included cnidarians (*Velella velella* was 8.1% by volume for coho in one year), pteropods (*limacine helecina*), amphipods, pandalid shrimp, benthic (Crangon spp.) shrimp, insects, juvenile rockfish, Pacific hake, myctophids (*stenobrachius leucopsarus*), cottids, sanddabs, rex sole, sand sole and other small flatfish species. In general, these results indicated that euphausiids and herring made up a greater proportion of the diets in salmon off of Washington state, with salmon off of Oregon and the Columbia River relying more on a mix of forage fishes (herring, anchovies, sandlance, osmerids and squid), and salmon off of California relying more on anchovies and rockfish. Brodeur and Pearcy (1990) also provided a comprehensive analysis of juvenile coho and chinook diet composition between 1981 and 1985 along the Oregon and southwest Washington coasts. They found that larval and juvenile fishes appear to make up the greatest amount of prey (roughly 70% by volume for coho, >80% for chinook), with 10 to 20% euphausiids or other macrozooplankton, and trace amounts of amphipods, pteropods, copepods and cephalopods. The most commonly encountered fish species in this period were juvenile *Sebastes*, northern anchovies and Pacific sand lance. The diet ultimately used in the 1960s model includes 61.2% forage fish, 10% euphausiids, 20% carnivorous zooplankton, 0.1% copepods, 0.1% amphipods, 1% cephalopods, 0.2% gelatinous herbivores, 0.2% gelatinous carnivores, 2.5% juvenile rockfish, 1% juvenile roundfish, 1% juvenile flatfish, 1% small flatfish, 1% sardine (necessary for inclusion in 1990s model), 0.2% benthic fishes, 0.1% rex sole, 0.2% hake, and 0.2% myctophids.

Pacific hake

Pacific hake (*Merluccius productus*), also known as Pacific whiting, is the most abundant stock of commercial importance along the U.S. west coast. The basic range is

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cited in Merkel 1957) found that Chinook salmon off of Washington in 1936 fed principally on sardines, herring and euphausiids.

from Baja California to (rarely) beyond the northern end of Vancouver Island, although juveniles (ages 0 to 2) are rarely found north of Cape Mendocino, CA (Bailey et al. 1982). Hake are summer migrants to NCC, and adults winter in deep, offshore waters off of Southern California and Northern Mexico. Stock size has fluctuated from nearly six million metric tons in 1987 to less than 1 million metric tons in 2000 (Helser et al. 2002); the average age 3+ biomass from early and more recent stock assessments is shown below as Figure A.3. Estimates of hake abundance are less reliable prior to the early 1970s, although assessments by Dorn and Methot (1990) and Dorn (1995b) estimated population biomass and recruitment as far back as 1958 based on data from the 1960s foreign fisheries. These early assessments suggested that the abundance of hake throughout the 1960s was indeed greater than that in the 1970s, ranging between ~2.5 and 5 million metric tons depending on the time and assessment. The population nearly tripled in biomass in the early 1980s as a result of two extremely large (1980 and 1984) year classes, and population declines in the 1990s presumably reflect a mix of poor current recruitment conditions (possibly associated with an increase in cannibalism) and relatively high fishing mortality.

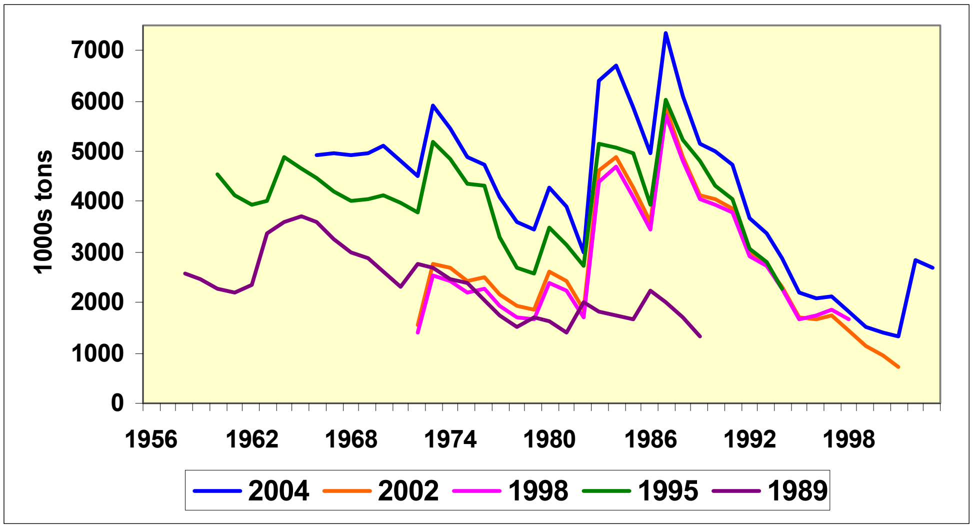

Figure A.3: Recent stock assessment estimates of Pacific hake (age 3+) biomass

For input to this model, assessing the correct proportion of the total hake biomass in the NCC, as opposed to that portion of the stock which migrate to the shelf waters off of Vancouver Island and the proportion that remains south of Cape Mendocino, is especially important. It has long been known that there is a strong latitudinal gradient in size, with older, larger fish (generally females) migrating further north than younger, smaller fish (Bailey et al. 1982, Francis 1983). It has also been shown that higher water temperatures are strongly associated with an increase in the northern distribution of the population. Dorn (1995) estimated that during the 1993 and 1992 El Nino years that much greater proportions of the hake biomass were found north of the US/Canada border (approximately 32 and 35% respectively) whereas during cooler years such as

1989 and 1990 this percentage dropped to 13 to 15%. Similarly, Ware and McFarlane (1995) estimated that every 1°C increase above average sea surface temperature (SST) in British Columbia resulted in an additional 170,000 metric tons of hake distributed north of the U.S./Canada maritime border. This pattern was exacerbated in the extremely warm El Niño year of 1998, when hake traveled deep into the Northwest and many of the larger, older fish were found as far north as the Gulf of Alaska. By contrast, in the cold subarctic-water year of 2001 few hake ventured beyond even the California-Oregon border (Swartzman and Hickey 2003). According to Dorn's analysis, the average proportion of the stock migrating to Canadian waters is between 22.7 to 23.8%. Data on the fraction of the population that is likely to have remained south of Cape Mendocino is also poor. Triennial surveys suggest a wide range of relative abundance (and total abundance for that matter) ranging from 4% of the surveyed biomass in the Monterey statistical area in 1992 to 76% in 1980. Most values are near 25% (which may include a large proportion of juveniles), and a fair estimate might be that 10% of the (adult) summer biomass is south of the NCC.

As discussed in Chapter 2, there are several possible means of accounting for migrations and other varying spatial patterns in the basic ecopath model, all of which can lead to unrealistic projections in the dynamic model (Aydin et al. 2003). Ecopath includes opportunities to explicitly account for migration rates, there is the option of "importing" a portion of the diet of migrants, or biomass (or P/B and Q/B) can be scaled back to account for the fraction of a year that the population is found outside of the modeled region (Christensen and Pauly 2000, Aydin et al. 2003). All of these were experimented with during various stages of modeling the NCC, and all give similar results for the static (mass balance) model. The latter method (scaling biomass relative to the amount of time spent outside of a system) is the final method chosen, based on observations of model behavior using all three methods, and the recommendation of Aydin et al. (2003). Consequently, it is estimated that 75% of the summer hake biomass is found in the region we consider the NCC, and (based on Francis 1982)[9] that 2/3rds of hake consumption and production occurs in the summer (April-October) foraging habitat. Thus, we will scale back 75% of the estimated biomass by 1/3rd, and estimate that 50% of the total hake biomass is present in the NCC "year-round."

The P/B ratio was estimated to be the natural mortality rate (0.23) in the 1960s model as this period was prior to fisheries targeting hake, and no obvious trends in production are known. For the 1990s model, P/B was estimated using stock assessment weight and numbers at age (see discussion in Chapter 2), which resulted in a value representing declining abundance. During this same period, the average weight at age of hake began

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[9] Using month-specific size at age data from the fishery, he also showed that hake of a given age typically gain 11 to 30% of their body weight in the summer (April-October) feeding period, and lose a minimum of 5 to 10% of their body weight during the November-March spawning season; a time at which feeding is inferred to be substantially reduced. Thus it follows both that most hake feeding occurs in the north during the summer, and that a significant proportion of the energy gained by hake in the NCC is exported out of this system.

to decline substantially, such that a twelve-year old fish which weighed (on average) over a kilogram in the late 70s and early 80s weighed barely 800 grams by the late 1980s and less than 700 grams by the early 1990s. However it is unclear whether the declining size at age is related to environmental factors, from density-dependent effects, some combination of the two, or other factors entirely. For estimating Q/B several options exist. Tanasichuck et al. (1991) estimate daily consumption rates for hake feeding off La Parouse bank in the summer as ~1.6% of body weight per day, the equivelent of 2.92 for a hake feeding at that rate for six months of summer, although this likely represented close to maximum feeding rates. Francis (1982) built a trophodynamic model for hake from which he estimated a range of summer consumption rates; 1.094% body weight/day (bwd) for age 2 fish, 0.939% bwd for age 4 fish, 0.796% bwd for age 6 fish and 0.713% bwd for age 8 fish. Finally, the Essington et al. (2002) method described in Chapter 2 (based on over 17,000 size at age samples) gave an estimated consumption rate of 2.43. Although this rate was sensitive to the age structure as well as various combinations of year-specific size at age data, it is also central to the distribution of other alternative rates, and is used here.

Because of early interest in interactions between hake and other commercially important species (notably pink shrimp) a great deal of food habits data is available for Pacific hake off of the west coast over the last 40 years (Gotshall 1967, Alton and Nelson 1970, Livingston 1983, Rexstad and Pikitch 1986, Brodeur et al. 1987, Buckley and Livingston 1997, Buckley et al. 1999, Tanasichuk et al. 1991, Mackas et al. 1997, Tanasichuk 1999). In all of these studies, it is widely accepted that younger, smaller hake feed primarily on euphausiids and shrimps, switching to an increasing proportion of herring, anchovies and other fishes (as well as other hake) as they reach 45-55 cm length (Figure A.4). Furthermore, many of these studies describe a pronounced change in diet composition with season, with fish replacing euphausiids as most frequently occurring prey items in late summer and fall.

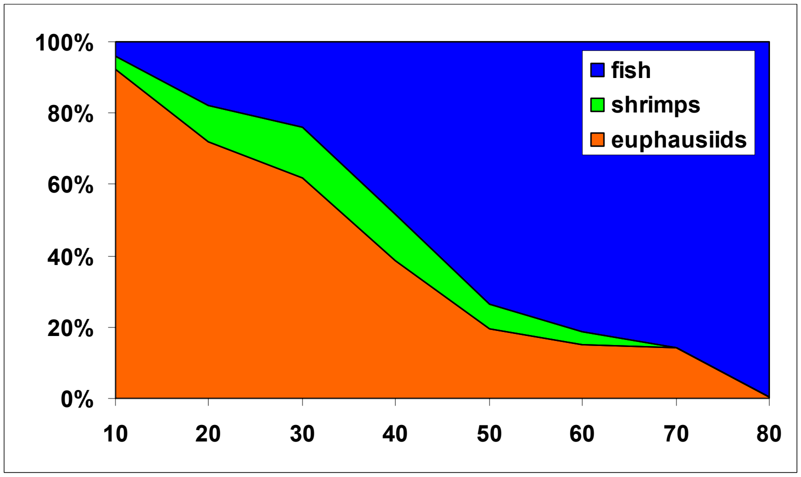

Figure A.4: Change in prey composition with size for Pacific hake

As even small changes in the percentage of an organism in hake diet can dramatically affect model balance and behavior, significant efforts were made to tune hake diet parameters carefully. The NOAA food habits database contains over 8000 records of hake stomach contents north of Cape Mendocino (and another 2700 south of Mendocino), but less than 1000 were taken prior to the late 1980s. Consequently, aggregating these results may disproportionately represent recent (possibly anomalous) years, and perhaps seasons (most 1990s samples were collected during fall slope surveys). For example, herring comprised 69% by volume of all the NOAA food habits database forage fish (north of 40.5°), sardine 8%, anchovy 3%, osmerids less than 5% and unidentified clupeids another 5%. However northern anchovy were the most abundant forage fish in 1967, and both anchovy and eulachon were the most important forage fish in the early 1980s (Livingston 1983, Brodeur et al. 1987). The most significant differences over time are with regard to cannibalism, (as also discussed in Chapter 3, with regard to Ecosim estimates of prey switching). Prior to the late 1980s, food habit studies reported little or no cannibalism, yet AFSC food habits data collected since 1988 suggests that hake represent nearly 30% (by volume) of hake prey, including up to 70% in 1997 and 1999. What is especially interesting is that this cannibalism occurred amongst all size classes; with 20 to 30 cm hake were feeding on 2 to 15 cm hake and several 60 to 70+ cm hake feeding on hake as large as 45 cm (Figure A.5). All of these factors complicate any ability to clearly delineate the diet composition of hake in the NCC at any given period of time.[10]

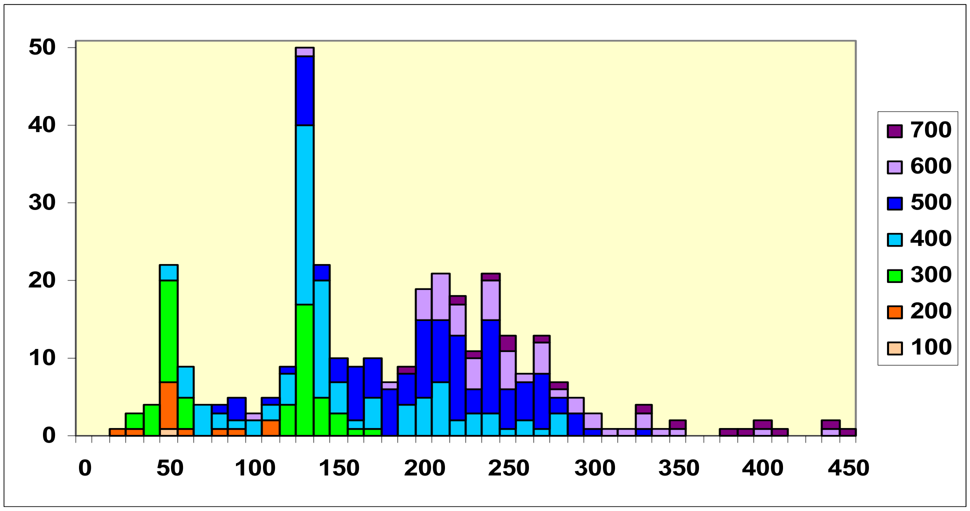

Figure A.5: Frequency distribution of size classes (in mm) of hake as prey (x axis) and the size of hake (in mm, legend) as predators

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[10] Although juveniles are not explicitly included in this model, as they are generally found off of southern and central California, food habits are available from Grover et al. (2002) who reported on juvenile hake (typically between 2 and 10 cm standard length) collected in midwater trawls between 1995 and 1999. Like adult hake, there was a clear shift in diet from primarily copepods (and some larval euphausiids) at smaller sizes (10 to 30 mm) to primarily euphausiids at sizes greater than 40 mm standard length. Minor prey included amphipods, pelagic shrimps, larvaceans, pteropods and other zooplankton.

In order to distinguish between predation by hake on juveniles and adults of prey species, we also estimated the number, weight and length distributions of flatfish and rockfish preyed on by hake (Figure A.6). Over all of these samples, there were 96 instances of predation on all flatfish species, shown in the top panel, which made up 2.29% of the total hake diet by weight. Predation occurred from all hake size classes over 20cm (legend refers to the size class of the hake as a predator), but was proportionately greater with larger size hake. Most of the prey appeared to be juveniles, as suggested by the size distribution of the prey relative to the size of the predators. Prey identified to species included arrowtooth flounder, dover sole, rex sole, rock sole, slender sole, and sanddabs; the latter two were those most commonly identified to species. However the vast number of prey were simply listed as unidentified *Pleuronectoidai*, so some predation on other species is both possible and likely. Clearly however, most predation is on the small flatfish assemblage, which includes sanddabs, slender sole, and rock sole. For predation on *Sebastes* rockfish (bottom panel), the total contribution to the diet was 0.2% over all time periods, and the size frequency of those prey items is limited to fish smaller than 17 cm, clearly juveniles, and likely including only pelagic-stage juveniles. None of the 58 Sprey items were identified beyond the genus level. For *Sebastolobus* rockfish, six instances of predation were noted (3 each on short and longspine) which comprised 0.07% of the total weight of all prey items; all were of juveniles between 6 and 11 cm.

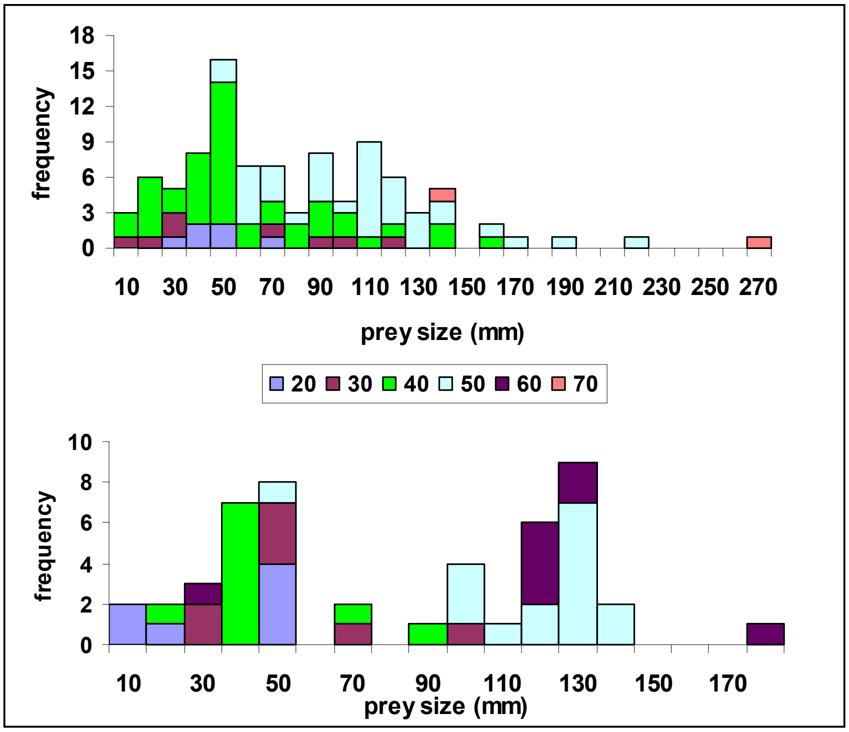

Figure A.6: Frequency distribution of size classes of flatfish (all species, top panel) and rockfish (all *Sebastes* and *Sebastolobus* species) as hake prey

Table A.1 shows the final prey habits used for the model. A further breakdown for some of these groups is necessary; epibenthic fauna is 0.7% benthic shrimps and 0.3% epifauna; “other fish” is 0.5% benthic fishes, 1% sardine, and 0.1% mackerel; flatfish is 2% small flatfish, 0.1% rex sole, and 0.1% juvenile dover sole; rockfish is split amongst all juveniles (including thornyheads). Finally, trace amounts (less than 1/20th of 1%) of other prey were not included as the resolution of the model makes it difficult to account for such minor proportions; including amphipods, carnivorous zooplankton, infauna, jellies, dungeness crab larvae and unidentified salmoniform fishes (unsure whether this was smelt or smolt). Clearly the wide range of prey that occur in hake stomachs indicate both that hake has clear food preferences and shifts in the same with size, yet additionally hake can be generalist predators of opportunity and prey on a wide range of food items given the opportunity (or the lack of preferred prey).

Table A.1: Summary of key hake food habits from
various sources and final model estimates

		All NOAA food habits		Alton	Rextad	Brodeur
	model	north of 40.5	coastwide	1965-66	1983	81-84
euphausiids	52.0	28.2	49.2	55	56	69
pelagic shrimps	2.8	1.4	7.6	4	0.6	
pandalid shrimps	2.0	1.8	1.0	5.7	1.3	
cephalopods	0.5	1.0	4.3	trace		
epibenthic fauna	1.0	1.0	0.2	trace	11.9	trace
forage fishes	34.0	45.1	13.2	35	36	15
flatfish	2.3	3.2	1.7		5	trace
rockfish	0.2	0.2	0.5			trace
mesopelagics	1.6	2.1	6.2		0.1	trace
hake	2.0	8.4	15.3			
other fish	1.6	7.4	0.6	trace	trace	13

A.6 Roundfish and Elasmobranchs

Lingcod

An important commercial and recreational species for well over 100 years, Lingcod (*Ophiodon elongates*) biomass estimates and catches were taken from the most recent assessment (Jagielo et al 2000). They used a split stock model to assess lingcod separately north and south of Cape Blanco, a problem considering that the boundary for this model is Cape Mendocino. This discrepancy was accounted for by using the entire northern stock with the percentage of the biomass estimated in the Eureka area (in contrast to all Eureka, Monterey and Conception areas) suggested by triennial survey data (28.9%) and the estimated commercial landings of the southern stock north of Mendocino based on Pacfin data (32.9%). The assessment time series begin in the year 1973, but given a very long history of exploitation a "known-biomass" surplus production model (MacCall 2002) was fit to the assessment values with historical landings (Lynde 1986) to hindcast biomass levels in the late 1950s and early 1960s (Figure A.10). Estimates of P/B and Q/B were derived based on Essington et al. (2001) with length-age data from the triennial survey and numbers at age data from the northern stock assessment, P/B was estimated to be 0.3 and Q/B 2.4 for the 1960s model.

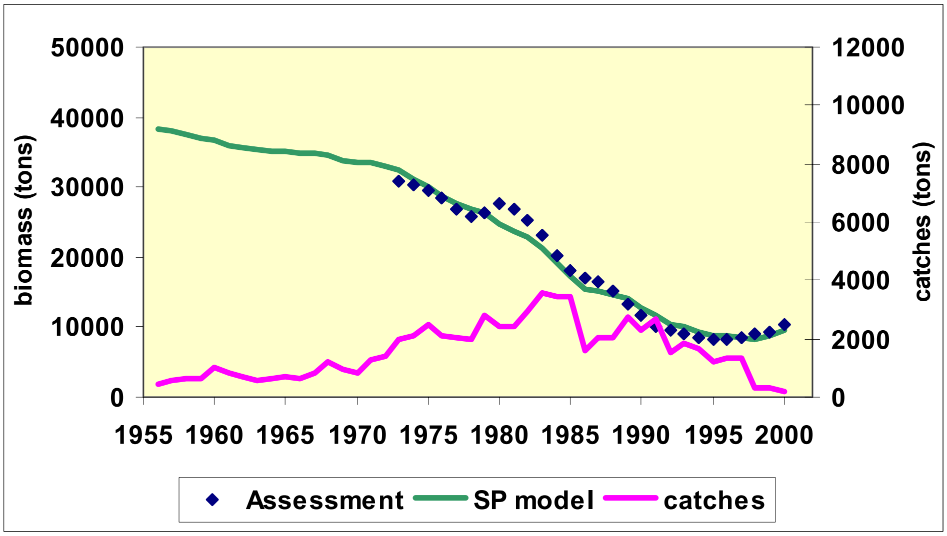

Figure A.7: Lingcod biomass and catches as reported in Jagielo et al. (2000) and the known-biomass surplus production method

Diet data for lingcod are problematic; lingcod are widely known to be voracious generalists, yet few published quantitative studies exist in the Northwest. Wilby (1937) reported that small juveniles off of British Colubia fed heavily on Neomysis and pandalid shrimp, with larger juveniles feeding primarily on young herring and other fishes. For adults, Wilby (1937) reported that "almost any live animals seem to be acceptable as food," he listed sand lance, herring, numerous flatfish species, dogfish, juvenile lingcod, gray cod (presumably Pacific cod), whiting, crabs, shrimps and squid as prey. Phillips (1959) reported that a 54 pound lingcod in Monterey, California had a 12 inch starry rockfish and an 18½ inch canary rockfish in its stomach, and noted that cannibalism could be one mechanism suppressing recruitment of smaller fish to reefs dominated by larger fish. Shaw et al. (1989) report that juvenile rockfish are amongst the most common food for California lingcod; other prey included squid, octopus, gastropods, crabs (Cancer sp.) and shrimp. Cass et al. (1990) summarized food habit studies from Canadian waters, which included primarily herring, flatfish, rockfish, sand lance, pollock, hake, Pacific cod, sablefish, tomcod and salmon as well as other fish and invertebrates described by earlier studies.

In the NCC, the best quantitative study is Steiner (1979) who evaluated food habits from 148 lingcod (over four seasons) caught at neritic reefs (typically 20 to 50 meters depth) off of the central Oregon coast. His work suggested a diet of 8.6% forage fish (mostly whitebait smelt, some anchovy and herring), 0.4% juvenile Sebastes, 3% adult Sebastes (not identified to species), 13.7% poachers, sculpins and other benthic fishes, 3.9% hexagrammid eggs (including eggs of other lingcods), 2.2% butter sole, 2.2% rex sole, 2.2% unidentified pleuronectids, 1.2% rock sole, 12.1% English sole, 1.2% sanddabs, 11.4% tomcod, 10.6% hake, 2.7% sablefish (presumably juveniles), 19.2% cephalopods (all octopus), 0.3% epibenthic fauna, and 0.3% pandalid shrimps. Finally, Wakefield (1984) described the diets of four lingcod caught off of Newport, Oregon as consisting entirely of pleuronectids (21% sanddabs, 4% unidentified pleuronectids) and unidentified fishes (75%). Diet is based on Steiner (1979), with consideration of other studies, as 10% forage fish, 10% hake, 25% benthic fishes, 15% cephalopods, 2.5% juvenile rockfish, 4.5% adult rockfish, 2.2% juvenile flatfish, 4% English sole, 10% small flatfish, 2% rex sole, 1% petrale sole, 1% dover sole, 0.5% juvenile roundfish, 5% epifauna 5% Dungeness crab, 1% benthic shrimps, 1% pandalid shrimps.

