Climate, ecology and productivity of Pacific sardine (*Sardinops sagax*) and hake (*Merluccius productus*)

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This is to certify that I have examined this copy of a doctoral dissertation by

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Abstract

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The volatility of pelagic fisheries in the California Current (CC) system has long been a challenge for the west coast fishing community. Over the last century, a number of west coast pelagic stocks have undergone large fluctuations in abundance. Faced with sudden collapses in once thriving fisheries (e.g. Pacific sardine in the late 1940s and Pacific hake in the 1990s), resource managers have struggled to understand the causes behind these fluctuations and develop appropriate responses. The overarching objective of this dissertation is to understand how climate, through its effects on pelagic habitat, influences production variability of sardine and hake in the CC system. I show that climate forcing of the CC system results in dynamic distributions of Pacific sardine and hake populations. I find pelagic habitat for these species to be dynamic, its boundaries changing according to time/space changes of the physical oceanographic variables defining it. By considering the oceanography of pelagic habitats I reveal important links between atmosphere-ocean variability and fishery productivity. A more complete understanding of these links could provide us with tools to better manage the fisheries. The focus of this study on two ecologically and commercially important species will allow for a better understanding of ecosystem variability as a whole, an understanding that will be relevant within the context of the current management structure.

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Dedication

For my parents, Barbara and Corrado, to whom I owe my spirit, passion and inspiration.

Water, stories, the body,
all the things we do, are mediums that hide
and show what is hidden.

Study them, and enjoy this being washed
with a secret we sometimes know,
and then not.

Rumi

INTRODUCTION

The volatility of pelagic fisheries in the California Current (CC) system has long been a challenge for the west coast fishing community. Over the last century, a number of west coast pelagic stocks have undergone large fluctuations in abundance. Faced with sudden collapses in once thriving fisheries (e.g. Pacific sardine in the late 1940s and Pacific hake in the 1990s), resource managers have struggled to understand the causes behind these fluctuations and develop appropriate responses. Scientist and managers alike are increasingly calling for a "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 in the management context." (Field, 2004). Pelagic species are the best indicators of climate forcing effects as their environment is directly influenced by atmosphere-ocean variability (Benson, 2002). The overarching objective of this dissertation is to understand how climate, through its effects on pelagic habitat, influences production variability of sardine and hake in the CC system.

West coast pelagic stocks have undergone wide fluctuations in abundance over the last century (figure 0.1). A classic example is the California sardine (*Sardinops sagax*): this stock dominated the west coast fisheries of North America for much of the first half of the twentieth century. The population then collapsed in the late 1940s, and remained at very low levels until the mid-1980s, when it began to rebuild. Pacific mackerel (*Scomber japonicus*) experienced two major peaks in abundance in 1932 and 1982 (Pacific Fisheries Management Council, 2004), with abundances remaining at very low levels in between. The northern anchovy (*Engraulis mordax*) began to increase in the mid-1960s and experienced a very brief period of high abundance in the mid-1970s (Jacobson et al., 1996, 2001). Pacific hake (*Merluccius productus*) abundance has also been highly variable over the last 30 years (1965-2003), with peaks occurring near the mid-80s and decreases in recent years to record low levels (Helser, 2004)

Climate variability has been known to impact production of a number of CC species (Beamish, 1993; Francis and Hare, 1994; Mantua et al., 1997; Francis et al., 1998; Hare and Mantua, 2000;

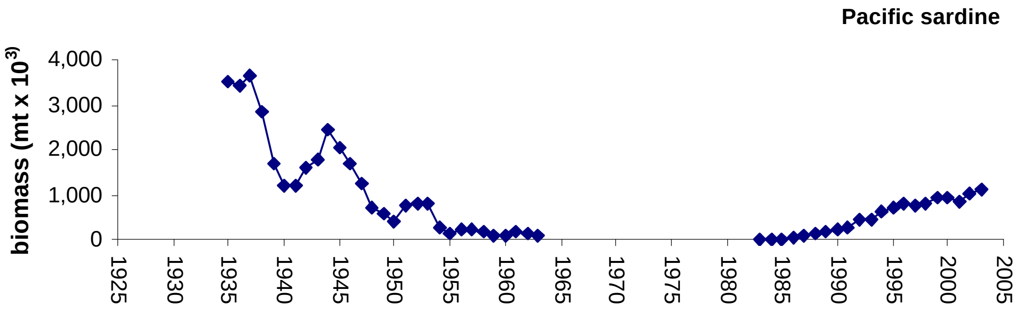
Hollowed et al., 2001; Smith and Moser, 2003). Studies have often attempted to link climate forcing directly with stock production variability, aggregating impacts across large spatial scales and range of species. The focus of these studies has been on directly linking climate with fish abundance metrics, often overlooking a more detailed analysis of how climate forcing impacts the ocean habitat of pelagic species. Habitat represents the common link between climate and production variability of marine ecosystems. Marine habitat is usually discussed as an area delimited by relatively static features (e.g. bottom type), but for pelagic species habitat is usually a dynamic entity. Its boundaries are changing according to time/space changes of the physical oceanographic variables defining it. Considering the oceanography of pelagic habitats has potential to reveal important links between atmosphere-ocean variability and fishery productivity. A more complete understanding of these links could provide us with tools to better manage the fisheries.

I have chosen to focus on Pacific hake and sardine for a number reasons. The two species spend different stages of their life histories in habitats located at both extremes of the CC system and migrate across the entire latitudinal range to reach those habitats. Both species occupy diverse habitats, making them good candidates for the study of climate-habitat interactions, and the influence these interactions may have on population dynamics of marine organisms. Also, their different life histories coupled with their worldwide distribution, will provide instructive comparisons. Finally, sardine and hake are important trophic links in the CC system, as well as important species in Pacific Northwest fisheries. The focus of this study on two ecologically and commercially important species will allow for a better understanding of ecosystem variability as a whole, an understanding that will be relevant within the context of the current management structure.

Changes in the physical environment can occur on a variety of spatial and temporal scales, and each one of those scales is likely to reveal a pattern. Ecologists are therefore challenged to understand how patterns are formed at whichever scales they manifest (Levin, 1992). Observing behaviors at different temporal and spatial scales will reveal a more complete picture of the system. While one scale might produce an image of noise, another will reveal a pattern. All these patterns then come together to produce the observed variability. The CC system exhibits great spatial diversity in physical and biological processes (Parrish et al., 1981; Strub et al., 1990; Mendelssohn et al., 2003). Thus, in this type of system, searching for patterns at a number of scales becomes crucial. However, it is important to recognize that while at times the scales of study chosen will be a product of the scientific question asked, most often these scales are imposed on us by technological or logistical constraints (Steele, 1978). For retrospective studies, the choice of analysis will ultimately not only be a product of the question asked, but also of the available data.

This dissertation will consider a variety of temporal and spatial scales to explore how sardine and hake use space to compensate for variability in their environment. Climate induced variability in the CC system creates a dynamic range of habitat suitability. Sardine and hake essentially seek out favorable areas within their larger habitat which allows them to optimize recruitment through various climate cycles. The adults conduct extensive migrations poleward in the summer to feed off the Pacific Northwest coast, and equatorward in