Sablefish

Sablefish (*Anoplopoma fimbria*) are one of the most important commercial species on the west coast, and are fished with bottom trawl, hook and line and pot gear, as well as being caught incidentally by midwater trawl gear and in shrimp trawl gear. Catches in the early 1960s averaged roughly 2800 tons coastwide, and increased to a peak of just over 25,000 tons (including estimates of discards) in 1979. Landings averaged over 10,000 tons through the 1980s and early 1990s, but have dropped in recent years to an average of 5500 tons between 1999 and 2003. Discards are high, largely due to trip limits in both open entry and limited access fisheries. Pikitch et al. (1988) estimated that total coastwide discard between 1985 and 1987 was as high as 30.7% of the total landed catch for the trawl fishery, and recent estimates have been even greater. Landings, biomass estimates, and estimates of discards are all taken directly from the most recent full stock assessment by Schirripa and Methot (2002). As the biomass estimates are for a coastwide stock, they are scaled to 67% of the coastwide biomass based on the observation that 75% of the shelf survey biomass and 59% of the slope survey biomass are estimated to be in the NCC. Additionally, 75% of the coastwide landings since 1981 have been north of Cape Mendocino, although historical catches may have been greater in southern areas.

Estimates of P/B and Q/B were generated based on Essington et al. (2001) and stock assessment numbers and weight at age data (Schirripa and Methot 2002). The estimated P/B for adults (age 1+) the 1960s model is 0.063 and for the 1990s model is 0.086. The estimated Q/B for adults varied both over time and by sex; values for the early 70s (used for the 1960s model) were 3.38 and 2.90, and for the 1990s were 3.41 and 2.93 for males and females respectively. The respective male:female population biomass ratios, (which were 38.7% male to 61.3% female in 1971, and 42.1% to 57.9% in 1990) were used to weight the adult Q/Bs, which resulted in mean values of 3.08 and 3.13 for the 60s and 90s model respectively. Interestingly, the resulting growth efficiencies for sablefish are very low, on the order of 2 to 3%. However there may yet be valid reason to question these values as applied to the bulk of the older population, as many of the older adults reside in low oxygen slope waters with limited food availability. Sullivan (1983) found both that sablefish seemed to be capable of surviving a wide range of oxygen and temperature conditions, as well as surviving long periods of starvation (up to 200 days at 8°C). Laboratory reared sablefish also had considerably lower transfer efficiencies (in contrast to other reared fish), on the order of 10%. Based on these observations, and the knowledge that a large fraction of the biomass exists in or near the oxygen minimum zone on the continental slope, we reduced Q/B rates to 1.95 for the 1960s, and 2.0 for the 1990s.

Food habits information for adults is available from Buckley (1999) who collected 731 stomachs between 1989 and 1992, and Laidig et al. (1997) who collected nearly 1900 stomachs between 1987 and 1992. Adult diet is extremely diverse, including a wide range of fishes, invertebrates, offal (presumably from factory trawlers processing hake, as cleanly severed hake heads are a common prey item) and even bird parts. Both studies found that *Sebastolobus* species, particularly *S. altivelis*, were the most important prey item, representing between 30 and 35% of the total prey volume. The data from Buckley et al. suggest a diet (by volume) of 21.5% longspine, 1.5% shortspine, 4.7% other rockfish, 5% benthic fishes, 12.7% hake, 6.1% forage fish (mostly herring), 2.4% juvenile sablefish, 0.6% dover sole, 0.4% rex sole, 1.3% other small flatfish, nearly 10% unidentified fishes, and trace amounts of juvenile salmon (or salmoniform) and mesopelagic fishes. Invertebrates included 10% epifauna (mostly unidentified benthic shrimps and crabs), 7.6% Tanner crabs, 7.3% euphausiids, 5.2% cephalopods, 2.2% infauna, 0.4% pandalid shrimps, 0.4% salps, 0.3% amphipods with trace amounts of copepods, Dungeness crabs and scyphozoans.

The data from Laidig et al. (1997 and pers. com) suggest that *Sebastolobus* species made up just over 26% of the diet by volume, another 26% was unidentified fishes, with 2.5% other rockfish (including several POP), 10% hake, 3.4% mesopelagics, 2.3% zoarcids (and other benthic fish), 0.5% forage fish, 0.5% flatfish, 0.28% dogfish, 0.15% macrourids, 10% cephalopods, 4% salps, 5.5% other gelatinous zooplankton, 2.5% echinoderms and other epibenthic fauna, 1% benthic shrimps, 0.5% pelagic shrimps, 0.1% pandalid shrimps, 0.6% infauna, 0.55% Tanner crabs, 1% euphausiids, 0.25% amphipods and 1% unidentified shrimp, crab and crustaceans. Both studies also demonstrated an ontogenetic diet shift from onecomposed largely of euphausiids, small fishes and other mid-water prey to a one composed largely of fishes (especially rockfish) and cephalopods. Given the highly confounding factors of changing metabolic rates with age (and depth distribution), no attempt was made in to accommodate changes in size and age distribution.

When early attempts to balance this model were made, the productivity of thornyheads was far lower than that necessary to balance the consumption of thornyheads as sablefish prey. To evaluate the potential for net feeding to have inflated these percentages, all prey items with a "recently ingested" digestion code were removed from the Buckley et al. (1999) data. This caused the total prey weight to drop from 9702 grams to 7667 grams, of the excluded data nearly 75% was *Sebastolobus*. The raw data from Laidig et al. (1997), who collected their data from trawl samples and found that *Sebastolobus* made up greater than 30% of prey (by volume), showed a similar result. Figure A.8 shows the size distribution (in mm length) of *S. altivelis* found as sablefish prey by Laidig (pers. com, note that size distributions from Buckley et al. were very similar). These data show predation over a broad range of size classes above the pelagic stage,[11] which would suggest that predation on midwater juveniles is low, but mortality for most size classes between settlement and full maturity by sablefish of all adult size classes is high. Figure A.12 shows the relative volume of prey assigned digestion codes for all (non-*Sebastolobus*) fishes that were identified to species, genus or family level contrasted to the same digestion codes for all invertebrate prey and all *Sebastolobus* species only. A digestion code of 1 suggests a recently ingested prey item, a code of 5 suggests bones fragments or other remnants of digestion. Over half (60%) of the *Sebastolobus* prey had a digestion code of 1, in sharp contrast to less than 10% of the total volume of all other fishes identified (not including unidentifiable fish) as sablefish prey.

Given that both of these independent studies showed an unusually high fraction of recently ingested *Sebastolobus* as sablefish prey, it is reasonable to assume that net feeding is a significant factor in assessing sablefish food habits. A reasonable estimate is that net feeding may account for approximately half of the thornyhead predation reported in earlier food habits studies. Why this bias seemed to occur in *Sebastolobus* only is unclear, as there did not appear to be evidence of significant biases towards net feeding of other prey species. The collection gear, trawl nets, may be a factor, as Caillet et al. (1988) collected sablefish samples from a variety of means (including traps, longlines, gillnets and trawls) and found that that rockfish made up a relatively small percentage of sablefish diet. However, Conway (1967) found high levels of predation on shortspine thornyheads from sablefish landed in Newport beach in the mid 1960s; his samples were collected from dory fishermen using setlines from which net feeding would not be expected. McFarlane and Beamish (1983) found that rockfish species made up approximately 60% and 40% of diets collected with sunken gillnets and bottom trawls respectively for sablefish off of British Columbia. Clearly rockfish,

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[11] *S. altivelis* are pelagic for the first 18 to 20 months of their life, settling at lengths of 40 to 60 millimeters and reaching lengths of 130 millimeters (size at earliest maturity) after approximately 6 years, and 250 millimeters (close to the size of full maturity) after roughly 23 years.

particularly *Sebastolobus spp*., are extremely important prey to sablefish, and the interaction between sablefish and rockfish of many species should be expected to be considerable.

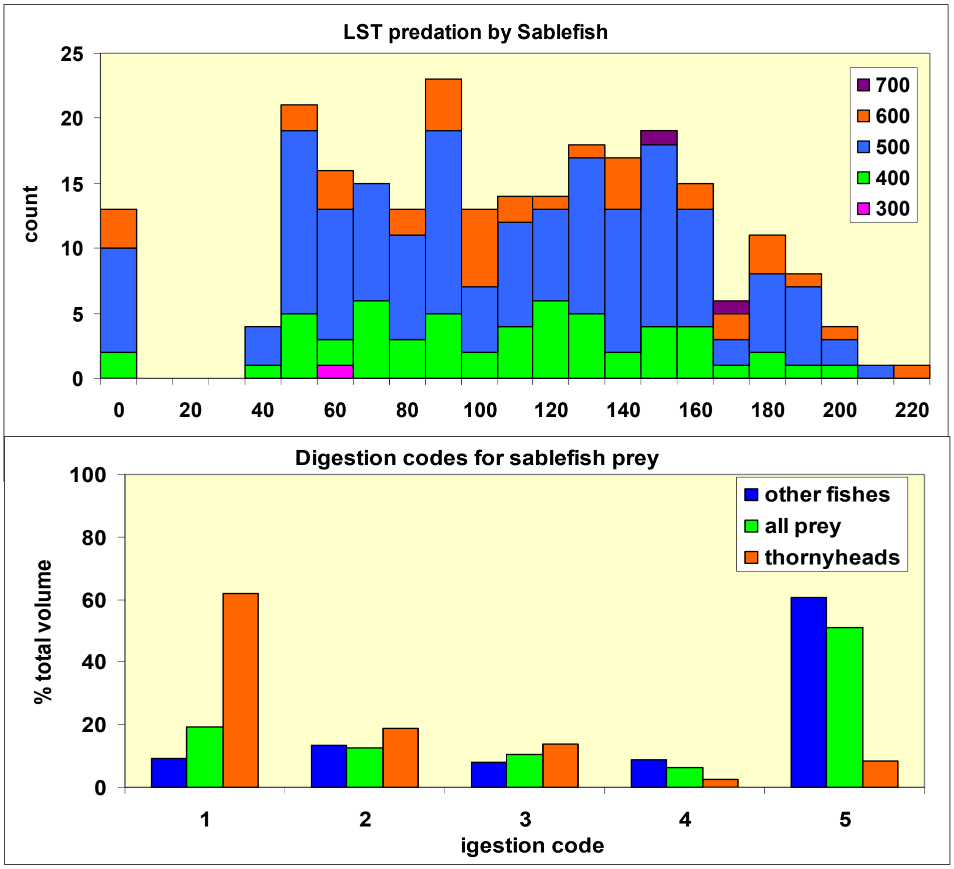

Figure A.8: Size of longspine thornyhead prey of sablefish (legend refers to size class of predators), and distribution of digestion codes

The filtered data were used to generate the final prey compositions, which were adjusted slightly to be consistent (aside from the high thornyhead predation) with the results of Laidig et al. (1997). There were many similarities between the two studies, as well as with Caillet et al. (1988); all studies suggested approximately 10% of sablefish diet was Pacific hake, and suggested similar levels of predation on mesopelagic and benthic fishes. Gelatinous zooplankton was also noted to be a substantial component of sablefish diet, both through personal observation of both Field and Buckley (pers. com) from collecting stomachs in the field (where gelatinous prey are either regurgitated, or the stomachs burst on contact, thus losing the sample for further analysis) and based on diets in the Gulf of Alaska. Thus, the final diet composition for sablefish is as follows; 4% gelatinous filter feeders, 5.5% gelatinous predators, 2% infauna, 4.4% epibenthic fauna, 5% cephalopods, 0.1% amphipods, 5% euphausiids, 0.1% macrozooplankton, 1.5% pandalid shrimps, 0.2% benthic shrimps, 0.2% Tanner crab, 0.1% Dungeness crab, 8% benthic fishes, 1% macrourids, 22% forage fishes, 0.6% juvenile salmon, 3% mesopelagic fishes, 12% Pacific hake, 2.4% juvenile roundfish, 0.1% lingcod, 5% *Sebastes* rockfish, 5% juvenile thornyheads, 2% juvenile rockfish, 0.5% shortspine thornyhead, 2% longspine thornyheads, 0.3% juvenile flatfish, 0.1% English sole, 1.9% small flatfish, 0.2% rex sole, 0.1% dover sole and 10% fisheries offal and detritus.

Macrourids

Grenadiers (family *Macrouridae*) include several relatively abundant deepwater species caught incidentally in deepwater trawls. Historical landings are minor, particularly as bottom trawling effort beyond the shelf break has been modest until fairly recently. Landings in the 1980s averaged roughly 90 tons per year, but increased to an average of nearly 500 tons per year in the early 1990s, triggered in part by increased demand in overseas markets. Over the last five years, landings have dropped from those relatively high levels, and now average 170 tons per year. As effort has increased in deeper waters in recent years, this is likely a function of reduced market demand and increased discarding at sea. According to data collected by Pikitch et al. (1988), macrourids made up only 0.4% of the total catch (by volume) in deepwater strategy tows greater than 200 meters, but made up 4.9% of the total catch (by volume) of deepwater strategy tows deeper than 400 meters.

Estimates of the abundance of macrourids, uncommon in waters shallower than 550 meters and most abundant in waters deeper than 900 meters, are available from the slope surveys done through the 1990s. These surveys consistently estimate a biomass on the order of 32,500 tons (ranging from 29,000 to 36,000 with no evidence of trends). The most frequently encountered species are the giant grenedier (*Albatrossia pectoralis*) which make up 51% of the biomass and Pacific grenadier (*Coryphaenoides acrolepis*) which make up 41%. Less abundant species include Popeye grenadier (*C. cinereus*), Smooth grenadier (*Nezumia liolepis*) and California grenadier (*N. Stelgidolepis*). In the absence of evidence to the contrary, we have assumed a survey catchability of 1 from slope survey estimates. Drazen (2002) constructed energy budgets and feeding rates for the Pacific grenadier which suggested that daily rations declined from 0.31% to 0.07% body weight per day with increasing length (which would translate into an annual Q/B between 1.13 and 0.25). As grenadiers are motile (rather than ambush) predators, we will justify using a higher rate, and estimate Q/B of 1 per year, (given the lower rate applied to thornyheads). Age estimates are not readily available for the two most dominant species, but Hoff et al. (2000) suggest relatively rapid growth rates and low maximum ages (9 for smooth grenadiers and 13 for California grenadiers). We will use the current P/B default value for the GOA and EBS models of 0.2.

Pearcy and Ambler (1974) reported that *Coryphaenoides* species on the abyssal plains off of the west coast fed primarily on cephalopods (as much as 67% of the diet of *C.*

acrolepis and up to 54% of the diets of other species), shrimp and other decapods (nearly 10% in *C. acrolepis* and up to 50% in other species), holothuroids (~7.6%), trace amounts of euphausiids and polychaetes, and unidentified fish remains (~12%). Buckley et al. (1999) reported on stomach contents of 89 *A. pectoralis* (60 of which had empty stomachs), and 40 *C. acrolepis*, (7 of which had empty stomachs). *A. pectoralis* fed primarily on mysid shrimp (37%) and other shrimps (30%), cephalopods (7.4%), brittle stars (0.3%), mesopelagics (bathylagids, 7.6%) and other unidentified fishes (17%). *C. acrolepis* fed primarily on cephalopods (29%), other epifauna (19.5%), pelagic shrimp (Seregestes sp., 8.2%), amphipods (1.2%), infauna (primarily polychaetes, 8.2%), Tanner crab (2.1%), euphausiids (0.3%), and 19% unidentified fish remains. Unidentified fish remains and organic debris made up substantial fractions of both diets, and may represent detritus or offal as grenadiers are notorious as scavengers of sunken carcasses. Drazen et al. (2001) reported on the food habits of 440 *C. acrolepis* and 304 *A. pectoralis* with non-empty stomachs sampled by size classes taken all along the entire west coast in 1997. They described substantial ontogenetic shifts in diet composition as generally developing from epifauna (microcrustaceans and polychaetes) to a diet dominated by fish (particularly hake) and squid (especially gonatid squid) at sizes greater than ~20 centimeters. Larger individuals had an increasingly greater percentage of scavenged material in their diets as well. Finally, Hoff et al. (2000) reported diets of *N. liolepis* and *N. Stelgidolepis* and found that these species fed primarily on amphipods (9 to 18%), benthic shrimps (20-30%), infauna (4 to 8%), other crustacean epifauna (20 to 30%), and unidentified organic material (10-14%). There was some change in diet observed with predator size for smooth grenadiers. As detailed age or size compositions of these populations are unavailable, the model inputs are a rather gross estimation of diet based on these detailed studies; 10% epibenthic fauna, 15% benthic shrimps, 5% amphipods, 10% infauna, 1% pandalid shrimps, 2% Tanner crabs, 5% mesopelagics, 5% hake, 5% benthic fishes, 30% cephalopods and 10% benthic detritus and offal.

Skates

Skates are commonly found throughout the NCC, and have become an increasingly important element of the groundfish fishery. Landings in the NCC averaged slightly over 100 tons through the 1980s, but increased rapidly in the mid 1990s and over the last five years (1999-2003) have averaged just over 1240 tons per year. Nearly all are from trawl gear, with very minor (average less than 10 tons per year) landings from longline and shrimp gear. Early landings off of Oregon and Washington varied substantially, ranging from several to several hundred tons per year from the 1940s through the 1960s (although most Washington skates were taken in Puget Sound fisheries). Skates have been a modestly important part of the trawl fishery off California since the 1920s, with annual landings ranging from 23 to 290 tons per year since 1916 (Martin and Zorzi 1993). Although there have been no obvious trends, Martin and Zorzi suggest that landings are probably affected by the effort and success of the target fisheries in which they occur as bycatch. Both Martin and Zorzi (1993) and Roedel and Ripley (1950) described California landings as being dominated by big skates (*Raja binoculata*), longnose skates (*R. rhina*) and California skates (*R. inornata*). Gaichas et al. (2003) observed that *R. rhina* and *R. binoculata* were also the most commonly incidentally caught skates in Gulf of Alaska fisheries, with the latter the most commonly landed species in directed fisheries.

Skates have frequently been caught incidentally in trawl fisheries for flatfish, rockfish and shrimp; raw data from bycatch studies of the Oregon trawl fishery in the mid 1980s (Pikitch et al. 1988 and unpublished data) showed that roughly 5.9 tons of skate are caught for every 100 tons of groundfish landed (rates were 23.5% for nearshore flatfish tows, 4.4% for deepwater complex tows, and 0.5% for bottom rockfish tows; this excluded midwater tows for hake and rockfish in which skate catches were extremely low). Figure A.19 shows the percentage of skate in the total catch (both retained and discarded) by starting depth strata for all bottom-trawl tows (excluding shrimp) observed by Pikitch et al., in which it is clear that the bulk of the skate catch is in the shallow strata. For tows between 10 and 50 meters, skates regularly comprise between 10 and 20% of the total catch by volume, in deeper waters the volume is considerably lower. Over 40% of all skates caught were in less than 55 meters depth. Figure 1.2 shows the species composition of all skates caught in the Pikitch study, illustrating that most of the skates caught in nearshore waters were big skate (*R. binoculata*), while most of those caught in deeper waters were longnose skate (*R. rhina*).Interestingly, the shrimp trawl trips observed in this study suggested fairly low bycatch rates (0.3% of the total landed catch), as did both earlier and later studies of bycatch in the shrimp fishery. (Morgan and Gates 1961, Hannah et al. 1996).

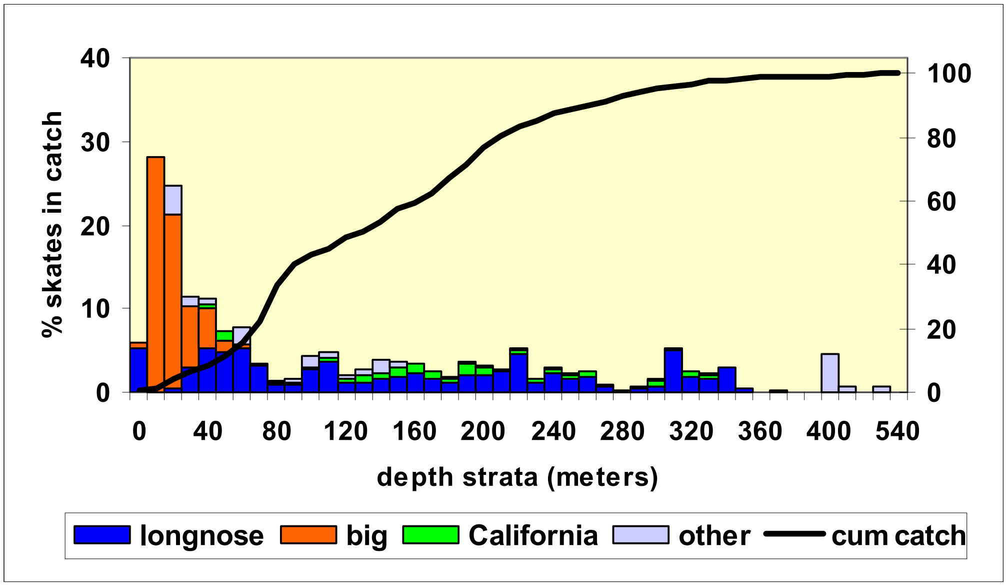

Figure A.9: Percentage of skates (by species) in catches, and cumulative total catches (all species, strategies) from the Pikitch bycatch study.

Overall, the Pikitch study estimated that only 3% of skates caught over the period of this study were retained. By contrast, the Oregon Enhanced Data Collection (OEDC) study of discards between 1995 and 1999 found that over half (55%) of skates caught incidentally in groundfish trawls were retained (Methot et al. 1999). This strongly suggests that the dramatic increase in landings over this period reflects increased retention rather than any targeted effort. Whether discarded skates have high or low survival rates is uncertain. Currently the NPFMC skate assessment (Gaichas et al. 2003) assumes a 100% mortality rate, although the authors acknowledge that some skates may survive depending upon catch handling practices. Roedel and Ripley (1950) suggested high survival rates, such that fishing might actually benefit skates, observing that "skates, like weeds, are very hearty and apparently thrive when returned to the water unharmed." Clearly many factors would affect possible survival rates, and no studies seem to have evaluated survival rates in the Northeast Pacific.

Data from the triennial shelf and irregular slope surveys suggest that the most abundant species in shelf waters seem to be the big skate (*Raja. binoculata*) and longnose skate (*R. rhina*); the latter is common in waters as deep as 700 meters. The California skate (*R. inornata*) and the Pacific electric ray (*Torpedo californica*) are less abundant yet common, and several other species are uncommon. In waters beyond the shelf break, several *Bathyraja* species are abundant (in addition to *R. rhina*), particularly the black skate (*B. trachura*) and the Bering skate (*B. interrupta*). The former tends to be more abundant in slope waters at depths greater than 900 meters, the latter in shelf waters between depths of 55 and 550 meters. Shelf survey estimates (55 and 366 meters) between 1977 and 2001 have averaged roughly 3200 tons since 1977, and these survey data do suggest an increasing trend over time (Figure 1.1).[12] Slope survey estimates (pooled into "effective" survey years) from the 1990s suggest an average biomass of 13,000 tons, with no apparent trend (over half of which is *R. rhina*, the rest predominately *Bathyraja* species). Interestingly, the slope surveys estimate a much greater biomass of R. rhina in the 180-366 meter strata than the shelf surveys do for the 1990s, a feature shared with dogfish (*Squalus acanthinus*) but not, apparently, with dover sole and many other major groundfish species. This may be associated with seasonal migrations to deeper water, perhaps as shallow waters warm or food becomes less abundant.

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[12] The shelf survey biomass estimates would suggest an upward trajectory, there is also some evidence that the average size of two of the more significant commercial species is declining. Although weight, length and sex information has not been collected on past surveys, counts and total weights have, and these data suggest that the average weight of *R. rhina* on shelf surveys has declined from 5.3 to 2.5 kg/skate between 1977 and 2001. Slope survey data show similar trends for both *R. rhina* and for several *Bathyraja* species. Taken in consideration with possible increase in biomass, this observation could simply reflect population expansion, however considering the vulnerability of skates and other elasmobranches, particularly species of larger size and with greater ages at maturation (such as *R. rhina* and *R. binoculata*), this could represent a troubling trend.

State groundfish surveys in the early 1970s (Demory et al. 1976, Barss 1976) included nearshore waters, and suggest higher biomass estimates of 17,000 and 13,000 tons off of the Oregon and Washington coast respectively for waters between 0 to 400 fathoms. Based strictly on their estimates of the trawlable area surveyed, this represents an estimated density of 0.87 and 1.05 tons per square kilometer respectively. These estimates are very similar to the densities estimated by AFSC slope surveys, which were 1.10 ton/km^2 for the 184-366 meter strata and 0.61 ton/km^2 for the 366-550 meter strata (the triennial shelf survey had a much smaller density, of 0.10 tons/km^2 for the 55-183 meter strata and 0.09 tons/km^2 for the 184-366 strata). Interestingly, the state surveys were also done in fall (early September to early October), consequently it could be that there are inshore/offshore movements in summer, or larger scale movements of skates in the fall relative to summer, such that the density of skates in shelf waters is higher in fall. In the absence of any estimates of nearshore skate abundance, and in recognition of the observation that the greatest skate bycatch is in the nearshore flatfish fishery in depths less than 50 meters, a point estimate for skate biomass will be made for the 1990s based on the average slope survey biomass for depths between 184 and 1280 meters (12,930 tons), the average shelf survey biomass between 1989 and 1998 for depths between 55 and 183 meters (1520 tons), and the average skate density (0.96 tons/km2) from the Oregon and Washington state surveys conducted in the early 1970s (14,990 tons). This would suggest a mean 1990s biomass of 29,440 tons, or 0.421 tons/km^2, although this estimate is obviously very uncertain. In the absence of any relevant information from the 1960s, the same estimate is used in the 1960s model.

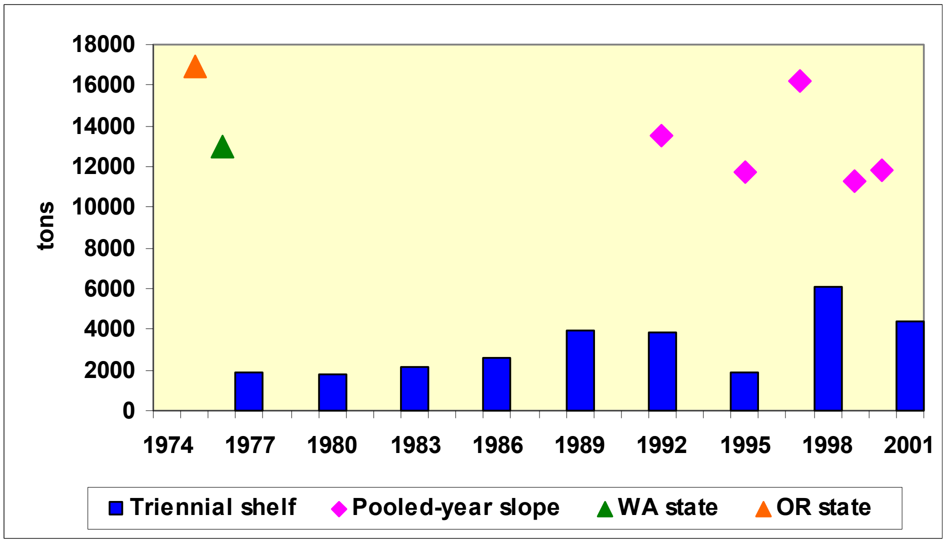

Figure A.10: Total skate biomass estimates from shelf, slope and early state surveys

Although skates are not explicitly managed by the Pacific Council, the three principle *Raja* species (*R. rhina*, *R. binoculata* and *R. inornata*) are included in the groundfish FMP. If we were to consider a “data-poor” assessment of skates, based solely on the information here, we could do so based on the NPFMC tier system. In the NPFMC system, skates are assessed as a tier 5 species, in which abundance from surveys and estimates of natural mortality are used to estimate target and limit fishing mortality rates (Gaichas et al. 2003). For tier 5 species (or assemblages) overfishing is defined as F=M, and the acceptable biological catch (ABC) is defined as F<=0.75 M, where F is estimated by both landings and estimates of bycatch. In the NCC, skate landings have been on the order of 1000 tons per year over the past decade, and were 1220 tons in 2003. Most recent bycatch information is unavailable, but if these landings reflect a roughly 50% retention rate (based on Methot et al. 2000), than the total catches are likely to be roughly twice that, or 2400 tons. Estimates of skate biomass over the 1990s based on shelf and slope surveys (~15,000 tons), and potentially optimistic estimates of inshore abundance (~15,000 tons, as described above) are on the order of 30,000 tons. Assuming an M of 0.1, based on Frisk et al. (2001) and Gaichas et al. (2003), the allowable catch by the NPFMC standards would be approximately 2250 tons, and the overfishing limit 3000 tons.

Thus, even a modest evaluation of catches based on skate life history information and very poorly quantified information on bycatch would suggest that this resource could already be approaching the limits of sustainability. This is particularly true given the characterization by some of skates and other elasmobranches as being “equilibrium” type life history strategists with low intrinsic rates of population increase (King and McFarlane 2003), as well as widespread agreement that species (particularly elasmobranches) with either (or both) large size and late age for maturation should be managed conservatively (Winemiller and Rose 1992, Frisk et al. 2001). In the northeast Atlantic, larger skate species have experienced substantial declines (including the barndoor skate *Dipturus laevis*, the smooth skate *Malacoraja senta*, and the thorny skate *Amblyraja radiata*). Several smaller species seem to have been increasing over recent years (Sosebee 1998). Although a natural mortality rate of 0.1 is likely to be the most plausible (Frisk et al. 2001, Gaichas et al. 2003), we will assume that P/B in both models is likely to be higher as a function of a long history of exploitation in which F is probably close to, possibly greater than, M, and estimate a P/B of 0.2, and a Q/B of 2 for both periods. These estimates are also consistent with the estimates being used for the Bering Sea and Gulf of Alaska models (Aydin pers. com., Gaichas pers. com.).

There is very little food habits data for the NCC. Wakefield (1984) reported on the stomach contents of several *Raja* species caught in nearshore waters off of central Oregon in May, 1979. Of the 51 stomachs examined, 42 were from *R binoculata* in 9 to 22 meters depth and 9 from 73 meters depth were from *R. binoculata*, B*athyraja interrupta* and *R. rhina*. Benthic shrimp (almost exclusively crangonid species) were the most important prey; accounting for 4 to 85% of the total stomach contents by species and depth and roughly 40% by weight over all species and depths. Dungeness crab were important for *R. binoculata* at all depths, averaging approximately 20% of stomach contents by weight, but were not observed in the other two species. Other invertebrate prey included small amounts (roughly 1.5% total prey volume) of amphipods, mysids, gastropods, cephalopods, other crabs, and other benthic infauna and epifauna. Sanddabs (*Citharichthys spp*.) were amongst the most important fish prey, making up an average of more than 10% of all prey over all species and depths. Other species included rex sole (25% by volume for *R. rhina*, not noted in other species), butter sole (20% in *R. rhina*), English sole, other unidentified pleuronectids, as well as sandlance, poachers and sablefish (presumably juvenile) and a large fraction (16.5%) unidentified fish.

There is no known data for any of the *Bathyraja* species that make up a large fraction of deepwater biomass in the California Current, although some food habits data exists from the Bering Sea and the Gulf of Alaska. These suggest that Bering skate (*B. interrupta*) from the Bering Sea fed principally on pollock (nearly 50%), with substantial predation on a variety of flatfish (~10%), benthic shrimps (~10%, including pandalids), crabs (~13%, including primarily *Chionoecetes* spp.), amphipods (~6%) and other benthic fishes and invertebrates (ranging from polychaetes, Pacific cod, sandlance and discards). Orlov (1998) reported on diet studies of seven *Bathyraja* species benthic skates off of the Northern Kuril Islands and southeast Kamchatka penninsula. His work shows clear shifts from diets dominated by small invertebrates (primarily amphipods, polychaetes and other annelids, and shrimps, including pandalids) and fish (primarily sculpins) to larger invertebrates (crabs and cephalopods, including *Chionoecetes* sp.) and fish (atka mackerel, pollock, myctophids, grenediers and other mesopelagic and benthic fishes) with increasing size for most species. Based on these unpublished and published food habits for *Bathyraja* species elsewhere, we will include Tanner crabs, hake, benthic fishes and some others to the diets used here. The estimated diet compostion will consequently be 20% epifauna, 20% benthic shrimp, 3% amphipods, 3% infauna, 2% pandalid shrimp, 1% cephalopods, 5% Dungeness crab, 2.5% Tanner crab, 5% forage fish, 2% juvenile roundfish, 5% benthic fishes, 5% hake, 15% small flatfish, 5% juvenile flatfish, 3% rex sole, 2% English sole, 2% Dover sole, 0.5% petrale sole, and 1% arrowtooth flounder.

Spiny dogfish

The spiny dogfish (*Squalus acanthias*) ranges from Baja California to the Bering Sea and western Pacific, and can make up enormous schools at times. Brown cat sharks (*Apristurus brunneus*) and other Apristurus spp. were also included in this group. Dogfish been exploited for centuries throughout the west coast for their livers (more specifically, liver oil); and a commercial fishery for dogfish has existed since the 1870s (Roedel and Ripley 1950, Ketchen 1986). The coastwide (U.S. and Canada) fishery grew rapidly in the 1930s and 40s with coastwide landings peaking at over 50,000 tons in 1944. Washington and Oregon landings were nearly 40% of the total, with most of the remainder from British Columbia and modest landings in Alaska. Perhaps half of the nearly 100,000 tons landed in Washington between 1935 and 1955 was taken from Puget Sound, with the other half from the coastal fishery (Ketchen 1986), which would suggest that dogfish populations may have been depleted in the 1960s as both landings and demand declined. Although dogfish bycatch is at times substantial, landings in the NCC were relatively low through the 1980s, averaging almost 200 tons/year. Over the last decade, landings have increased substantially, peaking at over 1000 tons/year between 1992 and 1994, but dropping to an average of nearly 600 tons/year over the last five years. Most landings are from the trawl fishery, with an increasing fraction of landings coming from the hook and line fishery, and are likely to reflect increased retention, rather than actual targeting of the species. Despite the high historical value of dogfish, the species has been described as a "poster child" for trash fish, often accused of preying on commercially valuable salmon, herring and crab (McFarlane and King 2003).

In NCC the shelf surveys have estimated the spiny dogfish biomass between 55 and 360 meters as ranging from ~10,000 to 60,000 tons, with no clear trend. Slope surveys done in the 1990s suggest a significantly larger biomass, ranging from 68,500 to 159,000 tons, most of which was in the shallow (184-366) strata (Figure A.11). These data suggest no clear trend in dogfish abundance over time, although fall surveys off of the Oregon and Washington coast in the early 1970s (Demory et al. 1976, Barss 1976) provide fairly modest biomass estimates of 8200 and 7800 tons respectively, which might be consistent with ongoing population recovery following the high exploitation in the 1940s and 1950s. Data from recent triennial surveys might suggest a modest decline, although no trend is clear from the slope surveys. Seasonal patterns of migration almost certainly account for the major discrepancy between shelf and slope survey biomass estimates.

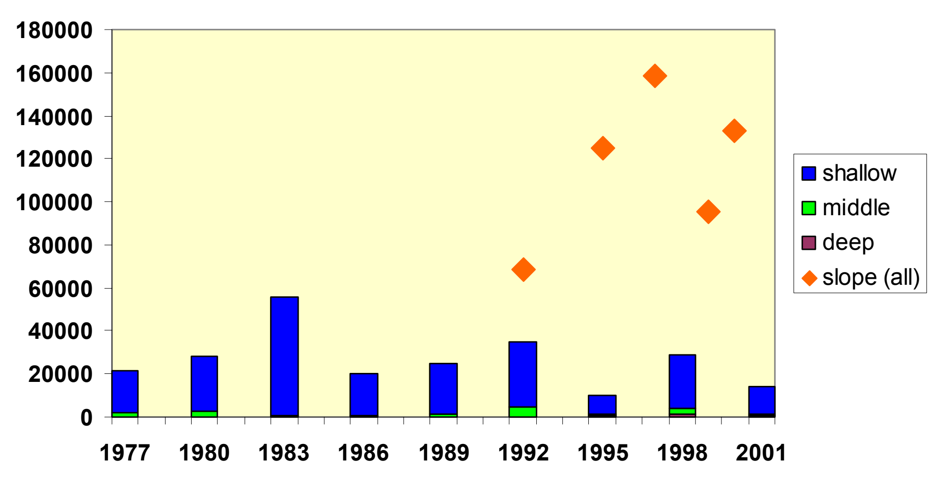

Figure A.11: Shelf and slope survey biomass estimates of dogfish in the NCC

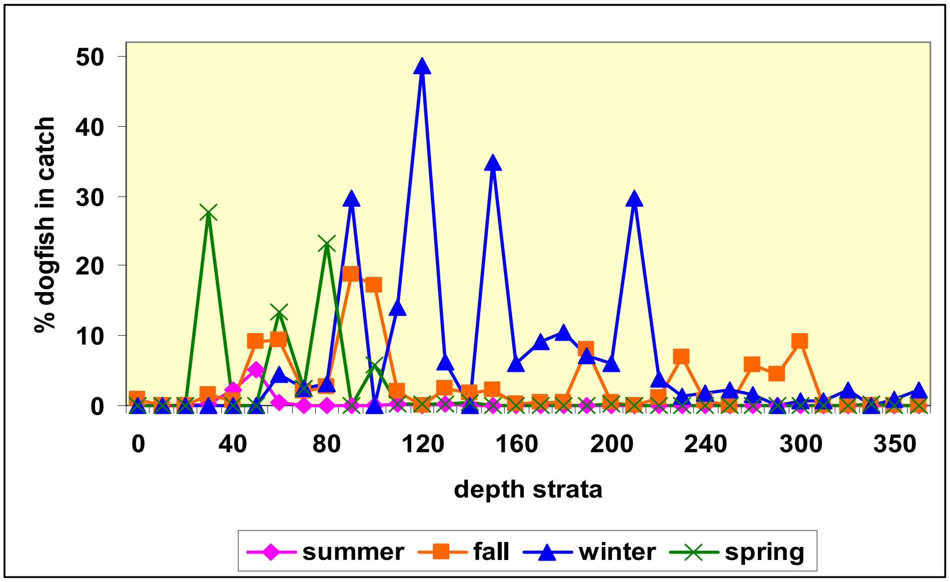

Figure A.12: Percentage of dogfish in commercial catches by depth strata and season

Several important tagging studies done in British Columbia demonstrated apparent seasonal patterns in movement and occasional lengthy migrations by some individuals (Ketchen 1986, McFarlane and King 2003). Fish tagged off of the southwest coast of Vancouver Island were regularly recovered in coastal Washington and Oregon waters; and the most recent study found that recoveries in U.S. waters were found to be substantially greater than early estimates when the data were standardized with relative dogfish catches (McFarlane and King 2003). Additionally, nearly 10% of the total recoveries including fish that traveled to California, Baja California, Alaska and Japan. With regard to the seasonality of migrations, the observations by Holland (1957), which are consistent with the recent results of McFarlane and King (2003), suggest that dogfish tend to migrate southward from the Vancouver Island and Washington coasts in fall and winter, and northward in spring and summer, generally over ranges of 400 to 800 kilometers. These observations are also consistent with the note by Roedel and Ripley (1950) who described the northern California dogfish fishery as especially important to the trawl fleet in winter (December-February) months. The raw data from the Pikitch et al. (1986) bycatch study in the Oregon trawl fishery suggests this pattern as well (Figure A.12). These data show that dogfish made up the greatest fraction of trawl catches, as much as 50% by volume, in winter months at depths ranging from 80 to just over 200 meters. They made up a considerable, but less dramatic, fraction of landings in spring and fall, when they tended to be caught more frequently in shallower (50 to 100 meter) waters, and dogfish were virtually absent from landings in the summer. Thus it would seem that the spring and summer biomass of dogfish in the NCC is low, and the fall and winter biomass high. As a starting estimate for the model, the averages of the summer shelf and the late-fall slope survey will be used for the 1990s, which suggest a total biomass of 70,000 tons, or 1 ton/km^2.

Although Wood et al. (1979) estimated natural mortality as 0.1, their history of fairly high exploitation during the 1940s would suggest a starting P/B greater than this, we will estimate 0.2. For Q/B estimates, Jones and Green (1977) estimate annual consumption rates ranging from 2.5 to 5 times adult biomass for dogfish along the British Columbia shelf, with younger, smaller dogfish consuming considerably more than adults.[13] We will use a value at the lower end of this range of 2.5, which gives a low, but plausible, growth efficiency of 0.075. For the NCC, early diet data are available from Bonham (1954), who evaluated 1100 dogfish stomachs along the Washington coast and Puget Sound (with the majority from Puget Sound). He found that ratfish, herring, flatfish, euphausiids, and crab were the most frequently encountered items from dogfish along the outer coast, with rockfish, other benthic fishes, and assorted benthic invertebrates also present. The most comprehensive study in the NCC was by Brodeur et al. (1987), who examined 175 dogfish stomachs between 1979 and 1984 along the Oregon coast, and found a wide range of prey, with unidentified fishes representing between 10 and 60% of the volume in any given year. Forage fish (herring and anchovy), Pacific hake, sanddabs, rex sole, english sole and unidentified pleuronectids were the most important prey items in most years; forage fish represented from 0 to 18% of total prey weight from year to year, hake represented 0 to 31% and flatfish represented 3.5 to 72% of (identified) prey weight. Lingcod were important in one year (5.6% by weight in 1982), other prey included cnidarians (*Velella velella* comprised nearly 50% of prey weight in 1981), cephalopods (1.1% in 1981, 0.3% in 1982), euphausiids (28.8% of weight in 1984, trace amounts other years), pandalid shrimp (0.3% in 1984) and other macrozooplankton (generally trace amounts). Based on these studies, diet was partitioned into 20% forage fishes, 20% hake, 10% small flatfish, 2% rex sole, 2% english sole, 1% dover sole, 0.5% petrale sole, 0.2% arrowtooth flounder, 2% juvenile flatfish, 1% juvenile rockfish, 0.1% shelf, slope, yellowtail, POP, widow and canary rockfish, 1% juvenile roundfish, 0.1% lingcod, 7% benthic fishes, 20% euphausiids, 0.1% pandalid shrimp, 2% Dungeness crab, 5% epifauna, 2% Dungeness crab, 0.5% cephalopods, and 5% gelatinous carnivores.

Coastal sharks

This group will include other large coastal sharks that occur in nearshore and shelf-break waters of the Pacific Northwest, including thresher sharks (*Alopias spp*), blue sharks (*Prionace glauca*), soupfin sharks (*Galeorhinus galeus*), salmon sharks (*Lamna ditropis*), basking sharks (*Cetorhinus maximus*), Pacific sleeper sharks (*Somniosus*

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[13] Diet data evaluated by Jones and Geen (>15,000 stomachs) for the BC shelf suggests that forage fish dominate dogfish diets (22% herring, 6% eulachon, also sandlance and anchovy), with euphausiids (14%), other plankton (10%), shrimp (8%), crab (7%), hake (7%), various flatfish (6%), cephalopods (5%) and gelatinous zooplankton (ctenophores and other jellies, ~3.5%) making up most of the rest. Minor prey items included ratfish, perch, rockfish, cod, polychaetes, eelpouts, sculpons, salmon and sablefish. They also demonstrated a clear ontogenetic shift in prey composition with age, and their estimates suggested that dogfish consumed on the order of five times the annual herring catch in British Columbia during the early 1970s.

pacificus), great white sharks (*Carcharodon carcharias*) and several others. The distribution of these sharks is variable; most commercially important species occur primarily in southern, offshore waters, although adult common thresher are described as being the seasonally abundant offshore of the 40 fathom isobath as far north as Cape Flattery (PFMC 2003). Historically, soupfin and other coastal sharks were also subjected to major fisheries along both the US west coast and in British Columbia (Bonham, 1949); their abundance is likely substantially less than historical levels, which may have been as high as 29,000 tons coastwide. Other large sharks, such as great whites, Pacific sleeper sharks, and basking sharks are known to be present or migratory to the NCC, but any meaningful representation of their role is hindered by a lack of data on abundance and life history characteristics. As the common thresher (*A. vulpinus*) and the soupfin shark represent those species of greatest historical and present abundance and commecial significance, this component of the model will be largely based on the pooled life history characteristics of these two species, with consideration of other species made where relevant.

Shark (and other elasmobranch) fisheries tend to be short lived, due to the rapidity in which fisheries are capitalized and the low productivity of most elasmobranch populations. Historical and recent shark fisheries on the west coast are no exception; fisheries for basking shark, soupfin shark, dogfish shark, angel shark and common thresher shark have all undergone dramatic increases in effort and landings followed by equally dramatic declines over the past century (Holts 1988, Ketchen 1986, see also Frisk et al. 2001). Soupfin sharks were taken in large quantities for their vitamin rich liver oil in the late 1930s and early 1940s when high demand drove what Ripley (1946) described as "a motley assortment of about 600 boats were avidly searching for soupfin up and down the coast." Catches in Washington and Oregon were on the order of 1500-2000 tons per year over most of this period, although much of this was from Puget Sound. Catches in California were on the order of 2000 to 3000 tons, with a modest (on the order of 20%) fraction taken from Eureka and Crescent City. Both declines in abundance and the development of synthetic vitamins during WW II were responsible for a decline in price, effort and landings in the mid 1940s, although soupfin have remained a small but significant element of both commercial and sport fisheries (landings have been on the order of 100 tons coastwide since the 1980s, although the vast majority are south of Cape Mendocino).

Common thresher (as well as pelagic and bigeye thresher) and other pelagic sharks became the targets of a significant drift-gillnet fishery (primarily targeting swordfish) that grew out of California in the 1970s and 1980s (Cailliet and Bedford 1983), and expanded to Washington and Oregon, where catches typically occur only in summer and fall months, in the late 1980s. Shark landings in the north have generally remained low, with sporatic landings of several dozen to as much as 100 tons per year in ports such as Crescent City and Ilwaco. These fisheries are currently managed under the PFMC Highly Migratory Species FMP (PFMC 2003), and the essential fish habitat (EFH) descriptions of observed shark catches in the NCC suggest that common thresher, and to a lesser extent blue shark, are the most frequently encountered species taken inside the 1000 fathom contour. Most of these catches (and most of the effort) appears to be concentrated offshore of the Columbia river, in depths of 100 to 1000 fathoms; by contrast bigeye and pelagic thresher, shortfin mako and blue sharks tend to be taken (with some exceptions) offshore of the 1000 fathom contour.

Given that perhaps tens of thousand of tons of soupfin doubtlessly occupied the NCC prior to exploitation, and several thousand tons of thresher (and other species) clearly occupy the NCC during the summer season, we will adopt a placeholder starting biomass value of 3500 tons (or 0.05 tons/km^2), acknowledging that this is little more than a starting guess. Age and growth of common thresher, shortfin mako and blue shark are also described in Cailliet and Bedford (1983), the natural mortality estimates used by the PFMC to estimate productivity are 0.234 for common thresher and 0.223 for blue sharks. No estimates are available for soupfin sharks, although Ebert (2002) found that females mature in about 11 years and provided an estimated maximum age of 60; considerably longer than the threshers maximum age of 19 (PFMC 2003). Cox et al. (2002) derived P/B estimates for blue and "brown" (silky and oceanic whitetip) sharks of 0.32 and 0.18, with corresponding Q/B estimates of 2.75 and 2.8 respectively. We will use the latter (lower) estimate as more likely to be consistent with the slower turnover rates for soupfin sharks.

A respectable amount of food habits information is available. Bonham (1954) reported on the food habits (by volume) of 200 soupfin sharks (75% of which were empty) landed between 1942 and 1943 along the Washington coast. Some 16% of the total prey by volume was Pacific sardine, followed by 14% salmon, 11% shad, 11% gadids (presumably largely hake), 8% Pacific cod, 6% ling cod, 6% rockfish, 5% anchovy, 5% halibut, 3% dogfish, 3% unidentified flatfish, 1% English sole, 1% rex sole, 1% sculpins, 9% unidentified fishes and trace amounts of crabs, snails, arrowtooth flounder and cephalopods. Similarly, Ripley (1946) reported that soupfin sharks off of California fed primarily on sardines (10-23% frequency of occurance by sex, M:F), midshipman (9-28% F:M), rockfish (5-9%, M:F), flatfish (6-12% M:F), squid (6% each), mackerel, hake, salmon, herring, halibut, skate, anchovy, barracuda, surf perch, sea-bass, sculpin, ratfish, flying fish, tuna and sheephead. Brodeur et al. (1987) examined the stomachs of 14 soupfin taken off of Oregon and southwest Washington in the early 1980s and found that prey were dominated by hake (>81% by volume) and shad (7%), with 10% unidentified fish and trace amounts of cnidarians (*velella vellela*), cephalopods, anchovies, sculpins and unidentified flatfish. From the same study (Brodeur et al. 1987), 14 blue sharks were found to also feed primarily on hake (53.9% by volume), as well as 10.4% anchovy, 2.9% herring, 8% sanddabs, 2.4% other flatfish, and small amounts of unidentified fish and squid. Finally, Preti et al. (2001) reported on the contents of 165 stomachs (107 of which contained food) of the common thresher shark sampled from the gill net fishery off of California and Oregon (primarily southern California) between 1998 and 1999. They found that stomach contents were dominated by anchovy (30.1% by volume), Pacific mackerel (24.7%), Pacific hake (9.2%) and

Pacific sardine (4%); other prey included Louvar (9.9% by volume, but comprised of 1 prey item), unidentified fishes (17.5%), jack mackerel (2.2%), market squid and other cephalopods (~0.1%) with trace amounts of grunion, croaker, sanddab, queenfish, rockfish, and pelagic red crab. We will estimate the diet of this component to be 25% hake, 25% forage fish 15% Pacific sardine (in the 1990s model, replaced by 5% sardine and an additional 10% forage fish in the 1960s model), 10% flatfish, 5% salmon, 5% rockfish, 2.5% mackerel, 5% cephalopods, 2.5% benthic fishes, 2.5% mesopelagic fishes, 1% dogfish, 1% skates and 0.5% lingcod.

Albacore tuna

Albacore tuna (*Thunnus alalunga*) are seasonal migrants to the NCC which are rarely found inshore of the shelf break. Variations in their distribution and relative abundance are indicated by the major latitudinal shifts in the location of US fishery effort; with relative abundance generally higer in the vicinity of the oceanic fronts and the 16° isotherm of the transition zone waters in the eastern North Pacific (Laurs and Lynn 1977). Consequently, despite the fact landings have been variable, yet substantial (up to 20,000 tons) off of Oregon and Washington, catches generally occur outside of the range of the NCC boundaries, between 50 and 2000 miles offshore (Laurs and Lynn 1977, PFMC 2003). Parrish (pers. com) suggests that albacore presence offshore of Oregon and Washington was likely considerably greater in the cool regime of the 1960s in contrast to the warm regime of the 1980s and 1990s. Catch records bear this out; Pacific Northwest landings averaged nearly 20,000 tons in the mid 1960s, dropping to less than 5000 tons in the early 1990s. Their role in the NCC is nearly impossible to quantify; consequently we will use a conservative estimate of 4000 tons present in late summer and early fall, scaling this back to just 1000 tons as an annual average, or 0.014 tons/km^2. Other biological parameters are borrowed from Cox et al. (2002), who estimated a P/B of 0.36 for large albacore and a Q/B of 7.3.

Albacore and the shark species in this assemblage feed on a variety of prey items, key among them being squid, forage fishes (especially saury), mackerel, mesopelagics and salmon. Early diet studies of albacore in British Columbia waters (Hart 1942) suggested that albacore will strick at “almost anything”, but that sardines were a key prey item off of the B.C. and Washington coasts when they were abundant; as were anchovy, herring, saury, myctophids, and cephalopods. Iverson (1971) described the feeding habits of albacore based on stomach contents analysis from fish landed in ports and caught between 15 and 150 miles of the coast in 1968 and 1969. For the region from Cape Mendocino to Cape Flattery, her analysis suggested that anchovies were the dominant prey item in 1968; providing some 71% of total prey, followed by sauries (20%), cephalopods (~6%, but a greater percentage frequency) and small crustaceans (~15%; principally seregestid shrimps). The following year samples were limited from this region, but suggested that seregestid shrimp were the most important prey item, followed by anchovies and two squid species. For the moment we will use for diet estimates 25% squid, 35% forage fish (in 90s model 10% of this will be sardines), 20% midwater fishes, 10% decapod shrimp, 8% mackerel and 2% rockfish.

A.7 Rockfish

Canary rockfish

The biomass of Canary rockfish (*S. Pinniger*) has declined tremendously over the past fifty years; from an estimate over 60,000 tons in the early 1960s to just over 5000 tons in recent years (Methot and Piner 2002). Biomass and catch estimates were taken directly from this assessment, with the biomass scaled to 87.5% of the assessment estimate to reflect the observation that 16% of the biomass (estimated by the triennial survey) and 8% of the landings (since 1981) have been south of Cape Mendocino. Length and age data from the triennial surveys, and numbers at age from Methot and Piner (2002) were used to estimate P/B and Q/B based on Essington et al. (2001), for a P/B of 0.113 and a Q/B of 1.66 in the 1990s and a P/B of 0.10 and Q/B of 1.66 in the 1960s.

Several sources of adult diet data are available. Brodeur and Pearcy (1984) describe the results of 368 stomachs sampled in spring and summer of 1980 as containing nearly 92% euphausiids by volume, with 0.6% pelagic shrimp, 0.4% pandalid shrimp, 0.1% mesopelagics, 0.4% sandlance and the remainder unidentified fish (and other) remains. An additional 60 stomachs sampled in 1986 are available in the NOAA food habits database, which suggested 48% euphausiids, 22% pandalid shrimp, 14.5% myctophids, 3.5% herring, and the remainder unidentified material. Finally, Lee (2002) evaluated the food habits of 104 Canary rockfish taken in different seasons between 1998 and 1999, and found 98.1% of the prey was euphausiids, which dominated prey over both years and all seasons, with approximately 0.4% pelagic shrimp, 0.4% pandalid shrimp, 0.2% unidentified gelatinous zooplankton, and trace amounts of amphipods, copepods, carnivorous zooplankton, bathylagids, and other unidentified fish. Clearly, canary tend to prefer euphausiids with other species being somewhat important at times; we will partition their diet into 92% euphausiids, 3% pandalid shrimp, 0.8% carnivorous zooplankton, 2% myctophids, 2% forage fish, 0.1% gelatinous zooplankton and 0.1% amphipods.

Yellowtail rockfish

Yellowtail rockfish (*Sebastes flavidus*) have been, and continue to be, one of the most important west coast groundfish species in terms of both biomass and landings; the species made up approximately 37% of landings between 1963 and 1971 (Lorz and Pearcy 1983), although that fraction dropped to less than 20% through the 80s and 90s as new fisheries developed. Recently, yellowtail have again been increasing in importance, in part as a result of their relatively healthy stock status and the poor status of many other *Sebastes* species. Tagart (1991) reviews evidence for stock differentiation in yellowtail rockfish that suggests a series of three stocks between Cape Mendocino and southern Vancouver Island, and stock assessments have been run both as a single coastwide stock and as a series of three separate stocks (Lai et al. 2003). Yellowtail rockfish in Canada are treated as two stocks, one shared jointly with the U.S. between southern Vancouver Island and northern Washington (consistent with the most northerly U.S. stock) and one that extends from central Vancouver Island to the Alaskan border. Yellowtail are not formally assessed south of Cape Mendocino, where landings have been modest over recent decades. Relative biomass data and catches were taken directly from the 2003 assessment (Lai et al. 2003). Length and age data from the triennial surveys, and numbers at age from the most recent assessment were used to estimate P/B and Q/B based on Essington et al. (2001). Adult P/B and Q/B were 0.146 and 1.7 for the 1990s, and 0.105 and 1.6 for the 1960s.

A large number of adult diet data are available. Pereyra et al. (1969) described an encounter with yellowtail rockfish off of Astoria Canyon in which prey consisted of over 75% myctophids, 13% pelagic shrimp and euphausiids, and 3% cephalopods (based on 22 samples). However the authors suggested that this occurrence may have represented either an opportunistic, or a site-specific feeding event, as they noted that yellowtail taken incidentally from the Pacific hake fishery fed primarily on euphausiids. Lorz and Pearcy (1983) examined stomachs of Yellowtail rockfish off of coastal Washington (as well as in Queen Charlotte Sound), and found that crustaceans comprised 93% by volume, with euphausiids representing the majority, trace numbers of pelagic and pandalid shrimps, and minor amounts of sandlance, herring, lampfish, cephalopods and gelatinous zooplankton. Brodeur and Pearcy (1984) described the stomach contents of 264 yellowtail rockfish collected from Oregon DFW and NMFS research surveys in 1980 and 1981. They found prey by volume to be 52.9% euphausiids, 0.9% amphipods, 1.4% pandalid shrimp, 0.9% pelagic shrimp, trace amounts of copepods, 12.9% cephalopods, 0.3% gelatinous predators (siphonophores and ctenophores), 9.7% herring and other forage fish, 5% myctophids, 0.3% juvenile Sebastes, 0.1% rex sole, and the rest unidentified remains. Livingston (pers. com.) also collected and analyzed 127 yellowtail rockfish stomachs in 1980; these suggested a diet of 39% euphausiids, 20% herring, 6% juvenile rockfish, 4% cephalopods, 1.7% pelagic shrimp, 0.3% pandalid shrimp, 3.7% benthic fishes, 1% epifauna, 0.8% jellies, 0.2% amphipods, and trace amounts of copepods, myctophids, small flatfish, and carnivorous zooplankton (with an additional 10% unidentified fish and 10% unidentified organic material). A smaller sample of 39 yellowtail rockfish from the 1986 shelf survey suggested a diet of 58% euphausiids, 22% herring, 7% pandalid shrimp, 6% myctophids, 5% other unidentified fishes and trace amounts of copepods and gelatinous zooplankton.

Finally, Lee (2002) evaluated 167 stomachs from fishing vessels during all seasons between 1998 and 1999, and an additional 360 stomachs from the 1998 triennial summer shelf survey. The seasonal study suggested a diet of 35.3% salps, 4.7% other gelatinous zooplankton, 27.9% euphausiids, approximately 10% slender sole and 5% rex sole (all from two of the six sampling periods), 5% juvenile hake, perhaps 1% sand lance approximately 2% each pandalid and pelagic shrimps, approximately 0.5% cephalopods, and trace amounts of amphipods, copepods and carnivorous zooplankton, sanddabs, dover sole, poachers, and bathylagids. The 1998 shelf survey stomachs suggested a diet composition of 22.1% salps, 10.6% heteropods, 20.2% euphausiids, 1.1% cephalopods, 0.3% pandalid shrimp, 0.1% pelagic shrimps, 32.5% hake, 6.9% unidentified fishes, 1% sandlance, 0.5% myctophids and trace amounts of copepods, carnivorous zooplankton, amphipods, sanddab, rex sole, slender sole, and dover sole. Trying to make sense of this wide range of information is difficult, but it is clear that yellowtail may be the most omnivorous of the (abundant) rockfish species. However it should also be considered that this omnivory might in part reflect the widespread availability of diet data over space and time. It is also clear from Lee's (2002) work that salps and other gelatinous zooplankton seemed to have been considerably more significant in rockfish diets in 1998 and 1999 than in earlier studies. As a starting point for our diet matrix we will suggest a diet of 55% euphausiids, 20% forage fish, 5% gelatinous filter feeders, 1% gelatinous predators, 4% cephalopods, 2% pandalid shrimp, 2.5% macrozooplankton, 5% mesopelagic fish, 3% juvenile rockfish, 0.2% juvenile roundfish, 1% benthic fishes, 1% hake, 1.2% small flatfish, 0.2% juvenile flatfish, 0.1% rex sole, 0.1% amphipods and 0.1% epifauna.

Pacific ocean perch

Pacific ocean perch (*Sebastes alutus*) was originally one of the most important commercial rockfish species on the west coast, taken both by trawl and hook and line gear. Stocks throughout the northeast Pacific were substantially overfished in the mid-1960s, largely by Japanese and soviet trawl fisheries that began in the Bering Sea in 1960 and expanded southward through the Gulf of Alaska, Queen Charlotte Islands and to the U.S. west coast by 1966; by 1969 stocks were widely acknowledged to be substantially depleted (Gunderson 1977). Relative biomass data and catches were taken directly from the 2003 assessment by Hamel et al. (2003), which used revised estimates of catches from the foreign fishery that subsequently lowered abundance estimates for the 1960s (and lowered potential yields of the current population). Adult and juvenile P/B and Q/B were estimated based on Essington et al. (2001), the adult P/B was estimated at 0.082 and Q/B at 2.07 for the 1990s.

Several sources of adult diet data are available. Livingston (pers. com.) described the diets of 93 POP taken off of Oregon, Washington and Vancouver Island in 1980, in which euphausiids dominated in weight (66.7%), followed by 9% myctophids, 4.9% cephalopods, 5% epibenthic fauna, 0.3% amphipods and 13.7% unidentified fish. A roughly equivelent number of POP sampled in 1986 had 37% euphausiids, 28% mesopelagics, 2% forage fish, 15% pandalid shrimp, 1.6% epibenthic fauna, 0.7% amphipods and the remainder either unidentified fish or unidentified organic debris. Brodeur and Pearcy (1984) sampled 73 POP stomachs off of Oregon and Washington in 1980, and found that euphausiids comprised 85% of prey by volume, with another 7.5% pelagic shrimp, 2.4% cephalopods, 0.6% amphipods and trace amounts of fish remains. Based on these estimates, we will attribute diet to 78% euphausiids, 7% carnivorous zooplankton, 3% pandalid shrimp, 6% myctophids, 3% cephalopods, 1% benthic fishes, 1% forage fishes, 0.5% epifauna and 0.5% amphipods.

Widow rockfish

Widow rockfish (*Sebastes entomelas*) are a semipelagic schooling species that were relatively uncommon in commercial landings until 1978, when the development of a midwater trawl fishery caused landings to increase from 1100 tons to over 28,000 tons in 1981 (Gunderson 1984). Currently widow rockfish are listed by the PFMC as overfished, as the stock is estimated to be at less than 25% of the historical spawning biomass (He et al. 2003). Estimated biomass and catches were taken from He et al. (2003), and biomass estimates were adjusted by scaling to 88.9% of the coastwide landings being north of Cape Mendocino. However, this may underestimate the fraction of the stock that is actually south of Mendocino, as the triennial survey data would suggest that perhaps only 66% of the stock is north of Cape Mendocino.[14] Adult and juvenile P/B and Q/B were estimated using the Essington method; values for the 1960s were estimated to be 0.14 and 2.1, and for the 1990s at 0.163 and 2.2 respectively.

Phillips (1964) reported that widow rockfish tended to feed primarily on macroplankton, particularly hyperiid amphipods, and suggested that this represented the use by widow rockfish of different habitats than other species (which tended to prey primarily on euphausiids and small fishes). Pereyra et al. (1969) noted that four widow rockfish caught and sampled incidently with yellowtail rockfish near the southern edge of the Astoria canyon fed heavily (>50% by volume) on myctophids, presumably most of the remaining prey were euphausiids and pelagic shrimps (as they were for yellowtail). Adams (1987) studied food habits of 381 widow rockfish collected in 1980 and 1981 off of Northern California, primarily from commercial catch sampling in the Eureka-Field Landing area. He found that four major taxonomic groups dominated prey by volume; results suggested a diet of 25.3% salps, 2.2% hydromedusae and ctenophores, 18.5% euphausiids, 21.7% shrimp (nearly all *Sergestes* or unidentified, but including 0.1% pandalid), 7% mesopelagics, 7% juvenile hake, 1% forage fishes, 2%

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[14] Based on years in which the survey sampled the Conception area, however this survey is widely acknowledged to poorly quantify semi-pelagic species, particularly widow. If the surveys are closer to representing the actual distribution, then it may be that widow rockfish have been more heavily overexploited in the NCC.

amphipods, 2% carnivorous zooplankton, 0.9% cephalopods, and 0.5% juvenile sablefish. He also described apparent seasonal diet shifts, and noted an increase in the percentage of both fish and salps in widow diets with size, associated with a decrease in the percentage of euphausiids.[15] A smaller number of samples from Fort Bragg, San Francisco and Monterey areas suggested similar patterns, although Fort Bragg area fish had a very high percentage (85% by volume) of salps and doliolids, San Francisco area fish had a high (70%) percentage of euphausiids, and Monterey fish had high percentages of both euphausiids (39%) and salps (46%). A small number (18) of widow rockfish sampled off of Washington and British Columbia by Livingston (pers. com.) in 1980 contained 92.5% euphausiids, 5.8% osmerid smelt (forage fish), 0.1% juvenile *Sebastes*, 1% amphipods and trace unidentified invertebrates. Lee (2002) sampled 274 widow stomachs off of the Oregon coast over different seasons in 1998 and 1999; his overall results suggested a diet of nearly 50% salps (49.7%), 28% other gelatinous predators (including siphonophores, ctenophores and heteropods), 17.5% euphausiids, small amounts of pelagic (0.5%) and pandalid (0.2%) shrimp, 1% cephalopods, 1.2% fishes (including sanddab, rex sole, dover sole, hake, juvenile sebastes, and bathylagids), and trace amounts of copepods and amphipods. The percentage of salps in the diet was greatest in the spring of 1999, when they comprised nearly 93% of the diet by volume (other gelatinous plankton made up much of the remainder). The clear importance of gelatinous zooplankton in both warm (1998) and cool (1999) years is impressive. In attempting to reconcile the two principle studies, we will assign the diet of widow to be 32% gelatinous filter feeders, 4% gelatinous carnivores, 30% euphausiids, 20% macrozooplankton, 3.5% amphipods, 0.1% pandalid shrimps, 0.5% cephalopods, 1.5% forage fishes, 3.5% mesopelagic fishes, 2% hake, 2% juvenile rockfish, 0.2% small flatfish, 0.2% juvenile flatfish, and 0.2% juvenile roundfish.

Black rockfish

This group includes the black rockfish (*Sebastes melanops*) and other nearshore rockfishes commonly caught in the NCC, such as blue, china, quillback, black-and-yellow, and gopher (*S. mystinus*, *S. nebulosus*, *S. maliger*, *S. chrysomelas* and *S. carnatus* respectively). For the moment, this assemblage also includes slightly more distantly related (but commercially important) cabezon (*Scorpaenichthys marmoratus*). The assemblage is based on Black rockfish population parameters and exploitation rates. Current assessments divide the west coast into two stocks, roughly north and south of Cape Falcon, Oregon, although the extent to which such divisions represent distinct populations is questionable (Ralston 2003). The most recent assessment for the north was by Wallace et al. (1999), and for the south by Ralston et al. (2003). Because the landings of Black rockfish south of Mendocino are on par with the landings of all

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[15] Adams (1987) also noted that the widow rockfish shares morphological characteristics with other *Sebastes* that tend to be associated with semipelagic habitat, notably blue rockfish (*S. mystinus*) which have also been noted to feed heavily on gelatinous zooplankton (Gotshall et al. 1965, Steiner 1979).

nearshore rockfish north of Mendocino, for this model the entire northern stock was combined with the entire southern stock to represent nearshore rockfish. Relative biomass data and catches were taken directly from the 1999 assessment 2003 assessment. Adult P/B and Q/B were estimated based on Essington et al. (2001), the numbers at age from the 2003 assessment and over 26,000 length at age samples provided by Ralston (pers. com). The resulting values for P/B were 0.088 and 0.129 for 1960 and 1990 respectively, and 1.94 and 2.01 for Q/B in 1960 and 1990 respectively.

Steiner (1979) examined 156 stomachs off of neritic reefs of the central Oregon coast and found that black rockfish fed on 65% forage fish (51.5% whitebait, 8.5% anchovy and 5% herring), 2.6% juvenile *Sebastes*, 3.2% benthic fishes, 4.6% benthic epifauna, 11.9% macrozooplankton (primarily megalopae), 0.6% gelatinous predators (hydrozoans), 6.4% gelatinous filter feeders, 1.7% butter sole and another 7% unidentified fishes. He also looked at 51 blue rockfish stomachs and found 25.5% gelatinous predators, 23.3% unidentified gelatinous prey, 11.2% forage fish (whitebait and anchovy), 5.2% macrozooplankton, 1.2% benthic epifauna, 2.3% benthic shrimps, and nearly 20% unidentified fishes or organic material. Eleven china rockfish fed on 97% benthic epifauna, principally crabs (*Cancer oregonensis* or other crabs), 2% benthic shrimps and 1% anchovy. 39 Cabezon fed on nearly 80% benthic epifauna (principally crabs), 10% benthic fishes, 8% hexagrammid eggs, 0.5% juvenile sebastes, 0.9% cephalopods, and 0.3% each pandalid and benthic shrimps. Brodeur et al. (1987) also evaluated 86 black rockfish stomachs collected from purse-seine studies off of the Oregon coast in the early 1980s, which fed on (roughly) 5.6% jellies, 1.1% amphipods, 5.6% carnivorous zooplankton, 10.6% crab megalopae, 0.1% cephalopods, 41% euphausiids, 0.1% pandalid shrimp, 9.5% benthic shrimp (primarily crangon species), 21% forage fishes (herring, anchovy, smelts and sandlance), 7.7% salmonids (both chinook and coho, all presumed to be smolts), 1.25% small flatfish (sanddabs, rex sole and sandsole are identified to species), and 1.7% benthic fishes (including tomcod, cottids and ronquils).[16] Taking primarily the black rockfish food habits into account, we will distribute the diet to 50% forage fishes, 3% benthic fishes, 2% juvenile *Sebastes*, 2% salmon, 1.8% small flatfish, 0.1% rex sole, 0.1% English sole, 15% euphausiids, 10% carnivorous zooplankton, 8% gelatinous herbivores, 2% gelatinous carnivores, 5% epifauna, 4.2% benthic shrimps, 1% cephalopods, 0.2% amphipods, 0.1% Dungeness crab, 0.1% pandalid shrimps, 0.1% pelagic shrimps,.

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[16] For nearshore species in other areas, Rosenthal et al. (1987) evaluated summer diets of ten species of rockfish in inshore waters off of southeastern Alaska between 1980 and 1982, their results suggested that benthic invertebrates and forage fish were among the most important prey items in these species. Love and Westphal (1981) did a study of Olive rockfish food habits off of California which also suggested that forage fish are amongst the most significant components; they reported as much as 43% fish (primarily forage fish and juvenile rockfish) and 8% squid, as well as 8.4% euphausiids, 18% other zooplankton, 16% octopus, and 10% isopods and amphipods (substrate oriented).

Shelf rockfish

For the moment, we will combine all of the remaining rockfish into two principle functional groups; shelf and slope rockfish, based on the designations suggested by Rogers and Pikitch (1992) and applied by the Pacific Fishery Management Council in the Groundfish FMP (PFMC 1993). Amongst the more abundant commercial species in the shelf assemblage are bocaccio (*S. paucispinis*), yelloweye (*S. ruberrimus*), chilipepper (*S. goodei*), stripetail (*S. saxicola*), redstripe (*S. proriger*), greenstripe (*S elongatus*), and silvergrey rockfish (*S. brevispinus*). Assessments have been done for yelloweye, bocaccio and chilipepper rockfish, yet these species have coastwide distributions, and the latter two are considerably more abundant south of Cape Mendocino. Assessments for yelloweye and bocaccio suggest substantial declines in abundance, with current stock sizes that fall within the overfished definitions of the Magnuson Act (Methot et al. 2003, MacCall 2003). Chilipepper rockfish, by contrast, appears to be closer to target levels, at approximately 50% of the unfished biomass (Ralston 1998), although the majority of the landings and biomass are south of Cape Mendocino. Preliminary stock status evaluations were done for several of the more commercially significant shelf rockfish species by Rogers et al. (1996), including northern bocaccio, yelloweye, yellowmouth, redstripe, sharpchin, silvergrey, and several slope species.

Rather than attempt to cobble together estimates from both surveys and assessments, we have based our estimate of these species for the 1990s on the total estimated biomass from shelf and slope surveys (Figure A.13, below), adjusted with a catchability coefficient (q) of 0.5 as suggested by Rogers et al. (1996). A more recent evaluation of catchability coefficients for west coast rockfish by Millar and Methot (2002) suggests that catchability coefficients vary substantially among species, and on average are likely to be significantly lower. The 1989 and 1992 survey years would suggest a biomass on the order of 58,000 tons, albeit with the recognition that this estimate is highly uncertain (and excludes shelf rockfish that might be in waters more shallow than 55m depth). To attempt to estimat the biomass in the 1960s, we constructed a surplus production using catchability-adjusted CPUEs from the shelf survey and the estimated total landings of shelf rockfish in the NCC since 1956. As the model would consistently attempt to fit the greatest initial depletion allowable, depletion was fixed at 0.9 and only r and K were free. Given plausible starting values, the model would consistently converge to an r of 0.24 and a K of 107,000; suggesting a biomass in the 1960s of 100,000 tons and a biomass in the 1990s of 38,000 tons. These results are obviously suspect for a variety of reasons, not the least of which being the aggregation of a wide range of species very poorly quantified in terms of landings or in terms of surveys. However in the absence of better information, the estimate seems to be plausible (if anything it might underestimate the 1960s biomass of other shelf rockfish). As such we will use it here with some trepidation.

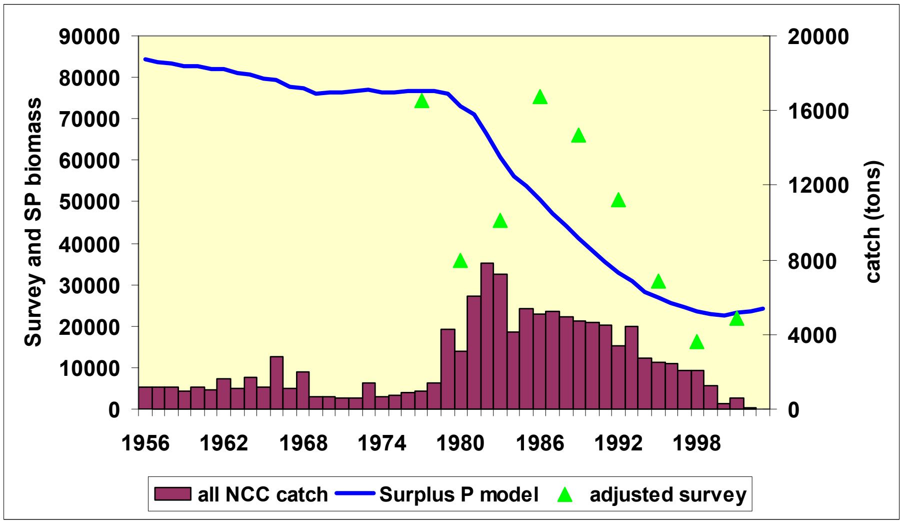

Figure A.13: Triennial survey biomass estimates (adjusted with an estimated q of 0.5) for all shelf rockfish, and surplus production model biomass estimates based on catches

Obviously, plausible estimates of P/B, Q/B and food habits are even more limited for this diverse assemblage, given a range of species and life history characteristics. We will assume that this assemblage has P/B and Q/B values typical for the other shelf species (canary, widow, and yellowtail) and assign a P/B of 0.125 for the 1990s, 0.10 for the 1960s, and a Q/B of 2 for the 1960s, 2.2 for the 1990s. Diet for these species of shelf rockfish is limited, and would be expected to be highly variable, given the large number of very different species in this assemblage.

Phillips (1964) found that adult splitnose, stripetail and shortbelly rockfish fed almost exclusively on macroplankton, primarily euphausiids, while chilipepper (and other shelf species, including those discussed elsewhere) fed on a mix of macroplankton and smaller fishes. Bocaccio were almost exclusively piscivorous. Shaw (1999) characterized diet data for greenstripe (*S. elongates*), redstripe (*S. proriger*) and rosethorn (*S. helvomaculatus*) rockfish (as well as several slope rockfish) and found that euphausiids made up the vast majority of prey items by weight in rosethorn (82%) and redstripe (nearly 99%), but a relative minor percentage in greenstripe (14%) where *Pandalus jordanii* made up nearly 85% of the prey by volume. Pooling the records from unassessed shelf species together in the NOAA food habits database (approximately 100 records, including those discussed in greater detail by Shaw 1986) suggests a diet for shelf rockfish of 35% euphausiids, 18% myctophids, 18% unidentified fishes, 16.4% pandalid shrimp, 12.5% herring, and trace amounts of amphipods and epibenthic fauna. More information is available from Steiner (1979) who reported on the stomach contents of 28 yelloweye (in addition to lingcod, black rockfish, blue rockfish and cabezon) caught on neritic reefs (20-50meters depth) off of the central Oregon coast. He found that the benthic epifauna made up the greatest fraction of diet at 34.3% followed by benthic fishes (particularly poachers and sculpins) at 27.2%, unidentified pleuronectids at 11.7%, 9.1 and 2.4% adult and juvenile *Sebastes* respectively, 7.5% pandalid shrimps, 1.2% cephalopods, 0.4% anchovies and the remainder unidentified fishes. Although few shelf rockfish seem to be piscivores, bocaccio are widely recognized to feed on other fishes, particularly on juvenile and adult rockfish. A starting point will be a diet of 35% euphausiids, 25% forage fishes, 12% pandalid shrimp, 10% myctophids, 1% benthic shrimps, 1% macrozooplankton, 5% benthic fishes, 2% small flatfish, 2% juvenile rockfish, 1% adult rockfish, 4% epibenthic fauna, 0.5% cephalopods, and 0.5% amphipods.

Slope rockfish

For the moment, we will combine all of the remaining slope rockfish in a single assemblage. Aside from Pacific ocean perch and thornyheads, the slope rockfish assemblage includes aurora (*S. Aurora*), blackgill (*S. melanostomus*), darkblotched (*S. crameri*), rougheye (*S. aleutianus*), sharpchin (*S. zacentrus*), shortraker (*S. borealis*), splitnose (*S diploproa*), yellowmouth (*S. reedi*), and several other species. For darkblotched, we will use the assessment results from the Rogers (2003) assessment. For all other species we will use survey estimates adjusted with a q of 0.5 as with shelf rockfish. Averaging the 89 and 92 shelf survey estimates with the 92 slope survey estimates, and adding the 1990 estimated biomass for darkblotched, gives us a total biomass of 41,000 tons in the 1990s. For the 1960s model, we again constructed a surplus production model to derive reasonable biomass estimates. This model estimated 60,500 tons in the 1960s, and 28,100 tons in the 1990s. Figure A.14 shows survey results (excluding darkblotched) from the NCC shelf and slope surveys, surplus production model estimates, and the combined surplus production estimates with the results from the Rogers (2003) darkblotched assessment.

For life history parameters, Rogers (2003) found the best model fits in her assessment were associated with natural mortality rates of 0.04 to 0.05. However estimates based on the relationship between mortality and gonadal-somatic index suggested mortality as high as 0.107 (Gunderson et al. 2003). Little data is available for other species. In the absence of better information, the model uses a P/B of 0.06 in 1990s, and 0.05 in the 1960s model. Survey-independent weight at age data was available for darkblotched rockfish from the triennial shelf surveys, using the Essington method with these data suggested a Q/B of 1.91, which was used for both time periods.

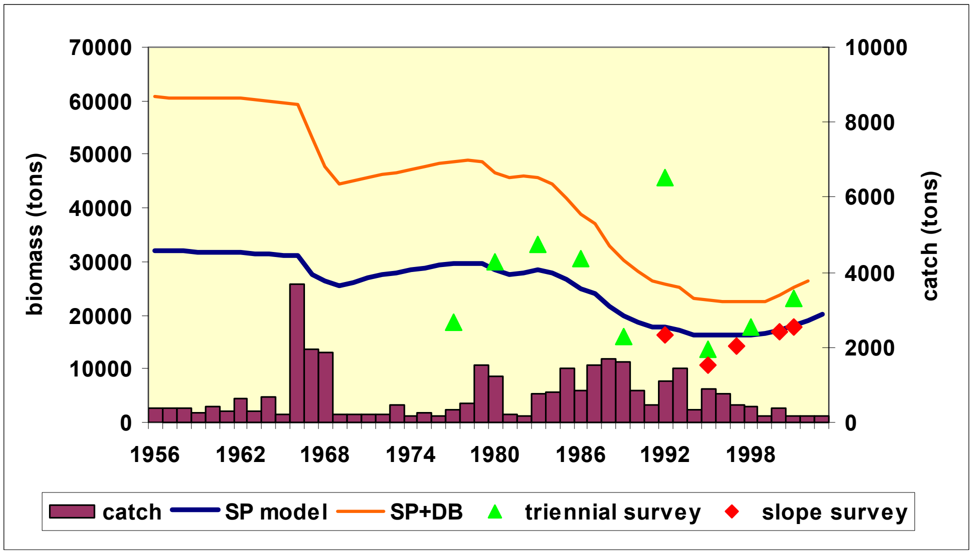

Figure A.14: Estimated survey (q-adjusted) biomass of slope rockfish, surplus production model estimates, and model plus darkblotch biomass estimates.

Shaw (1999) reported on the stomach contents of 8 non-empty sharpchin rockfish (*S. zacentrus*, collected in 1986), which contained 85% euphausiids, 14% unidentified fish and 1% pandalid shrimp. Seven rougheye rockfish from the same year fed on 44% euphausiids, 37% pandalid shrimp, 13% amphipods, and 7% unidentified fishes. Brodeur and Pearcy (1984) examined diets 62 splitnose in 1980 that suggested a diet of 74.1% euphausiids, 17.4 % pelagic shrimp (mostly *Seregestes similes*), 2% amphipods, 2.7% mesopelagics, 0.3% sand lance, 0.2% cephalopods, trace amounts of copepods and trace amounts of other fish remains. They also sampled 30 darkblotched rockfish, which had diets of 27.3% euphausiids, 2% amphipods, 1.5% copepods 1.1% pelagic shrimp, 4.3% sand lance and 62.5% unidentifiable remains. All of these suggest that slope rockfish may be more dependent on euphausiids, although sample sizes are low over both space and time. The diet we will use will be 70% euphausiids, 8% pandalid shrimp, 8% pelagic shrimp, 8% forage fish, 5% amphipods, 0.6% myctophids, 0.2% cephalopods, 0.2% copepods

Shortspine thornyhead

Shortspine thornyhead (*Sebastolobus alascanus*) are a deep-water, continental slope rockfish species. Wakefield (1990) evaluated the abundance of both short and longspine thornyheads off of central California, while Jacobson and Vetter (1996) evaluated length composition, density and biomass in regions of central California and Central Oregon. Both found high densities of both species beyond the continental shelf, with *S. alascanus* off of Oregon having the greatest biomass in the 200 to 400 meter depth range. The latest assessment (Piner and Methot 2002) suggests a biomass in the early 1960s of 100,000 tons coastwide, dropping to approximately 45,000 tons in 1990 and just over 25,000 tons in 2000. The species is widely distributed coastwide, the average of the most recent (coastwide) slope survey estimates suggest that only 44% of the biomass is nouth of Cape Mendicino. Based on Pacfin data since 1981, 68% of landings were made north of Cape Mendocino. As a starting point, we will estimate that the average of these two (56%) is found in the NCC.

Shortspines regularly live as long as 80 years, and may approach 100 years in age (Love et al. 2002). Estimates of natural mortality were set at 0.06 by the stock assessment team (Piner and Methot 2002). Using age data from the Alaska Center slope surveys, numbers at age from the assessment, and the Essington et al. (2001) approach for estimating life history parameters suggested a P/B of 0.065 and Q/B of 0.45 in the 1960s model, and a P/B of 0.08 and Q/B of 0.47 in the 1990s model. These low estimates are consistent with the extremely low metabolisms and growth rates thought to typify fishes living in the waters of the continental slope (Jacobson and Vetter 1996). However, these estimates may not be low enough, as estimates generated from godadosomatic indices and otolith ages evaluated in Pearson and Gunderson (2003) indicate considerably lower mortality rates, ranging from 0.01 to 0.017.

Jacobson and Vetter (1996) noted that *S. alascanus* prey heavily on *S. altivelis* where the two overlap in distribution, particularly in slope habitats between 600 and 800 meters where the average length of *S. alascanus* is double that of *S. altivelis* (and the average weight nearly 10 times greater). Cannibalism of juvenile *S. alascanus* by adults is also significant. Diets in the south tended to vary somewhat from those in the north, and *S. alascanus* also show a significant ontogenetic shifts in dietary preference with size (Buckley et al. 1999). Larvae and juveniles are thought to have an extended pelagic phase, as long as 14-15 months after which settlement occurs at approximately 100 meters of depth (Jacobson and Vetter 1996). Diet for pelagic *S. altivelis* juveniles included primarily euphausiids (Smith and Brown 1983). Buckley et al. (1999) found that north of Cape Blanco, adult *S. alascanus* fed primarily on Tanner crabs (15.2%), other crabs (3.3%), benthic shrimps (6.2%), pandalid shrimp (5.4%), cephalopods (0.6%), amphipods (0.1%), other epifauna (0.4%), infauna (0.4%), hake and unidentified gadids (14%), benthic fish (2%), forage fish (primarily herring, 1.4%), mesopelagics (0.2%), flatfish (including arrowtooth and rex sole, 0.3%), rockfish (22%), LST (2.1%), SST (0.5%), other unidentified fish (16.5%), and offal (primarily hake heads, 8.9%). South of Cape Blanco (which includes the Eureka INPFC area, and thus part of the NCC) diets were relatively similar, with a greater proportion of Tanner crabs (60%), benthic fish (6%) and macrouriids (2.5%). Laidig (pers. com.) found that *S. alascanus* preyed primarily on Tanner crabs (16.3%), pandalid shrimp (5.5%), other benthic shrimp (18%), pelagic shrimp (1.3%), other epifauna (5%), infauna (6.5%), amphipods (1%), gelatinous zooplankton (0.9%), cephalopods (3.2%), benthic fishes (3.6%), macrourids (0.5%), mesopelagics (0.9%), small flatfish (including deepsea sole, 1.1%), longspine thornyheads (9.2%), shortspine thornyheads (0.2%), other rockfish (1.8%), hake (0.9%), trace forage fish, and unidentified fish (22.9%). The adult diet for this model was set to 20% Tanner crabs, 15% benthic shrimps, 5% pandalid shrimp, 2% cephalopods, 1% carnivorous zooplankton, 0.2% amphipods, 5% epifauna, 5% infauna, 0.5% gelatinous herbivores, 6.5% offal (discards!), 12% hake, 5% benthic fishes, 0.5% adult rockfish, 5% juvenile thornyheads, 5% juvenile rockfish (none were greater than 100mm SL), 1% forage fish, 0.2% mesopelagics 5% longspine thornyheads, 0.5% macrourids, 0.1% rex sole, 0.1% arrowtooth, 0.1% dover and 0.7% small flatfish.

Longspine thornyhead

Longspine thornyhead (*Sebastolobus altivelis*) are closely related to shortspine, another deep-water, continental slope rockfish species of growing commercial importance that tend to have a greater depth distribution. Wakefield (1990) discuss abundance and habitat associations of both short and longspine thornyheads off of central California, while Jacobson and Vetter (1996) evaluated length composition, density and biomass in regions of central California and Central Oregon. Both found high densities of both species beyond the continental shelf, with *S. altivelis* more abundant at the 800 to 1000 meter contours. Wakefield estimated the density of longspines could be extremely high; ranging from 0.1 mton per km^2 at 400 meters depth to 9.4 tons/km^2 at 1000 meters depth. Jacobson and Vetter (1996) estimated deinsities of nearly 1 ton/km^2 at 400 to 600 meters, up to nearly 3 tons/km^2 at depths of 800 to 1000 meters. The most recent assessment for longspines was by Rogers et al. (1997), which suggested a total biomass of approximately 77,500 tons in the early 1960s and 59,500 tons in the early 1990s. However, these may be modest underestimates, as slope survey results for the late 1990s estimate a total coastwide biomass on the order of 98,700 tons (with no apparent trend). These data also suggest that roughly 52% of the biomass, or 50,900 tons is north of Cape Mendocino. However, 77% of the landings (since 1980) have been north of Cape Mendocino. For the 1960s model we will taking the average of these two ratios (64%) applied to the 1997 assessment estimate of the unfished biomass for a starting value of 67,400 tons (0.963 tons/m^2). For the 1990s model we will assume that standing biomass is equivelent to survey observations, for a standing biomass of 0.75 tons/m^2.

S. altivelis is a much slower growing species than *S. alascanus*, with larvae spendings as long as 20 months in the pelagic environmenta before settling. Settled (age 1) juveniles were estimated by Wakefield (1990) to be 4.5 to 5cm, and roughly 8 cm at age 2. Adults are rarely found at sizes greater than 40 cm. Smith and Brown (1983) found that *S. altivelis* had very low oxygen consumption and metabolic rates, as low as 1/3rd of those for a similar size Pacific grenadier (*Coryphaenoides armatus*), and reviews by Jacobson and Vetter (1996) of the effects of pressure on enzyme function suggest that *S. altivelis* is better adapted to deep water. The 1997 assessment (Rogers et al. 1997) estimated mortality rate for *S. altivelis* of 0.1, however the observation that these species occur at greater depths, and likely have substantially slower metabolism than even shortspine thornyheads, suggests that this estimate may be too high. Pearson and

Gunderson (2003) generated estimates of natural mortality rates using gonadosomatic indices to arrive at an estimate natural mortality rate of 0.0146 (standard error 0.0018), similar to their estimate for shortspine thornyheads. However, in recognition of their significance as prey to both sablefish and shortspine thornyheads, this value would appear too low. Instead, the starting estimate for P/B will be between the two very different natural mortality rate estimates, 0.05. The estimate for Q/B will be generated by assuming the same GE as shortspines in the 60s model, or 0.35.

Smith and Brown (1983) found that pelagic juvenile *S. altivelis* in the Southern California Bight fed primarily on euphausiids, while adults fed primarily on ophiuroids (38 of 39 fish examined). Other prey included fish fragments, crustaceans, bivalves and polychaetes. Laidig (unpublished data, but see Laidig et al. 1997 for discussion of sampling methods) found that key prey were primarily benthic shrimp (22%), pandalid shrimp (1.7%), Tanner crabs (1.5%), benthic epifauna (primarily echinoderms and benthic crustaceans, 20%), infauna (26%, primarily polychaetes), amphipods (6.2%), cephalopods (1.8%), euphausiids (0.3%), salps (1.9%), pelagic shrimp (1%), other thornyheads (presumably juveniles, 1.4%), benthic fishes (1.7%), trace amounts of small flatfish and 6.6% unidentified fishes. Buckley et al. (1999) found that north of Cape Blanco, *S. altivelis* fed primarily on benthic shrimps (27.7%), Tanner crabs (10.8%), other epifauna (10%), cephalopods (9.2%), amphipods (0.2%), infauna (2.9%), pelagic shrimp (0.9%), offal (5.5%), mesopelagic fishes (18.4%), juvenile rockfish (1%), benthic fishes (2.6%) and other unidentifed fishes (11%). South of Blanco, diets were very similar, although there were higher proportions of Tanner crab (21.2%), rockfish (5%) and infauna (8.5%). We will assign their diet to be 10% Tanner crabs, 25% benthic shrimp, 1% pandalid shrimp, 1% carnivorous zooplankton, 20% epibenthic fauna, 16% infauna, 3% amphipods, 5% squid, 1% gelatinous zooplankton, 2% offal, 10% mesopelagic fishes, 1.5% juvenile rockfish, 5% benthic fishes and 0.5% small flatfish.

A.8 Flatfish

Dover sole

Dover sole (*Microstomus pacificus*) were most recently assessed by Sampson and Wood (2002). The average Dover sole biomass for the 1960's is over 300,000 tons; for the 1990's the estimate is approximately 150,000 tons. However, attributing the percentage of Dover sole north of Cape Mendocino is difficult, as different indices provide different information. Although early landings were initially greater in the Monterey and Conception areas, pooling the total landings since 1956 suggests that 73.7% of the total landings have been from the NCC. Using the 1990s slope survey abundance trends as an index of relative abundance in the NCC, we estimate that the proportion of the population in the NCC is approximately 76% of the biomass; or

147,000 tons in the early 1960's and 80,000 tons in the 1990's. Landings of Dover sole between 1960 and 1966 in the NCC averages 5300 tons/year, and landings for the 1990's averaged 11,100 tons. P/B and Q/B were estimated based on Essington et al. (2001) and the numbers at age from the assessment by Sampson and Wood (2002). P/B was estimated to be 0.08 and 0.12 in the 1960s and 1990s models respectively, Q/B was 1.01 and 1.07 for the same.

Diet data from 846 Dover sole stomachs reported by Buckley et al.(1999) suggested that 52% of Dover sole diets was polychaetes, 29% Ophiuroidea (or other echinoderms), 7% clams and other infauna, 4% epifauna (various crustaceans, snails), 1% amphipods, 0.5% euphausiids, 0.5% pandalid shrimp, 0.3 non-pandalid shrimp, and the remainder unidentified material. Data presented in Pearcy and Hancock (1978) similarly suggested that 64.4% of Dover sole diet was polychaetes, with an additional 11.2% crustaceans (primarily amphipods by number, but with substantial numbers of pandalid shrimps and other benthic epifauna), 18.3% mollusks (primarily suspension-feeding bivalves, but including some gastropods), 3.4% echinoderms (primarily ophiuroids) and 2.6% coelenterates. Gabriel (1978) and Gabriel and Pearcy (1981) also reported that ophiuroids (brittle stars) were a more important prey item for Dover sole than polychaetes, mollusks and crustaceans; as the former made up 83% of the total dry weight of all prey items, polychaetes made up 13%, with mollusks and crustaceans making up the remainder.[17] Finally, Wakefield (1984) reported on 27 Dover sole which had fed primarily on ~20% polychaetes, 10% other infauna, 25% amphipods, and ~10% epifauna (the remainder was unidentifiable). Based on all of these studies, which are all relatively consistent in their results, we estimated that 85% of Dover sole diets is infauna, 10% epibenthic fauna, 3% amphipods, 1% benthic shrimp, and 1% pandalid shrimp. Clearly, it will ultimately be beneficial to further segregate infaunal and epifaunal groups to account for variability in prey selectivity between many of these groups.

English sole

The English sole population (*Parophys vetulus)* off of the Oregon and Washington coast was assessed by Sampson (1993), however the biomass estimates from this assessment for 1990 seem extraordinarily high (approximately 200,000 tons in 1990) for this species, particularly if trends inferred from the triennial survey were followed. Surveys off of the Oregon coast by ODFW between 1971 and 1974 were designed specifically to sample flatfish, and estimated a biomass in the survey area of 19,713 tons; a similar

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[17] Their work also confirmed that larger individuals tended to consume larger size prey, and may even be energetically advantaged to remove deeper infauna from the sediments than smaller individuals. Furthermore, by comparing location-specific diets with infaunal biomass estimates from sediment cores, Gabriel and Pearcy suggest that Dover sole are not simply opportunistic predators, nor do they appear to be selecting for prey items of greatest caloric value, implying that search and handling time costs play a role in determining diet preferences (in other words, despite their lower caloric values and apparently slower digestion rates, ophiuroids tend to be an easy to capture and readily available prey items).

survey off of the Washington coast was completed in 1975 that estimated biomass was 17,292 tons (Demory et al. 1976, Barss 1976). In both surveys, peak biomass estimates were in the 30-39 fathom depth range. The triennial surveys, initially intended to survey rockfish, estimated substantially lower biomasses for the late 70s; although the 1977 survey did not sample inside of 90 meters, later surveys sampled from 55 meters outwards. The 1980 and 1983 surveys would have suggested an NCC standing biomass of 2200 and 3600 tons respectively, applying the CPUEs from the shallow strata to the nearshore would increase that estimate to 3500 and 6200; still considerably less than the ODFW surveys.

In order to attempt to reconcile these conflicting data a surplus production model was used with landings and survey data as indices of abundance. Free parameters were r, k, initial depletion and q for the shelf survey. The combined Oregon and Washington shelf surveys from the early 1970s were given one data point (the 1975 data point, shown as a triangle rather than a diamond), weighted at three times the significance of the shelf survey data points and a q of 1. The results are shown as Figure A.15, the resulting r, k, q, and initial depletion were 0.187, 92,500, 0.35 and 0.13. Although this simplistic estimate is certainly highly sensitive to changes in assumptions (such as data weighting and the setting of boundaries for parameters), the model did converge and does provide results that seem to be consistent with available data. The results suggest a point estimate for the 1960s model of 35,500tons, and for the 1990s model of 40,500tons (or 0.51 and 0.58 tons/km^2 respectively). For population rates, Sampson's (1993) estimate of M was 0.26, based on an earlier assessment, although even earlier assessments had used an estimate of 0.29. To reflect the likely Z, given the long history of the fishery, we assumed a P/B of 0.35. As no fishery independent age data were available for estimating Q/B, and the age data from the fishery reflects highly selective discarding of smaller and younger fish, we assumed a Q/B similar to rex sole (2.12) which gave us a plausible growth efficiency of 15%.

For adults, Kravitz et al. (1977) report on 50 English sole food habits collected off of central Oregon, however they do not provide volumetric estimates or frequency of occurrence. They suggest that English sole feed primarily on polychaetes and amphipods, along with mollusks, ophiuroids and crustaceans. Wakefield (1984) reported on 51 English sole collected at two stations off of Central Oregon, and found a diet composition of roughly 33% infauna, 35% epifauna, 20% amphipods, 6% copepods, 0.6% benthic shrimp, 0.5% Dungeness crab and the remainder unidentified material. Based primarily on Wakefield, we will partition the diet to be 34% infauna, 36% epifauna, 25% amphipods, 4% copepods, 0.5% benthic shrimp and 0.5% Dungeness crab.

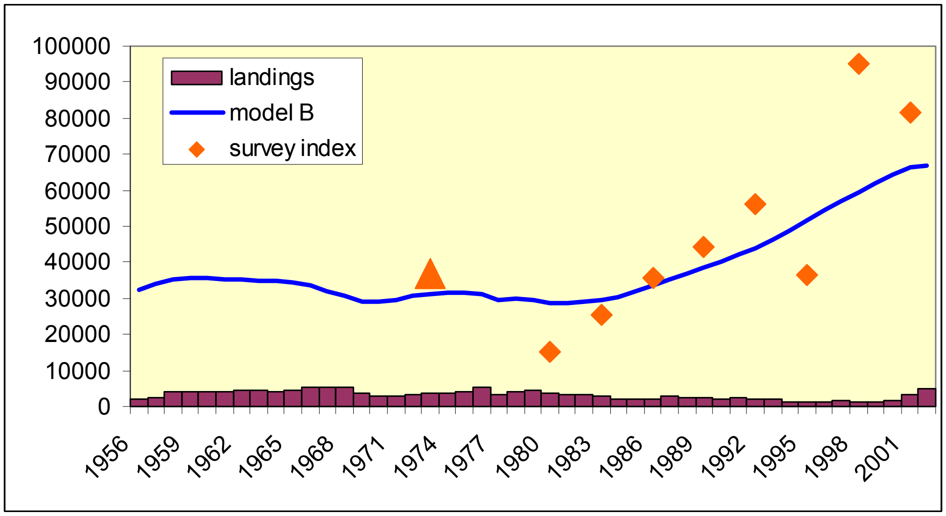

Figure A.15: English sole surplus production model estimates

Petrale sole

Petrale sole (*Eopsetta jordani*) have been an important component of the nearshore flatfish fishery for nearly a century, and reliable landings data extends back beyond the 1950s. They are found in depths of roughly 15 to 550 meters, and comparison of early flatfish survey results (Demory et al. 1976, Barss 1976) to later triennial shelf survey results would suggest that much of the biomass is in shallow water during the summer. Petrale sole migrate to discrete spawning sites in deeper water (300-500 meters) in winter, and these areas are fairly well known by fishermen. A stock assessment for the Columbia and U.S. Vancouver areas by Sampson and Lee (1999) suggests an average biomass through the 1960's of approximately 21,000 tons, and through the 1990's of approximately 8200 tons, with an increasing trend since the early 1990s. These estimates were scaled upwards by 1.27 to reflect the estimated survey biomass and catches in the Eureka region (19% and 36% of those in Columbia and U.S. Vancouver, respectively), and these estimates in turn were fit to a known-biomass surplus production model (MacCall 2002) in order to generate an estimate of abundance for the 1960s model (Figure A.16). As petrale sole have been commercially important since well before 1956, a depletion estimate of 0.8 was used in fitting the model (a likelihood profile of depletion suggested that values between 0.6 and 1 were reasonable).

Ketchen and Forester (1966) estimated natural mortality rates for Vancouver Island Petrale sole of 0.18 to 0.26 for males, and 0.19 to 0.21 for females. Sampson and Lee (1999) used estimates of 0.20 for both sexes, as did earlier assessments. The growth information and numbers-at-age from Sampson and Lee (1999) were used to derive

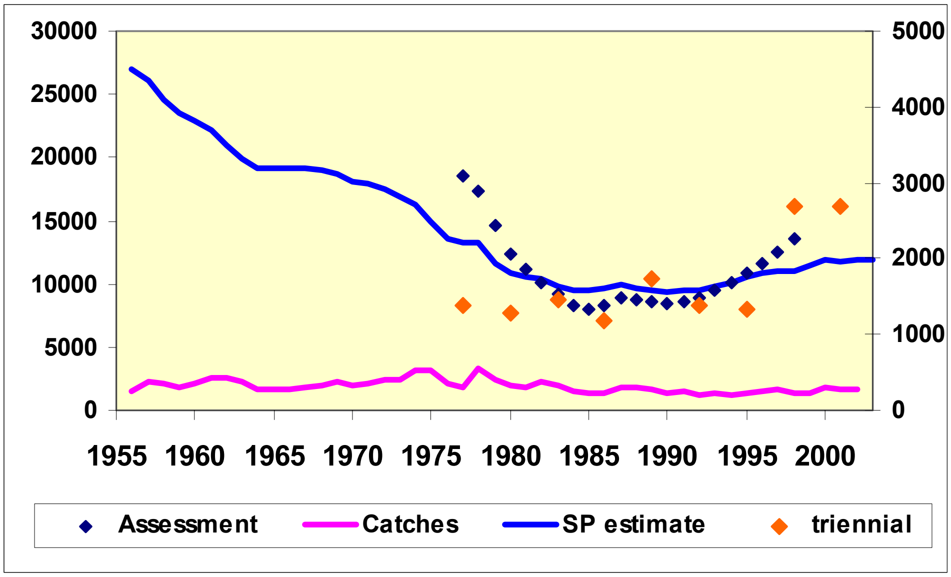

Figure A.16: Petrale sole surplus production model biomass estimates, based on assessment results of Sampson and Lee (1999) and survey biomass estimates.

estimates of P/B and Q/B based on Essington et al. (2001), using length at age data from the PacFIN Biological Database (W. Daspit, pers. com). These suggest a P/B of 0.36 and a Q/B of 1.7; we will use the same estimate for both periods. For food habits, petrale sole were found by Kravitz et al. (1979) to feed heavily upon fishes (including poachers, sculpins, anchovy, and rex sole), and decapod crustaceans (particularly benthic shrimps and crabs). Wakefield (1984) also evaluated Petrale sole diets off of the Central Oregon coast, collecting 33 individuals from 73 meters depth. He found roughly the following, 0.4% cephalopods, 10.4% mysid shrimps, 2.2% epibenthic fauna, 0.2% amphipods, 14.7% benthic shrimps, 5.7% sculpins and poachers, 12.9% tomcod, 17.2% sanddabs, 12.7% unidentified pleuronectids, 2.7% petrale sole, 1.1% rex sole, 12.2% butter sole, and the remainder unidentified fishes. Based on this information, we will partition Petrale sole diets to 15% epibenthic fauna, 25% benthic shrimps, 2% pandalid shrimps, 0.5% Dungeness crabs, 0.5% amphipods, 0.5% euphausiids, 0.5% cephalopods, 10% forage fishes, 15% benthic fishes, 21% small flatfishes, 2.5% English sole, 2.5% rex sole, and 1% dover sole.

Rex sole

Rex sole (*Glyptocephalus zachirus*) are an important commercial species and a key prey item for many piscivorous fishes (sablefish, arrowtooth flounder, lingcod). Landings are available back to 1956, and biomass estimates are available from the west coast shelf surveys undertaken since 1977, and the slope surveys undertaken since 1989 (Figure A.17). The shelf survey results in particular suggest a notable increase in rex sole abundance over the past two decades; from less than 5000 tons in the late 70s and early 80s to over 20,000 tons over the past 3 years. Based on survey estimates, the 1990s biomass estimate is 16,500 tons (or 0.23 tons/km^2), although this is likely to be conservative at it includes no estimate for fish shallower than 50 meters, and does not adjust catchability. Hosie and Horton (1977) also reported on the basic biology of rex sole, which rarely grow longer than 45 cm, and rarely live beyond 23 to 24 years. They estimate total mortality rates (Z) using several methods, catch curve analysis suggested a Z from 0.53 to 0.7 for males and 0.44 to 0.55 for females. Using the Essington method to estimate both P/B and Q/B from rex sole collected and aged in the Gulf of Alaska (no west coast fishery-independent age data is available) suggests an estimate of 0.37 for P/B and 2.12 for Q/B; we will use these as starting values in the model.

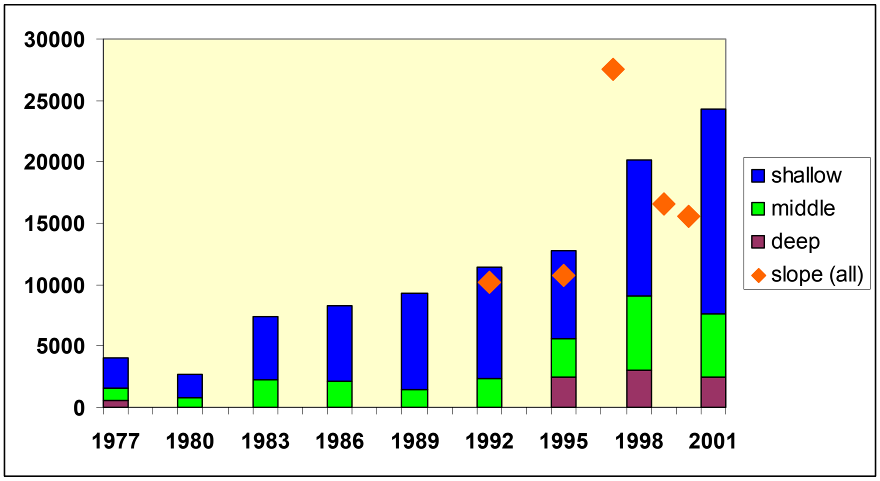

Figure A.17: Biomass estimates of Rex sole from NCC shelf and slope surveys

Pearcy and Hancock (1978) reported on the stomach contents of 614 Rex sole off of central Oregon between August of 1968 and 1970 (both winter and summer sampling was conducted). They reported that diet by volume was 64.8% polychaetes, 31% crustaceans (primarily amphipods, but including cumaceans and juvenile crabs), 1.4% mollusks (presumably infauna), and trace amounts of echinoderms and larvaceans. Kravitz et al. (1977) reported that rex sole off the central Oregon shelf fed primarily on amphipods and secondarily on polychaetes and other infauna, as well as on minor fractions of fish, but did not provide volumetric estimates of prey composition.[18] Finally, Wakefield (1984) reported on 37 rex sole diets off of the Oregon coast from

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[18] These authors also suggested two general feeding types for flatfish, with dover and rex soles feeding principally on polychaetes and amphipods, as opposed to flatfish such as slender sole, sanddabs and petrale sole which fed primarily in the water column. At a finer scale, they found that Dover and rex sole diets appeared to differ substantially as well, with Dover sole feeding on more pandalid shrimps, amphipods, pelecypods and ophiuroids, while rex sole supplemented their diets with crab larvae, cumaceans and larvaceans.

1979, and found that key prey items were 22% polychaetes, 44% amphipods, 22% brachiyurans, 4% benthic shrimps, 3% other infauna, 1.2% copepods, 10% other epifauna (isopods, cumaceans, ophiuroids), 1.9% sanddabs and 0.1% flathead sole. It seems reasonable to give more weight to the diet with significantly larger sample size, so we will assume 55% infauna (primarily polychaetes), 30% amphipods, 12% epibenthic fauna, 2% benthic shrimps, 0.5% larvaceans and 0.5% small flatfish.

Small flatfish

This is a functional group that includes all remaining flatfish, most of which are found in shallower waters (although the slender sole and some others are found to relatively deep depths). Species include, but are not limited to, Pacific sanddab (*Citharichthys sordidus*), other *Citharichthys* species, slender sole (*Lyopsetta exilis*), sand sole (*Psettichthys melanostictus*), butter sole (*Isopsetta isolepis*), starry flounder (*Platichthys stellatus*), and rock sole (*Lepidopsetta bilinieata*). Figure A.18 (below) shows the trend in small flatfish (perhaps 90% of which is *Citharichthys* spp) abundance suggested by the shelf survey. Adding the 1989-1992 average biomass in the shallow strata from the shelf survey to the inferred nearshore average (by extrapolating shallow strata CPUE estimates) and the 1990s average from the slope survey (which is primarily slender sole, and shows no sign of trends) suggests a total biomass on the order of 52,600 tons, or 0.75 tons/km^2. However, as the biomass is likely greater inside of 55 meters, catchability is likely less than one, and predation pressure on small flatfish is high, a top-down balance was used to estimated a biomass of 3.7 tons/ km^2 in the 1960s.

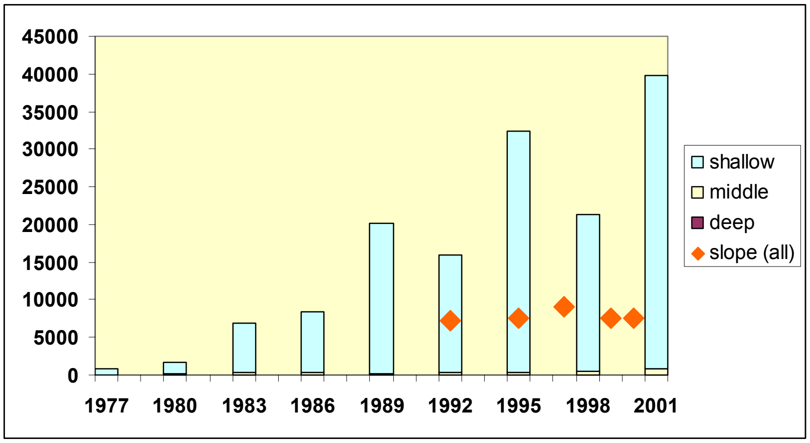

Figure A.18: Shelf and slope survey estimates of small flatfish biomass

Kravitz et al. (1977) evaluated the feeding habits of five species of flatfish on the Oregon shelf, and found that Pacific sanddabs feed (at times) heavily on northern anchovies, in addition to euphausiids, shrimps, amphipods and crab larvae. They also found rock sole feeding heavily on ophiuroids and to a much lesser extent on polychaetes and mollusks. Pearcy and Handcock (1978) assessed the food habits of slender sole and Pacific sanddab, both of which they characterized as chiefly pelagic feeders. Their results suggest that sanddabs and slender sole both consumed about 75% crustaceans, 7.2 and 15.6% polychaetes respectively, and trace amounts of mollusks, echinoderms and other (principally benthic) taxa. Euphausiids and calanoid copepods comprised a majority of crustacean prey items in Pacific sanddabs and pandalid shrimp comprising a larger proportion of prey in slender sole. Wakefield (1984) also reports on diet data for Pacific and speckled sanddabs, the former (based on 33 stomachs) consumed 2.7% cephalopods, 30.6% mysids and other epibenthic fauna, 7.1% copepods, 16.2% euphausiids, 5% carnivorous zooplankton, 9.3% gelatinous zooplankton, 6% amphipods, 3.2% benthic shrimp, 4.6% sculpins and poachers, 1.3% tomcod, and 13.5% butter sole and other pleuronectids. The latter consumed 1.5% infauna, 87% mysid shrimp, 0.5% other epibenthic fauna, 0.2% amphipods, 0.1% benthic shrimps, 3% other crabs, and 6.6% butter sole.

Wakefield also reported on a number of other small flatfish (with sample sizes from one to two dozen) and found that sand sole fed on 40% mysid shrimps and other epifauna, 2.2% amphipods, 9.3% benthic shrimps, 3.7% sandlance, 1.2% sculpins and poachers, and 32% tomcod; butter sole fed on 21% infauna and 30% epifauna, 12.6% amphipods, 15% benthic shrimps, 9% Dungeness crab, 5% sanddab, and 5% English sole; starry flounder fed on 23% infauna, 51% epibenthic fauna (much of which was crabs), 19% amphipods, 3.7% benthic shrimps, 2% Dungeness crabs, and 3% unidentified fish; and finally, rock sole fed on 6% infauna, 8.5% epifauna, 9.3% amphipods, 15.6% benthic shrimps, 24.2% sanddabs, 5.6% unidentified pleuronectids and 24.8% butter sole (Rock sole are uncommon in the region, yet these habits appear to be more similar to Petrale sole). Although these significant differences in food habits would suggest distinguishing pelagic feeding flatfish from benthic feeding species, we will assign the diet as follows; 12% infauna, 40% epifauna, 8% copepods, 10% euphausiids, 1% carnivorous zooplankton, 1% gelatinous zooplankton, 10% amphipods, 6% benthic shrimps, 1% pelagic shrimps, 1% pandalid shrimps, 2% Dungeness crabs, 0.5% cephalopods, 5% forage fishes, 5% benthic fishes, 2% small flatfish, and 0.1% English sole.

Arrowtooth flounder

Arrowtooth flounder (*Atheresthes stomias*) are at southernmost extent of range in the California Current, with fairly high levels of abundance in the U.S. Vancouver and Columbia provinces, and declining abundances in Eureka. It is possible that Arrowtooth was in greater abundance in the 50s and 60s; as Best (1958) describes the animal food fishery in Northern California in the 1950s as consisting of 17 to 30% arrowtooth in the Eureka province. Arrowtooth were assessed in 1993 (Rickey 1993), but the assessment was not age structured and did not produce biomass estimates beyond those available from survey data. Stock structure was discussed in the assessment, but no conclusions were reached.

Surveys off of the Oregon and Washington coast in the early 1970s (Demory et al. 1976, Barss 1976) suggest reflective biomass estimates of 7500 and 15000 tons respectively, numbers consistent with 1977 shelf survey biomass estimate of nearly 20,000 tons. Abundance estimates from the triennial shelf survey suggest significant variability in abundance, from lows of approximately 5300 tons in 1983 and 1992 (warm years) to highs of 15,500 and 17,500 during 1977 and 1989 (cool years). Pooling these estimates with the mean slope survey biomass (185-1200 meters depth) of 4200 tons gives us an average biomass of 16,000 tons over all years (15,700 for 1989-1992). There is no apparent trend over time in either shelf or slope surveys, although the most recent surveys (1998 and 2001) suggest increasing biomass, with the latter giving the highest biomass estimate ever (nearly 21,000 tons) and the former (also a very warm year) suggesting a biomass of nearly 15,000 tons. The North Pacific Council's stock assessment for arrowtooth (Wilderbuer and Sample 1999) uses a catchability coefficient (q) of 1. The results of the state surveys (22,500 tons) will be used for the 1960s model, and the mean triennial biomass estimate, with the cpue data from the shallow strata extrapolated as an estimate of nearshore biomass, will be used for the 1990s for a total of 16,000 tons.

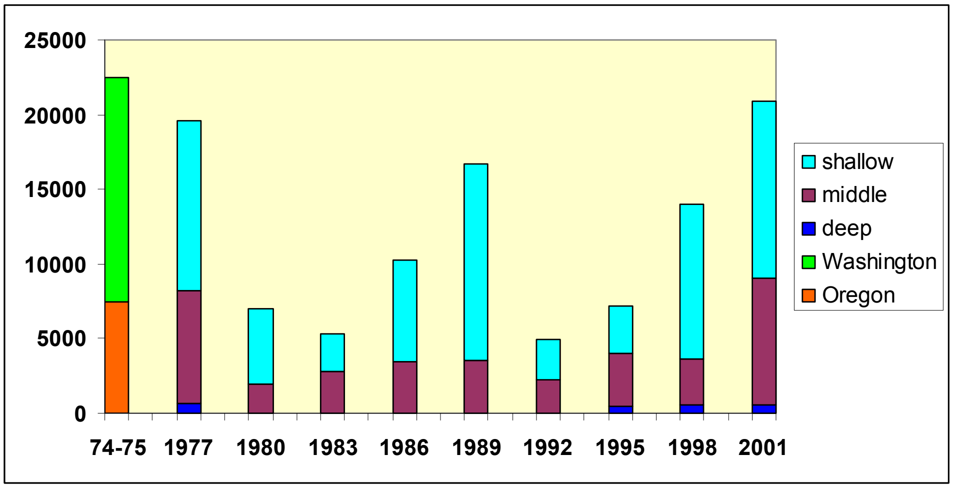

Figure A.19: Biomass estimates of Arrowtooth flounder from Oregon and Washington state surveys (1974-75) and from triennial surveys by depth strata (1977-2001)

Despite the poor quality of arrowtooth for human consumption, landings in the NCC have been significant for nearly 50 years, beginning with substantial landings in the 50s and 60s during fisheries for animal feed. Landings declined substantially in the 1970s, coincident with the decline of domestic mink farming (Rickey 1993) but have been increasing through the 1990s. Reported landings in the NCC between 1958 and 1962 were ~1450 tons per year (Lynde 1986), however actual landings may have been higher as Arrowtooth may have made up a significant quantity of ~1000 tons per year of unspecified groundfish. Between 1988 and 1992 landings averaged 4000 tons per year. Rickey (1993) cited a number of studies suggesting discard rates ranging from 60 to 80% in Oregon trawl fisheries; a figure comparable to arrowtooth discard rates elsewhere. It may be that recent landings represent increased retention rates rather than development of new fishery. Most recent landings are taken in offshore waters of the US Vancouver province. Because Arrowtooth is at the southern end of its range, and these landings suggest high exploitation rates (on the order of 20 to 30% per year) on the available biomass, there is likely to be either a movement of Arrowtooth into the NCC from the north, or more Arrowtooth than estimated by the surveys in the NCC region.

As there is no age structured assessment for west coast arrowtooth, nor weight at age data from surveys, the biological parameters (P/B, Q/B) for this species will be borrowed from S. Gaichas (pers. com) who estimated for P/B of 0.335 and a Q/B of 2.12 for arrowtooth in the Gulf of Alaska. This P/B value is near the mean of a wide a range of estimates of Z generated by various methods in the stock assessment by Rickey (1993). Buckley et al. (1999) evaluated 380 arrowtooth stomachs collected in 1989 and 1992, in which hake and unidentified gadids dominated stomach contents (45 and 22% respectively) followed by herring (19%), mesopelagics (0.5%), rex sole (1%), slender sole and other small flatfish (3%), other arrowtooth (1.5%), other unidentified flatfish (1%), pandalid shrimp (~3%), euphausiids (3%), benthic shrimps (trace), and various other fish and invertebrate prey. Similarly, Yang (1995) found that larger (>40cm) arrowtooth in the Gulf of Alaska fed primarily on pollock (50 to 82% by depth), as well as a variety of invertebrates (particularly euphausiids and other crustaceans for smaller arrowtooth), a substantial amount of herring, and notable amounts of other flatfish. In an earlier study off of Northern California, Gotshall (1969) examined 425 arrowtooth stomachs throughout the 60s, and found pandalid shrimp to make up nearly 40% of the prey by volume, along with other shrimps, crabs, euphausiids, sanddabs, slender sole and other items. However his samples were taken directly from shrimp beds, and consequently would be biased towards shrimp. Based primarily on Buckley et al., we will assign the diet as follows; 50% hake, 30% forage fish, 4% euphausiids, 4% pandalid shrimp, 1% rockfish, 1% rex sole, 6% small flatfish, 1% juvenile flatfish, 1% Dover sole, 0.5% English sole, 0.2% petrale sole, 0.2% juvenile roundfish, 0.4% myctophids, 0.4% benthic fishes, 0.2% benthic shrimp, 0.1% carnivorous zooplankton, 0.2% Dungeness crab, 0.1% infauna and 0.1% epifauna.

Pacific halibut

Pacific halibut (*Hippoglossus stenolepus*), like the arrowtooth flounder are near the southern extent of their range, however unlike arrowtooth flounder they are a highly valued and important resource. The International Pacific Halibut Commission (IPHC) statistical area 2A, which includes shelf and shallow slope waters of Oregon and Washington, is the equivelent to our NCC boundaries, and catch data is based on Halibut Commission estimates of catch, bycatch and sports catches. Although the biomass of halibut in the 2A statistical area is not formally assessed, Clark and Hare (2003) estimated it to be approximately 13% of the area 2B stock. The 2B stock, like most halibut stocks, declined slowly from the 1950s into the 1970s, then increased rapidly over the 1980s and 1990s, a pattern confirmed by commercial CPUE data and by trends in halibut estimates from the triennial shelf surveys (Figure A.20). Biomass estimates based on the area 2B assessment corresponds with roughly 5200 tons in 1960 and 9100 in 1990 (based on age 6+ fish only). Using the numbers at age from the area 2B assessment, and the average weight at age for age 1-5 fish from Southward (1967), it was estimated that the biomass of age 1 to 5 fish averaged 19.8% of that of age 6+ fish in the 1960s. Consequently, the estimates used in this model reflect a 19.8% increase in biomass from the "assessment" estimates, or 6220 tons in the 1960s and 10900 tons in the 1990s. That these estimates are consistent with, but greater than the estimates of halibut biomass from the triennial survey is consistent with observations that trawl survey estimates underestimate larger halibut due to gear avoidance (Myhre 1969). For the moment, production and consumption rate parameters are borrowed from arrowtooth, for a P/B of 0.335 and a Q/B of 2.12. Depletion and accumulation terms for population trajectories in the 1960s and 1990s were estimated based on assessment data.

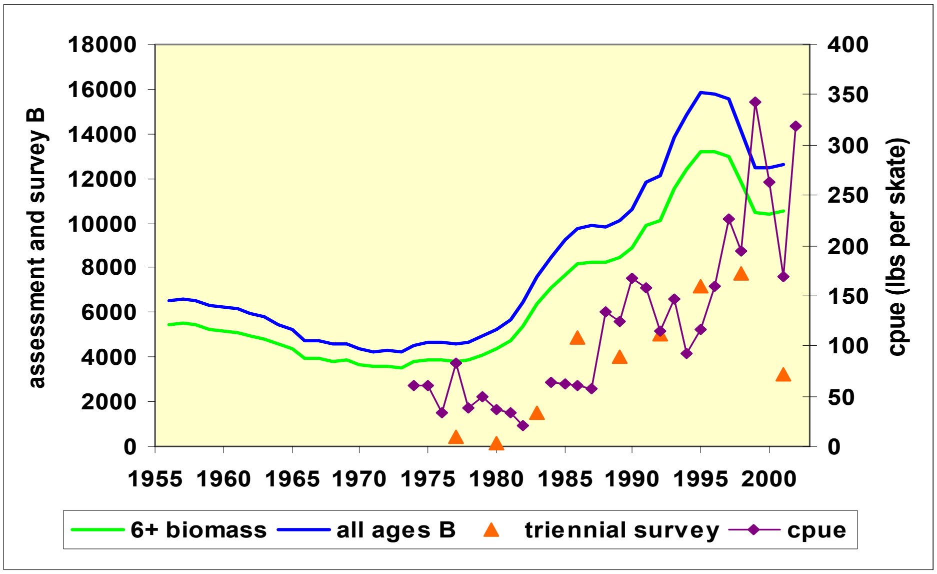

Figure A.20: Halibut biomass and CPUE estimates in the NCC

Halibut are known to feed on a wide range of prey items, primarily other fishes, cephalopods and benthic epifauna, but the only data found specific to the NCC was anecdotal accounts by Rankin (1915). Rankin described prey items of Pacific halibut caught off of the Oregon coast as including starfish, octopus, small halibut, small rays, crustaceans (shrimps in particular), hake, coho salmon and a yelloweye rockfish (the latter three items were all from a single 130 pound halibut, and said to weight at least 10 pounds each). An extensive IPHC study and review of halibut prey and predators (Best and St-Pierre 1986) did not examine halibut south of British Columbia, but reported food habits for 1250 fish taken from the Bering Sea, Gulf of Alaska and British Columbia. In general, they found that halibut smaller than 30 cm fed primarily on shrimp and other crustaceans, while larger halibut fed primarily on walleye pollock, various forage fishes (particularly sandlance) and small flatfish; with octopus and Tanner crabs the most commonly observed invertebrate prey. From halibut taken from the Hecate Strait and Dixon Entrance areas of British Columbia, sand lance, herring and other forage fishes were by far the most commonly observed prey, other prey included Pacific cod, unidentified rockfish, rock sole, rex sole, other unidentified flatfish, octopus and various unidentified crabs. In the eastern Gulf of Alaska, prey included primarily pollock, herring, Tanner crab, and various flatfish (arrowtooth flounder, flathead sole, and many unidentified species).

More recently, Yang (1995) examined 467 halibut stomachs from the Gulf of Alaska (as well as arrowtooth flounder stomachs, described above), and found that walleye pollock was the most important prey item (57% by volume). Other fish prey made up nearly 20% of the remaining prey, including coho salmon, forage fishes (including eulachon and capelin), Pacific cod, rockfish (including Pacific ocean perch), flatfish (including Dover sole and young halibut), zoarcids and other benthic fishes. Invertebrates made up only about 20% of the total prey items, including Tanner crabs (roughly 6% by weight), octopus (4.8%), other crabs (~6%) and trace amounts of polychaetes, shrimps, squids and other invertebrates. Perhaps more importantly, Yang characterized the differences in arrowtooth flounder and Pacific halibut; despite the observation that both preyed heavily on walleye pollock (over half of the prey by volume for both species), the species composition of other prey items suggests that arrowtooth feed primarily in the water column while halibut feed principally on benthic prey. Taking into account inferred predation on salmon, rockfish, hake and skates (Rankin 1915), we will assume a prey composition similar to arrowtooth with regard to high predation on hake, but similar to the Gulf of Alaska with regard to other prey, for a prey composition of 45% hake, 15% forage fish, 3% salmon, 4% adult rockfish, 1% sablefish, 2% Dover sole, 1% rex sole, 1% arrowtooth flounder, 0.2% Petrale sole, 0.3% English sole, 3.5% small flatfish, 1% juvenile flatfish, 1% juvenile roundfish, 5% benthic fishes, 0.5% skates, 0.5% dogfish, 5% cephalopods, 5% epibenthic fauna, 2.5% pandalid shrimp, 2.5% benthic shrimp, 2.5% Dungeness crab, 0.1% Tanner crabs (although important elsewhere, the spatial overlap of halibut and Tanner crabs in the NCC is minimal, suggesting little to no predation), 0.6% infauna and 4% detritus.

A.9 Seabirds

Gulls and allies

Estimates of gulls and their allies (including kittiwakes, fulmars and albatross) for the 1990s are based on at-sea surveys by Briggs et al. (1992). Average counts are shown as annual averages in Table A.3, along with corresponding mean body weights and energetic requirements (assuming a mean prey density of 5kj/gram) estimated by Hunt et al. (2000). Although colony counts and other data are available for some (breeding) species, at sea-sightings may be more appropriate, as they should more accurately account for those individuals actively foraging at sea. For example, at sea counts (annual averages) from Briggs et al. (1992) were found to be similar, yet slightly less, than colony counts from Wahl et al. (1993) for glaucus-winged (*Larus glaucescens*) and western gulls (*L. occidentalis*).[19] The estimated P/B will be set at 0.12, based on Schreiber and Burgers (2002) who suggest a taxonomic order level survival rate for gulls of approximately 74-97% per year.

Table A.3: Estimates of Gull and allies in the NCC from Briggs et al. (1992)

	density (birds/sq. km) 0-200 m.	200-2000 m.	mean wt. (kg)	numbers at sea	density (mt/km^2)	QB
California gulls	0.235	0.055	0.607	10832	0.00009	145
Herring/thayer gulls	0.214	0.120	1.135	12044	0.00020	123
Western gulls	0.263	0.028	1.011	11078	0.00016	126
Glaucous-winged gulls	0.315	0.043	1.413	13591	0.00027	90
unidentified gulls	0.554	0.067	1.042	23603	0.00035	116
Black-legged kittiwakes	0.208	0.240	0.407	15551	0.00009	162
Black-footed albatross	0.041	0.064	3.148	3592	0.00016	93
Northern fulmars	0.792	0.259	0.544	38841	0.00030	150
all gulls and allies	*2.621*	*0.877*		*129132*	*0.00163*	*122*

Quantitative diet studies for gulls in the NCC are not available, and Hunt et al. (2000) only report on diet preferences for western gulls in the Southern California Current. They suggest a diet composition of 2% invertebrates, 1% crustacean zooplankton, 17% small cephalopods, 65% fish (ranging from low to high energy density), 6% birds and mammals (primarily eggs and chicks, presumably of other gulls, murres, etc.), and 8%

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[19] The number of both of these species estimated at nesting sites off of the Washington and Oregon (excluding N. California) coasts was on the order of 33,000; the count data for these two species from at-sea sightings (extrapolating average densities to the California portion of the NCC) was 25,500. Presumably, this reflects the likelihood that some birds forage partially or exclusively in terrestrial, littoral or estuarine environments. Other comparisons can be made with the seabird densities estimated by Hunt et al. (2000).

offal or discards. Anchovy and *Sebastes* spp. (presumably juveniles) are cited as key prey items by Ainley et al. (1993); herring, anchovy, smelts, saury, sandlance and (juvenile) rockfish are the most common overall prey items listed in Hunt et al. (2000) in the Northern California Current; with salmonids, bathylagids, myctophids and some pleuronectids also listed as general prey items. Based on this general pattern, we will attribute the diet to 1% each euphausiids, pelagic shrimps and carnivorous zooplankton, 17% cephalopods, 55% forage fish, 10% juvenile rockfish, 2% mesopelagics, 1% sardines, 1% salmon, 2% juvenile flatfish, 1% birds (murres and other alcids, although this presumably represents only chicks and eggs), 1% euphausiids, 1% pelagic shrimp, 1% epifauna and 8% offal and discards.

Common murres and other alcids

The common murre (*Uria aalge*) is one of the most abundant seabird species in the NCC, and alcids such as Cassin's auklets (*Ptychoramphus aleuticus*), rhinoceros aukles (*Cerorhinca monocerata*) and tufted puffins (*Fratercula cirrhata*) are included in this group as well. Several plausible estimates of abundance exist. Taking strickly the average at-sea density of seabirds off of Oregon and Washington waters from Green et al. (1992) suggests an at sea population of approximately 150,000 birds. However, Green et al. (1992) cite unpublished counts by USFWS personnel for Oregon colonies on the order of 262,000, (and additional 21,000 in Washington) in 1989. Multiplied by 1.67 to account for birds at sea results in an Oregon/Washington estimate of 460,000 birds. However, this does not include California birds north of Cape Mendocino. On the ourter Washington coast Wahl et al. (1993) estimated as many as 88,000 Cassins auklets, 24,000 rhinoceros auklets and 24,000 tufted puffins, as well as smaller numbers of comorants, guillemots, murrelets and other species. With regards to at-sea densities, Green et al. (1992) only includes densities for Cassin's auklets, however these estimates are comparable (73,000 birds) with the colony estimates in Washington reported by Wahl et al. (1993). For our purposes, we will estimate a total of 600,000 murres, and 150,000 auklets and other alcids in the NCC. Using mean body weights in Hunt et al. (2000) to convert these numbers to biomass suggests an NCC biomass of slightly over 600 tons of alcids, or 0.0087 tons/km^2. Using the daily allometric requirements reported in Hunt et al. (2000) suggests a Q/B of 129. The winter mortality rate reported by Wiens & Scott (1975) for common murres is 0.1, we will use this as an estimate of P/B for the moment.

Diet data for murres is reported in a variety of sources. Wiens and Scott (1975) report on seasonal variability in murre diets for the Oregon coast in the early 70s. Forage fish (particularly anchovies, smelts and herring) comprised the greatest fraction in any given season (22 to 86% by volume), gadids made up an average of perhaps 10% of prey over all seasons, and rockfish nearly 15% (peaking at 27% of prey during July and August). The 'other' fish category was not expounded upon, but cephalopods made up a minor fraction, and euphausiids made up a significant fraction in July-August, but were not present in other seasons. Matthews (1983), as cited in Ainley et al. (1996), reported on murre diets from three separate locations along the Oregon coast between spring and autumn. Tomcod, rockfish, smelt, sandlance, salmon, anchovy, market squid and herring as dominant prey, euphausiids were an uncommon prey item. Ainley et al. (1996) found that juvenile rockfish, hake, squid and various forage fishes dominated diets of murres in the Gulf of the Farallones in the late 1980s, with euphausiids, surf perch, butterfish, lingcod, zoarcids, sanddabs, and midshipman included as occassional prey. Ainley et al. (1993) also reported on interannual variability in the percentage of juvenile rockfish in summer (June-July) murre diets in the Farallon Islands, where juvenile rockfish were described as a preferred summer prey item that represented between 10 and 90% of prey for nesting murres between years. This variability was strongly linked both with juvenile abundance as assessed by midwater trawl surveys as well as ocean conditions. Diet data for Oregon and Washington was also compiled coastwide by Parrish and Loggerwell (pers. com); their early results suggest the following; for the 1970s, 68% forage fish (primarily herring, followed by sandlance, smelts and eulachon), 35% juvenile rockfish and other juveniles (salmon and flatfish; we might say 1% each). For the 1990's, their data suggest 92.4% forage fishes, 1.8% sardine, 4.6% rockfish and other juveniles and 1.1% juvenile salmon. The other alcids in this group (auklets and puffins) tend to feed on similar prey items. Rhinoceros auklets in British Columbia fed principally on herring, salmon smolts, argentines, sauries, sandlance and juvenile rockfish, (with many other species commonly occurring as prey) according to Vermeer and Westrheim (1984), and Hunt et al. (2000) suggest that Cassin's auklets eat primarily (~75%) crustacean zooplankton. For our final diet matrix, we will base estimates on Parrish (pers. com), but include crustacean zooplankton (to account for small number of Cassin's auklets and possible predation by murres), such that we have 80% forage fish, 10% juvenile rockfish, 3% cephalopods, 1.8% sardine, 1% mesopelagics, 1% juvenile salmon, 1% small and juvenile flatfish, 1% euphausiids, 1% copepods and 0.2% benthic fishes.

Shearwaters

Shearwaters, particularly Sooty Shearwaters (*Puffinus griseus*) are common summer migrants off the Oregon and Washington coast, their numbers typically peak between July and September. At sea density estimates were taken from Briggs et al. (1992) for sooty and pink-footed shearwaters (the two most abundant species), as well as petrels and phalaropes (minor numbers of other birds were excluded). These estimates suggest that approximately one million shearwaters are present between July and September; averaging these numbers over a year and including the considerably smaller estimates for pink-footed shearwaters, petrels and phalaropes results in a total density of 0.00289tons/km^2. According to Parrish (pers. com) summer shearwater numbers off of the Pacific Northwest coast during the summer ranged from 1.3 to 1.7 million in the 1970s, whereas surveys in the 1990s suggest a greater abundance in waters off of California and declines off of Oregon and Washington. Hunt et al. (2000) provide summer ‘dark shearwater’ (short-tailed and sooty) numbers and abundance estimates of 6.02 birds/ km^2 in the NCC and 27.2 birds/km^2 in the sout. These too are comparable to the Briggs et al. (1992) observed summer densities, consequently we feel these estimates to be reasonable for this time period.

Table A.4: Estimates of shearwaters and allies in the NCC in the 1990s

	density (birds/sq. km)		mean wt.	numbers	density	QB
	0-200 m.	200-2000 m.	(kg)	at sea	(mt/km^2)	
sooty shearwaters	6.039	0.518	0.787	250671	0.00282	135
other shearwaters	0.095	0.028	0.543	4580	0.00004	150
petrels	0.261	0.560	0.055	27587	0.00002	281
phalaropes	0.608	0.202	0.0338	29877	0.00001	320
all shearwaters and allie	7.003	1.308	1.419		0.00289	138

Consumption rates were estimated from the mean body weights and daily energy requirements reported in Hunt et al. (2000), assuming mean prey energy density of 5kj per gram (an ‘average’ energy density fish). The results suggests a mean annual consumption rate of 138 for this guild. For production estimates we will use the annual mortality for Manx shearwater of 0.1, as estimated from Furness and Monaghan (1987). Some diet data for the Oregon coast is reported in Wiens and Scott (1975), who attribute 8% of sooty shearwater diet to cephalopods, 80% to anchovies, and 12% to ‘other’. They also report on the diet of storm petrels as comprising of 44% hydrozoans, 38% euphausiids, 9% other crustaceans, 1% cephalopods, and 8% ‘other’. Chu (1984) reported on sooty shearwater diets in the southern California Bight and in Monterey Bay in the late 1970s, and found that juvenile rockfish were the most important prey in May and June, with market squid and anchovy being the most important prey from July through September. Euphausiids, polychaetes, lingcod juveniles and other cephalopods were amongst the other observed prey. Briggs et al. (1984) also reported on phalarope diets off of central and northern California, which included primarily fish eggs and euphausiids, as well as trace amounts of hydrozoans and gastropods. Diet here is estimated as 75% forage fish, 10% cephalopods, 10% rockfish, 3% euphausiids, 1.5% macrozooplankton, and 0.5% gelatinous carnivores.

A.10 Marine Mammals

Harbor seals

The most recent estimate for harbor seal (Phoca vitulina richardsi) abundance along the Washington and Oregon coast is 26,180 animals in 1997 (Carretta et al. 2002, using a correction factor for animals in the water). This population was historically depleted by bounty hunters from the turn of the century into the 1960s (Bonnet 1928), but has increased substantially since the 1970s. The population is thought to have peaked in 1992 at 28,500 animals and has been declining slightly since that time. The California population is thought to be greater than 30,000, having also increased substantially over the last several decades from a low of perhaps hundreds in the early 1960s (Carretta et al. 2002). Harbor seals are found in great abundance in large estuaries such as the Columbia River, Grays Harbor and Willapa Bay, especially when when salmonids or eulachon are abundant (regional counts are available in NMFS 1997) so it might be reasonable to assume that much of the population is not consistently present in the coastal waters modeled here. A reasonable approximation might be to assume that approximately 4000 of the California animals are present in the NCC, and then scale the total number of animals down by one-half to account for animals living and foraging in estuaries and littoral environments. This would suggest the equivalent of 16,250 animals in the NCC. The mean body mass for harbor seals is approximately 60 kg (Hunt et al. 2000), which suggests a total biomass of 975 tons, or 0.014 tons km^2. As the 1977 population was slightly over 1/3rd the 1997 population (Carretta et al. 2002), a reasonable estimate for the 1960s model would be approximately 1/5th of the 1990s biomass amount, or 0.003 tons km^2. Using the Siler life history table model as applied by Barlow and Boveng (1991) suggests an average mortality of 0.0826, which seems reasonable given that population growth rates have been observed to be as high as 7% over recent decades.

NMFS (1997) summarizes nearly two-dozen food habits studies throughout the northwest over time, with nearly all of the studies focusing on samples obtained from inland or estuarine waters. The focus was often on salmonid predation, and the data suggesting the greatest percentage of salmonid remains (~50%) came from seals caught incidentally in the Grays Harbor salmon gillnet fishery. Salmonid predation was also high in the Columbia river estuary (up to 60% occurrence) where eulachon were also important (especially in winter) and a wide range of other prey species was common. The most frequently occurring (in descending order) other prey items for Washington and Oregon estuarine or river sites were forage fish (sandlance, eulachon, herring, anchovy, whitebait smelt, other osmerids), hake, flatfish (rex sole, sanddab, dover sole, English sole, starry flounder), rockfish (no species listed, presumably nearshore species), lampreys, sculpins, eelpouts, surf perch, cephalopods and crustaceans. The current estimates for the diet matrix are consequently based on loose interpretation of these results, with an attempt to focus on the prey items most likely occurring in the coastal, rather than estuarine, waters. These estimates are- 35% forage fish, 25% flatfish (mix of English, dover, petrale, and other small flats), 10% hake, 10% salmonids, 5% cephalopods, 5% rockfish, 1.5% lingcod, 5% benthic fishes, 2% epifauna, 2% Dungeness crab.

Sea lions and elephant seals

Steller sea lions (*Eumetopias jobatus*) are the most abundant breeding phocid in the Northern California Current, and we will include the small number of (non-breeding) seasonally migrating California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*) with this group. Hill and DeMaster (1999) estimated Stellar sea lion stocks in California, Oregon and Washington to be 2042, 3990 and 523 respectively (6555); we will estimate that 20% of the California stock is north of Mendocino for a total of 4921 animals in the NCC. These numbers are minimum estimates, as they are not adjusted for animals that may have been at sea due to the lack of a reliable correction factor. Bonnell et al. (1992) estimated comparable, albeit slightly lower counts at Oregon and Washington rookeries and haulouts; their transects had a total of 209 sightings which suggested in turn a density on the order of 0.0049 to 0.0059 animals/km^2. This would suggest that the number of animals at sea during the breeding season was ~700, with ~1500 animals at sea during the non-breeding season. Most sightings (89%) were over the continental shelf, and within 30 to 40 km of a rookery. Although Steller sea lioins have historically been hunted or culled throughout the NCC range (Bonnet 1928, Cass 1985), recent population trends over the last two decades have been described as "stable" for California and Oregon, and the British Columbia and SE Alaska stocks seem to have increased over the same period. Nevertheless, we will assume that the 1960s biomass was slightly less (2/3rds) of the 1990s biomass. Hunt et al. (2000) suggest a mean biomass for Steller sea lions of 198 kg, with a corresponding Q/B of 24. Using the Siler life history table model as applied by Barlow and Boveng (1991) suggests an average mortality of 0.074, which we will use for a P/B value of the entire group (as Steller sea lions are the most abundant breeding biomass in the system).

The most recent estimates of the California sea lions population are of over 200,000 animals (204,000 to 214,000 based on pup counts reported in Carretta et al. 2002). Early 1990s estimate may have been closer to 178,000 animals (based on Barlow et al. 1996), and estimates for the 1970s were on the order of one-third to one-quarter of those from the mid-90s. The net productivity of the stock was been estimated at some 11% per year between 1980 and 1995 (Barlow et al 1996). California sea lions breed off southern CA and Mexico, where most juveniles and adults are found year-round, however some adult and sub-adult males spend fall and winter off of Northern California, Oregon, Washington and British Columbia. Bonnell et al. (1992) had sightings of a total of 50 animals in OR/WA waters in the mid-1990s, and estimated that a maximum of 3% of the population spent part of the year in northern waters (and then only seasonally). Consequently it seems reasonable to assume no more than 1500 (year round) animal equivalents in the NCC. Given a lack of insight regarding the distribution of California sea lions during the 1960s, we will estimate the abundance as ¼ of the estimate for the 1990's (or 500 animals). Hunt et al. (2000) estimate the mean size of California sea lions as 69 kg, with a corresponding Q/B of 24.

Northern elephant seals make biannual migrations from the breeding beaches in California to deep waters in the Gulf of Alaska. Males generally travel further north than females, as females generally stay south of 45 deg N. The total California breeding stock was estimated at approximately 84,000 animals in 1996 (Barlow et al. 1996), having recovered from extremely low levels in the 1900s (Stewart et al. 1990). Abundance estimates for the 1960s are not available, but pup counts reported in Barlow et al. suggest that the population was perhaps one tenth of its current size in that period. Condit and Le Bouef (1984) reviewed captures and sightings at sea that suggested that a significant proportion of animals from the central California colony were found in the coastal and offshore waters between Cape Mendocino and Cape Flattery (as well as further north along the BC shelf and even in the Strait of Juan de Fuca).[20] Recent work by Le Boeuf et al. (2000) generally confirms this. Of 23 males and 17 females tracked with satellite tags, two males foraged along Oregon and one along the Washington shelf break, and one female appeared to spend a substantial quantity of time along the Oregon shelf (although she moved west after one month). Eight other tags stopped transmitting at sea. At a very crude level, we might assume that 5% of the population (4200 animals) spend the majority of their foraging time (approximately 8 to 10 months per year) in the NCC. We will assume this fraction for both the 1960s and the 1990s period. The average weight of elephant seals based on Hunt et al. (2000) is 371kg, and because elephant seals rarely feed when hauled out or while in transit we will assume that Q/B for elephant seals is the equivalent of a full year (11.07).

The resulting ‘general’ sea lion estimates for the NCC are given above in Table A.5. Food habits data are scattered, but some data exists. Some food habits were reported by

Table A.5: Sea lion and elephant seal estimates for NCC

	number individuals	mean wt. (mtons)	B/area (mt/km^2)	QB
Steller sea lions	4921	198	0.0139	24.07
California sea lions	1500	69	0.0015	24.04
Northern elephant seals	4200	371	0.0223	11.07
all sea lions, elephant seals	10621		0.0377	16.38

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[20] Bonnell et al. (1992) reported only 19 sightings of elephant seals, generally further from shore and in warmer, deeper waters during summer and early fall (they also reported one elephant seal haul out, at Shell Island off Cape Arago, Oregon). They also report that their sightings per unit effort was less than half (43%) of that commonly observed in California waters. However, they also noted that dive duration studies suggest that elephant seals spend upwards of 85% of their time underwater (and, consequently, unobserved).

Fiscus and Baines (1966) for Stellar and California sea lions, however only one of the Stellar sea lions was taken off of Oregon; that specimen had two *Sebastes* spp. rockfish. Three other Steller sea lions from California had various rockfish and flatfish (specimens were taken in March), the rest of the sea lions were taken off of Alaska. Six California sea lions were found to have been eating anchovies, squid, hake and rockfish, these were amongst the most common prey items for California prey items in the food habits summary by NMFS (1997), along with herring, mackerel, lamprey, dogfish, skates and salmonids. Fiscus (1979) citing his earlier study and another study off of British Columbia suggested that Steller sea lions in the Oregon and Washington regions fed primarily on lamprey, herring, salmon, hake, rockfish, flatfish, squid, octopus and other species; but offered no quantitative estimates of relative importance. Diet data for elephant seals has been published based on animals returning to rookeries in California (Condit and LeBouef 1984) these studies likely illustrate only prey consumed in transit and LeBouef et al. (2000) suggest that the implications of these studies could be misleading. The studies which have been done indicate that elephant seals feed primarily on cephalopods, hake, sharks, skates, shrimps, crabs, and other invertebrates. The diet composition used in this model will consequently be 25% forage fish, 20% squid, 20% hake, 10% rockfish, 5% flatfish, 5% salmonids, 2% sardine, 2% mackerel, 2% mesopelagics, 2% benthic fishes, 2% dogfish, 2% skates, 1% sablefish, 1% lingcod and 1% epifauna.

Fur seals

Fur seals (*Callorhinus ursinus*) are amongst the most abundant pinnipeds in the North Pacific, and have a significant presence in the California Current throughout the winter (non-breeding) season. They have been intensively harvested since the end of the 18th century, yet despite land-based harvests of up to 50,000 animals (mostly pups) per year, the population was reportedly thriving into the late 19th century, when land harvests increased sharply, pelagic sealing peaked and the population began to dwindle. By 1909 the herd was at what is now considered to be a low point of approximately 300,000 animals (York 1987, NMFS 1993). The North Pacific Fur Seal Convention, which banned pelagic sealing and set limits on land harvests, was negotiated in 1911, and although harvests remained significant the population grew throughout the 20th century. The population reached a historical peak of perhaps 1.25 million animals in the early 1970s following the end of commercial harvest in 1968 (Angliss and Lodge 2002). This was followed by a decline in the early 1980s to a stock size of approximately 877,000 animals. Although some subsistence harvest continues, most sources of human mortality are thought to be associated with entanglement in fishing gear. The latest stock assessment is estimated as the number of pups at rookeries multiplied by a series of expansion factors (Angliss and Lodge 2002), and suggests a population of 942,000 animals in 2001. A smaller stock of approximately 4300 animals on San Miguel Island (off of Southern California) apparently originated from the Pribilof island stock in the late 1950s or early 1960s.

Estimating the number of northern fur seals in the California Current, and the corresponding trophic impact, is a difficult task. Most mature animals are in the Pribilof Islands, in the Eastern Bering Sea, during the breeding season (roughly May-September for males, June- November for females) and spend the remaining 7 to 8 months at sea.[21] To be consistent with existing models of the Eastern Bering Sea, Gulf of Alaska and elsewhere, we distributed fur seals throughout the North Pacific for all seasons based on the migratory patterns and data presented by Bigg (1982) and Bigg (1990). These two documents present detailed information regarding Northern fur seal migration and distribution, based on three data sets collected between 1955 and 1977 (sightings and kill data from the Fur seal commission, data from research and whaling vessels, and observations from ocean station Papa). Bigg (1982) presents the number of fur seals seen per hour in monthly 1° latitude by 2° longtitude grids, we used these data to distribute the density of fur seals into the PICES areas in the Northeast Pacific (BSC, ASK, CAN, CAS, ESA), average the densities regionally, then multiplied these mean densities by the total area of the PICES region to arrive at a total number of "animals years" per unit area (where an animal year would be the energetic requirements of one animal over a year period, but could represent two animals for six months, etc., in any given region). We did not attempt to correct these distributions for changes in foraging rates, sex ratios or mean size of animals.

Despite patchy distribution of effort in the sightings data (which did not cover much of the Gyre) the results, listed in Table A.6 below, seemed consistent with the general assumed patterns of distribution. Nearly half of the animal years are distributed in the Bering Sea, just over one third of the animal months in the Alaska Gyre and transition zone, and the remainder (approximately 96,000 and 56,000 respectively) of animal years in the Gulf of Alaska and California Current. As this seems consistent with even the emerging knowledge of fur seal distributions over space and time, we have used this approach to apportion fur seal densities and trophic impacts throughout the different regions modeled here. Consequently, the number of fur seal animal-years in the NCC is estimated to be 11,667. This is lower, yet comparable, with the peak estimate of approximately 7000 animals observed in April for the Oregon and Washington coast, based on 172 animals observed on winter surveys reported by Bonnell et al. (1992). For the 1960s model we would assume similar numbers, given that the population was then on its way to the 1974 peak. Based on Hunt et al. (2000) consumption rate is estimated

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[21] Bigg (1990) discusses the three primary migration patterns for different groups of animals. Older (4+) males leave the Pribilofs in September-October, winter offshore in the Gulf of Alaska, and begin re-entering coastal regions in April-May, returning to the Pribilofs between June and July. Mature females (generally age 3+) winter in the CCS between December and January through as late as June, returning to the Pribilofs between July and September. Juveniles tend to spend their first few years in the Alaska gyre, with some excursions into coastal regions. These patterns are generalized, as satellite tagging studies by Loughlin et al. (1999) and R. Ream (pers. com.) shows that some adult males and females overwinter in transition zone waters.

at 39.03, and the P/B ratio is set at 0.091 based on mortality estimates from Barlow and Boveng (1991).

Table A.6: Estimated fur seal distribution in the NE Pacific

PICES Region	surface area (sqkm)	biomass/area (mtons/sqkm)	fur seal numbers	fur seals/hour all months
EBS	1022000	0.0111	403914	3.917
GOA	429000	0.0063	96591	2.232
CCN	166000	0.0047	27667	1.652
CCS	129000	0.0063	28880	2.219
ESA	3622000	0.0030	384704	1.053

For diet information, Perez and Bigg (1986) reported on the stomach studies of over 18,400 fur seals caught from Southern California through Western Alaska between 1958 and 1974; and report detailed food habits by subregions. Their work suggests that off of Northern Oregon and Southern Washington their diets were approximately 15% market squid, 5% herring, 25% anchovy, 15% salmonids, 5% capelin, 25% rockfish and the remainder “other”. Off the northern Washington coast and La Perouse Bank, about 5% of their diet was market squid, another 5% miscellaneous squids, 30% herring, 10% salmonids, 3-4% shad, 10% rockfish, 5% sablefish and 10% miscellaneous fishes. Off of Oregon, diets were 18% market squid, 18% onychoteuthid squids, 22% anchovy, 4% saury, 15% hake, 18% rockfish and the remainder other prey. Off of Northern California, diets were nearly 25% market squid, 8% anchovy, 50% hake, 10% sablefish and the remainder other prey. Far beyond the shelf break, the diet was dominated by onychoteuthid and gonatid squids, which regularly comprised over half of the stomach contents, with lesser amounts of anchovy, myctophids, saury, hake, jack mackerel, salmonids, rockfish, and other prey. Although sardines were not noted in these diets, Clemens and Wilby (1933) described the contents of 25 fur seal stomachs off of Vancouver Island as consisting primarily of herring, salmon, squid and sardine. Interestingly, no flatfish species was mentioned as potential prey in this or other fur seal food habits papers. The final diet distribution used in the model was an average of these values (with the addition of sardines and a small amount of 'other' attributed to benthic fishes), such that the diet is 30% squid, 26% forage fish, 14.8% hake, 7% salmon, 12.6% rockfish (distributed amongst species), 3% sablefish, 2.4% mesopelagics, 0.6% jack mackerel, 2.5% sardine and 1.1% benthic fishes.

Gray whales

Nearly the entire Eastern North Pacific stock of roughly 22,000 gray whales (*Eschrichtius robustus*) migrate southward through the NCC in early winter and northward in mid to late spring. While most animals are thought to not feed during their migration, a small (but perhaps growing) number of animals appear to remain and feed in small groups between Northern California and British Columbia throughout the season. Calambokidis et al. (2002) estimated the numbers of animals involved in these summer feeding aggregations, currently referred to by NMFS as "Pacific coast feeding aggregation' whales, and suggested that between 61 (unique Ids) to 178 (Ids) animals may use the NCC for their principle summer feeding grounds. We will use the average of these two values, for an estimate of 120 animals. The average body weight of gray whales was taken by Hunt et al. (2000) as 19.6 tons, for a biomass in the NCC of 0.033 tons/km^2. Because there is no estimate of the number of whales that might have remained in the NCC in the 60s when the total population biomass was considerably smaller, we will estimate that approximately ¼ of these animals were present, and give the 60s population a rate of increase of 4.6% to put the population at the 1990s level in 30 years. Based on the same source, Gray whales Q/B is estimated at 8.872, and P/B is estimated at 0.037. Diet is primarily benthic amphipods in the Eastern Bering and Chukchi seas, although other stomach contents have included polychaetes, isopods, decapods, gastropods, bivalves, holothuroidians, echinoderms, cumaceans, fish larvae and other organisms as well as wood, sand, algae, pebbles and kelp (S. Harkness, pers. com). For this model, diet will be assumed to be 95% amphipods, 2.5% infauna, and 2.5% epifauna.

Baleen whales

Humpback (*Megaptera novaeangliae*), minke (*Balaenoptera acutorostrata*), and fin (*B. pysalus*) whales are the most frequently occurring baleen whales (other than gray whales) that occur in the NCC, although Blue (*B. musculus*) and sei (*B. borealis*) are occasionally noted. Green et al. (1992) estimated that humpbacks were the second most abundant large cetacean (after gray whales) off of the Oregon and Washington coasts based on aerial surveys. Barlow et al. (1996) estimate that the entire North Pacific population of humpback whales was estimated to be ~15,000 pre-exploitation, reduced to perhaps 1,200 by 1966. Recent estimates are that the North Pacific population exceeds 6,000 (Carretta et al. 2002). Currently there are thought to be three relatively separate populations in U.S. waters, the eastern North Pacific stock is the dominate stock in the NCC, which winters off of Central America and is distributed along the coast of California as far as British Columbia in the summer (Calambokidis et al. 1996, Carretta et al. 2002). Between 1910 and 1965 roughly 7000 humpbacks were taken in the California Current (see discussion in Chapter 1), the best estimate of the California Current stock size was 1024 in 2001. Mark-recapture estimates suggest that this population may have increased by as much as 8% per year from 1988 to 1998, and suggest an abundance of nearly 600 animals in 1991. Given a five to six-fold increase in the population since the 1960s, we will estimate the 60s population at 110 and give the 60s population a growth rate of 5.3% per year (equivelent to a biomass accumulation of 0.0011 tons/km^2/year).

A visual examination of sighting locations in Carretta et al. (2002) would suggest that nearly half of the sightings have occurred in the NCC between 1989 and 1996. Most of the sightings were well within the EEZ (and presumably within 1280 meters of depth) although many were likely to be far offshore. We will assume an average of 250 humpback whales in the NCC in the 1990s, and 50 in the 1960s. At 30 tons per whale, this is a biomass of 0.107 tons/km^2 in the 1990s and 0.021 tons/km^2 in the 1960s. From Hunt et al. (2002), a 30 ton humpback eats approximately 441 kg/day of food with a caloric density of 1000kcal/gram (which would be a fat euphausiids or a thin fish- given the propensity to eat herring, saffron cod, saury and other fish this could even go up a bit), which in turn translates into an annual Q/B of 7.58. We will assume all of this is consumed during their period on summer feeding grounds.

There have been only a few sightings of minke or fin whales, and there are no recent blue whale sightings north of Cape Mendocino (although there are many in the south) and only one west coast sighting of a Sei whale. The pre-exploitation abundance of fin whales in the North Pacific has been estimated to be on the order of 42,000 to 45,000 animals, which was reduced to an estimated 13,620-18,680 by the early 1970s (Carretta et al. 2002). The 2002 assessment suggests a total population of 1851 along the U.S. west coast, although the vast majority of sightings are south of Cape Mendocino (and of those that are in the north, most are quite far offshore). Green et al. (1992) estimated fin whales to be the fourth most abundant cetacean in Oregon and Washington coastal waters, although of perhaps 100 sightings between 1991 and 1996, only 4 were in the NCC. A gross starting estimate would be 1/25th of the total numbers, or 74 animals. With an average weight of 49 tons, the mean biomass per unit area would be 0.052 tons/km^2. For Minke whales, the most recent minimum assessment estimates 440 for the California, Oregon and Washington (including inland waters) stock (Carretta et al. 2002); whales in northern waters are thought to be migratory (although whales in inland waters, such Puget Sound and the Strait of Georgia, seem to have established home ranges). Of the sightings reported in the 2002 assessment, six of twenty were between Cape Mendocino and Cape Flattery, although all but one of these were likely offshore of the shelf. Consequently, we will estimate that only 1/20th of the 440 whales occur in the NCC. There are no data on trends in minke whale abundance or productivity; consequently parameters will be borrowed directly from the humpback and fin whales.

Table A.7: Baleen whale estimates for the 1990s NCC

	number individuals	mean wt. (mtons)	B/area (mt/km^2)	P/B
Humpback whales	250	30	0.1071	0.0377
Fin whales	74	49	0.0518	0.0377
Minke whales	22	6	0.0019	N/A
all baleen whales	346		0.1608	0.0377

Clapham et al. (1997) summarized food habits reported in of over 1500 humpbacks, 169 fin whales and 26 sei whales taken from California shore fisheries in Monterey Bay and Trinidad, California in the 1920s. California sardines, shrimp (presumably euphausiids), anchovy and herring were the most important prey items. Although there was significant variability between years and locations, sardines represented (the percentage of sardines in the diet of whales taken off of Trinidad, California was significantly less), sardines represented roughly 50% of the prey, followed by euphausiids (nearly 50%), anchovy, herring and unidentified fishes. Fin whales ate mostly euphausiids (65%), sardines (32%) and other prey, as did sei whales (77% euphausiids and 23% sardines). Food habits reported from California whaling stations in the 1950s did not include sardines, not a surprising result given the stock collapse that was even then diffcult to acknowledge. Instead, humpbacks were reported to contain primarily anchovies (64%) and euphausiids (36%), based on 149 whales examined by Rice (1963). During that same period, 237 fin whales also fed principally on anchovies (10%) and euphausiids (90%), and 83 sei whales fed on anchovies (36%), sauries (10%), sardines (1%), euphausiids (50%) and copepods (3%).

Food habits summarized by S. Harkness (pers. com) suggests that minke whales also feed primarily on euphausiids sand shoaling fishes, and to a lesser extent on copepods and pelagic squids. Arctic cod, saffron cod, Pacific cod, Atka mackerel, rockfish, smelt and salmon are also infrequent prey items for fin (as well as humpback) whales in the Bering Sea and Gulf of Alaska. In the absence of regionally specific information, we will estimate that in the 1960s, 65% of baleen whale diets in the NCC are euphausiids and 30% forage fishes, and 5% sardines (intended to "seed" sardines into the dynamic simulation).

Toothed whales, dolphins and porpoises

For purposes of simplicity, and because diets and other aspects of life history are not known in greater detail, the five principle species of toothed whales are aggregated into one group. Dall's porpoise (*Phocoenoides dalli*), harbor porpoise (*Phocoena phocoena*) and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) are amongst the most abundant toothed whales in the NCC, with Risso's dolphin (*Grampus giseus*) and northern right whale dolphin (*Lissodelphis borealis*) being the only other smaller toothed whales to occur in the NCC with any regularity. Abundance estimates are taken principally from Carretta et al. (2002), with insight from Green et al. (1992); mean body weights and consumption/biomass ratios are taken from Hunt et al. (2002). Barlow and Boveng (1991) using the Siler life history table model with data from both striped dolphin and harbor porpoises to arrive at toothed whale mortality rate estimates from 0.04 to 0.09, we will assume that 0.07 is a reasonable mortality rate. For most of these species, there are no estimates of population trends over time. Some mortality is inflicted on stocks as a result of fishing operations, such as marine set gillnet mortality to harbor porpoise in Washington, and mortality in California and Oregon shark drift gillnet fisheries as well as groundfish (whiting) fisheries for Dall’s porpoise, but mortality estimates are generally low (on the order of only 12 animals per year in each of these instances).

Dall’s porpoises are commonly seen in the shelf, slope and offshore waters of the California Current, with significant north-south movement on seasonal and internannual time scales in response to changing ocean conditions (a tendency to be further offshore during winter and spring). Carretta et al. (2002) estimates the size of the coastwide stock to be 116,016. The sightings data presented in Carretta et al. (2002) suggest that perhaps 1/6th to 1/4th of the Dall’s porpoise sightings occurred in the NCC. Yet this would suggest a significantly greater number of animals than the estimate made by Green et al. (1992), who estimated between 1550 and 2980 animals for the Oregon and Washington shelf and slope. Evaluating the sightings figure closer, we see that a cluster of large number of sightings in Northern California between Cape Mendocino and the Oregon border, which gives us reason to believe higher densities in that region. We will estimate 19,336 animals, or 1/6th of the population, in the NCC based on a low estimate of the percentage of sightings in the NCC.

Harbor porpoise are another abundant small cetacean throughout coastal and inland waters, and generally within 200 meters of depth. Carretta et al. (2002) estimated the abundance of the Washington/Oregon stock of harbor porpoises to be 44,644, again well below the estimate by Green et al. (1992) of 15,046. A relatively distinct northern California stock occurs between approximately San Francisco Bay and the Russian River, the abundance of that stock has been estimated at 15,198. Based on the rough distribution of area, we will estimate that 1/3rd of this stock, or 5066 animals, occurs in the NCC. Using the most recent assessment estimates rather than Green et al. (1992) estimates would thus suggest a total population of 49,710 animals in the NCC.

Pacific white-sided dolphins are another abundant species throughout the California Current; population estimates coastwide have been made as approximately 25,825 animals during 1990-1991 (Carretta et al. 2002). Sighting patterns suggest that the population is largely off of central and southern California in winter, movement in spring and summer months to the waters off of northern California. There are very few sightings north of Cape Blanco in any season, and perhaps 75 to 85% of all sightings were south of Cape Mendocino. We will estimate that 1/5 of the population may be present in the NCC at any given time; for a total of 5165 animals (and in the absence of trend data, we will use these estimates for both time periods).

Northern right whale dolphin are often associated with Pacific white-sided dolphin, and were described by Green et al. (1992) as the third most abundant small cetacean off of the Oregon and Washington coast (although due to the high variability of sightings, a total abundance was not estimated). The most recent assessment estimated the coastwide population at 13,705 (Carretta et al. 2002), but the majority (on the order of 75 to 80%) of sightings were south of Cape Mendocino. As sightings frequently occur outside the 2000 meter isobath, we will estimate that 1/5th of the population occurs in the NCC, for a total population number of 2741. Finally, Risso's dolphin are commonly seen on the shelf in the southern California Bight and in the slope and offshore waters of California, Oregon and Washington; the greatest concentrations of sightings are south of Cape Mendocino, although the distribution appears to be highly variable in response to changes in ocean conditions. Carretta et al. (2002) estimate a total WOC population of 16,483 animals, based on visual examination of the sightings data we will estimate that 5% of this population (824 animals) occurs in the NCC at any given time.

Table A.8: Small toothed whale abundance estimates for the NCC

	number individuals	mean wt. (kg)	B/area (mt/km^2)	QB
Dalls porpoise	19336	62	0.0171	27.47
Harbor porpoise	49710	31	0.0220	32.67
Pacific white-sided dolphin	5165	79	0.0058	25.82
Northern right whale dolphi	2741	105	0.0041	24.14
Rissos dolphin	824	224	0.0026	19.93
all small toothed whales	77776		0.0517	28.85

Diet data for toothed whales is available from Stroud et al. (1981) for 44 Pacific white-sided dolphin and 9 Dall's porpoise stomachs collected off of Oregon and Washington between 1958 and 1972. Salmonids and Onycorhynchus spp. squids were most commonly encountered prey items off of Washington in Pacific white-sided dolphin, although the authors point out that the Washington collections took place over a small area during a short time period and might not represent a major interaction between those species. Other prey off of Washington included capelin, eulachon, flatfish and trace amounts of squids. Further south, northern anchovy, hake, market squid and other squids were the most abundant prey items for white-sided dolphins. Additionally, these authors cited descriptions of predation on large sardines, Pacific saury and jack mackerel from earlier studies. Dall's porpoise off California also fed on anchovy, hake, saury and squids; off of Washington their diet also included eulachon, rockfish, sablefish, flatfish, shad, capelin, and gonatid squids. Fiscus and Niggol (1965) reported on the stomach contents of five Dall's porpoises off of central and northern California, for all the only identifiable stomach contents were squid and squid beaks. A short paper by Scheffer (1953) reported the stomach contents of two Dall's porpoise taken off Oregon, each of which contained 45cm long hake. No data are available for harbor porpoise, although Pauly et al. (1998) describe a 'generalized' harbor porpoise diet as comprised of 5% benthic invertebrates, 20% small and large squid, 30% small pelagics and 45% miscellaneous fishes. Based on this extremely imperfect information, we will make a rough estimate of the diet composition of this assemblage to be 20%

cephalopods, 35% forage fish, 15% hake, 5% mackerel, 5% sardine, 7% rockfish, 5% mesopelagics, 2.5% sablefish, 2.5% shelf flatfish, 1% salmon and the remainder miscellaneous fishes (benthic fishes, dogfish, etc.).

Sperm whales

Sperm whales breed in the lower latitudes in the winter, migrate throughout the North Pacific in the summer, and are regularly seen throughout the Northern California Current in all seasons but winter (Green et al. 1992); the most recent estimate of total numbers along the west coast (California, Oregon and Washington) was 1407 (Carretta et al. 2002). A visual inspection of the locations of sightings would suggest that approximately 10% of these sightings were in the NCC, or somewhere on the order of 140 animals. The average biomass of sperm whales into the waters offshore of the shelf break throughout the North Pacific, were they to be evenly distributed over space and time, would be 0.202 tons/km^2 (assuming a population of 930,000 evenly spread throughout the North Pacific Basin, including the Bering Sea, with an average weight of 18.5 tons based on Trites and Pauly 1997). Considering only the slope waters in the NCC model (those between 183 and 1280 meters), the corresponding number of sperm whales would be 315, more than double the rough estimate based on the most recent NMFS assessment. Spread evenly throughout the NCC model, the biomass per unit area would be estimated at 0.083 tons/ km^2. However in the interest of being conservative, we will be consistent with the most recent stock assessment and assume 140 animals in the NCC, for a total biomass of 0.037 tons/km^2. Sperm whales have been hunted in the North Pacific since the 1800s, with the greatest reported take between 1947 and 1987 (approximately 250,000 animals in the North Pacific). The population is thought to have grown since the cessation of large-scale pelagic whaling (Carreta et al. 2001), however as there are no published estimates of trends either basin-wide or locally no trends will be assumed for either period in the model.

Consumption rate is assumed to be 6.609, based on Hunt et al. 2002, and P/B 0.02. Clapham et al. (1997) reported that 12 sperm whales caught off of central and northern California fed primarily on “octopus,” sardines, sharks (presumably dogfish) and squid. Rice (1963) reported that of 54 sperm whales taken off of central California in the late 1950s and early 1960s, 52 (96%) had fed on squid, 11% had fed on octoputs, 24% had fed on longnose skate, 11% had fed on brown cat sharks or angel sharks, 4% had fed on sablefish, 4% had fed on lingcod, and a few had evidence of feeding on myctophids and unidentified fishes. Kajimura and Loughlin (1988) also report that sperm whales taken off British Columbia fed on sablefish, brown cat shark, longnose skate, hake, rockfishes and king-of-the-salmon. Based on these qualitative descriptions, we will assume a diet of 65% squid and 35% fishes; with the latter broken out to 10% rockfish, 5% hake, 5% sablefish, 5% dogfish (and cat) sharks, 5% skates, 2.5% lingcod and 2.5% mesopelagics.

Killer whales

Killer whales (*Orcinus orca*) are infrequently observed off of Oregon and the Washington coast, and observations may be from any of three distinct Northeast Pacific resident and transient stocks (there are two more Alaskan stocks). Most California, Oregon and Washington sightings are thought to be of either the Eastern North Pacific transient stock or the Eastern North Pacific offshore stock, although sightings can include animals from the Eastern North Pacific Southern resident stock (based in Washington and British Columbia inshore waters) as well. Based on summer/fall shipboard line transects in the 1990s, the total number of killer whales within 300 nautical miles of California, Oregon and Washington coasts was estimated as 819 animals (Carretta et al. 2002); and photo identification of 161 animals suggested 2/3rds of those photographed (105 of 161) belonged to the transient stock. The majority of these sightings (perhaps 2/3rds) were off of the California Coast south of Cape Mendocino, and more modest numbers were offshore of perhaps 100km or so. Green et al. (1992) also found killer whales to be widely distributed along the Oregon and Washington coasts, with five pods (total of 33 animals) observed during their surveys, usually at or near the shelf break. In the absence of better information, we will estimate that some 100 killer whales are found in the NCC (very possibly an overestimate), and use an average weight of 2280 kg, and a Q/B of 11.15 based on Hunt et al. (2000), for an estimate of 0.0033 tons/km^2.

The residents and transients have obvious differences in food habits, the latter are widely held to be mammal eaters, and the former primarily fish and squid eater. Yet both residents and transients occur in this system, and the extent to which transients may consume fish is uncertain. Added to this, very sparse diet data is available. Fiscus and Niggol (1965) report on the stomach contents of an Orca collected off of the Farallon islands, which contained at least one California sea lion, one toothed whale, and as many as four elephant seals. Transient orcas have also been frequently observed preying on porpoises, grey whales and other baleen whales in the California Current. Pauly and Christensen (1996) estimated the diet of transients to be 20% toothed whales, 5% baleen whales, and 75% pinnipeds. Hunt et al. (2000) provide diet estimates of killer whales of 10% squid, 10% forage fishes, 40% misc. fishes and 40% marine mammals, and we will use this estimate as the basis for our diet. In the Bering Sea, Orcas were observed to prey on sablefish, arrowtooth flounder and halibut off of longlines, while ignoring pollock, cod, grenadier, rockfish and thornyheads (Dahlheim 1995, Yano and Dahlheim 1995); while there is no reason to expect similar habits in the NCC, we will attempt to be consistent with these observations. For non-mammal prey, we will assume 10% squid, 10% forage fishes, 10% salmonids, 10% sablefish, 5% skates, 5% dogfish, 5% arrowtooth flounder, and 5% halibut. Since gray whale predation in the California Current has been observed several times (including off of Newport, OR, as cited in Green 1992), we will partition the mammal prey into 5% gray whales, 5% baleen whales, 20% pinnipeds (5% harbor seals, 5% N. fur seals and 10% sea lions/elephant seals) and 10% toothed whales.

A. 11 Key balancing issues

Balancing the model required substituting poorly defined estimates of standing biomass for juvenile groups of rockfish and flatfish with top-down balances. It was also necessary to do a top-down balance for Tanner crabs; as estimates based on survey results were insufficient to balance the model and doubtlessly underestimated the biomass (particularly of juveniles) substantially. One particular problem related to interactions between small flatfish and benthic fish, both of which ostensibly prey on each other. Although this is true, it creates some odd dynamics and consequently the diet of each on the other was reduced to 1% (down from 2-5%). Cannibalism within each of these groups was also reduced to to 1% (for small flats increased infauna, epifauna, euphausiids and amphipods by 1% each, for benthic fish increased infauna and epibenthic fauna by 1% each, amphipods by 0.5%). I also reduced benthic fish consumption of small flatfish, moving most of that predation into juvenile flatfish (as well as trace predation on juvenile rockfish and juv. Roundfish), and reduced small flatfish cannibalism, moving most of that into predation on juvenile flatfish

The biomass of rex sole and the P/B of rex sole and of small flatfish was also raised slightly, to account for increased productivity of juveniles (which are the likely source of most of the mortality for these assemblages). Rex sole biomass had essentially been adult biomass estimated (poorly) from surveys and a surplus production model; as juveniles or small adults were un- or under sampled this biomass estimate was increased from 0.21 to 0.28; the P/B of rex sole was also increased from 0.37 to 0.5 and from 0.5 to 0.7 for small flatfish; note that these maintain the P/B estimates within the ‘upper bounds’ of estimated adult mortality rates, and thus are a reasonable estimate of combined juvenile and adult production/mortality. Predation on rex sole by skates and yellowtail rockfish was also reduced to balance rex sole production.

As many marine mammal populations were depleted in the 1960s (gray whales, baleen whales, sea lions, harbor seals) from whaling and culling it was necessary to either increase predation by Orcas on finfish or reduce the biomass of Orcas significantly; the latter was ultimately chosen as the preferred option and the biomass was reduced to 0.001 (perhaps 25 animals). While there is no evidence for trends in transient orca populations in the area, the presumption would be that these highly migratory animals simply spent more time elsewhere during periods of low marine mammal abundance; obviously there is no evidence of this. Even with this reduction, the marine mammal proportions in the diet compositions had to be altered; with predation on gray whales, harbor seals and sea lions reduced substantially; compensated for by increased predation on fur seals, toothed whales and baleen whalesIt was also necessary to slightly adjust Orca diet habits; the percentage of fur seals was reduced from 5% to 2%, harbor seals were reduced from 5% to 3%, sea lions were increased to 11%, baleen whales were increased from 5% to 8%, gray whales were reduced to 4.5%, and small toothed whales was increased from 10% to 11%.

Other balancing problems included too much predation on thornyheads by sablefish (a consequence of the significantly higher sablefish biomass in the 1960s relative to the 1990s) which was compensated for by increasing sablefish predation on other juvenile and adult rockfish (also in greater abundance in the 60s relative to the 90s, especially canary, POP, and shelf rockfish), as well as juvenile and adult lingcod (which had very little trophic impact). English sole also had too much predation pressure on them; given that their biomass was not significantly greater than it was in the 1990s, but many of its predators (sablefish, lingcod) were at much higher biomass levels; for these two predators in particular some of the diet composition was shifted from English sole to Dover sole, rex sole and petrale sole (all of which were more abundant in the 60s). Both sablefish and shortspine thornyheads also required a reduction in the amount of fisheries offal in their diets; in both cases this was reduced to ~1% (from ~8%), and this was compensated for largely by an increase in forage fish and rockfish predation for sablefish, and primarily rockfish predation in thornyheads. Finally, to account a presumably complete (or nearly so) lack of sardines in the 1960s model, sardine predation was reduced to low levels for all sardine predators (and redistributed to either mackerel or forage fish), minor fishing pressure was maintained (essentially "faux" fishing, although based on the fact that sardines were indeed encountering unsustainably high exploitation rates relative to their low productivity in the 60s) and sardines were given a very high EE in the expectation that this would act as a proxy aid in their "recovery" when fishing was removed.

Hake in the 1990s present a new sort of problem- in that the population was declining, substantially, in the face of heavy fishing mortality and low recruitment. The P/B rate for this period was roughly 0.18, as estimated by increase in the mass of the population, and consequently was considerably lower than the natural mortality rate (0.23). To address this, the observed population decline over the 1988-1992 period was incorporated into the biomass accumulation term, and the GE from the 1960s model was used to estimate Q/B, rather than assume Q/B had remained constant. Although the assumption of a constant GE is also a poor one, given the greatly reduced size-at-age of hake in the 1990s it is clear that consumption rates and growth were much reduced from historical levels. Consequently, the assumption of a constant GE would be more consistent with a larger hake population that had a lower (per capita) consumption rate. The same approach was used for sablefish, but for a different reason. For sablefish, P/B had increased over time, and consequently Q/B would be expected to be greater in the 1990s (consistent with the idea that many of the older individuals had been removed, and the population was skewed towards a younger age composition). For the other assessed species (primarily rockfish) P/B and Q/B for the 1990s were estimated from the growth data and population age composition as described in Chapter 1, these two species were treated with greater care as a result of their disproportionately greater impact on model structure.

Given that the 1990s model had less rockfish and more rockfish predators, the diet composition from the 1960s led to significant model imbalances. Predation on most rockfish had to be reduced, often significantly, from 1960s levels (although this does not infer a decline in predation rates from the same predators). More specifically, the percentage of sablefish, POP, canary, widow, yellowtail, black/nearshore, shelf and slope rockfish was reduced slightly to significantly in the prey compositions of toothed whales, sperm whales, sea lions, harbor seals and fur seals. This predation was re-allocated to the species that are known to be both significant historically in the diets of these animals, as well as more abundant in the 1990s than the 1960s; primarily Pacific sardine, Pacific hake, Pacific/jack mackerel and modest increases for harbor seals (that feed closer to shore) in small flatfish and English sole.

VITA

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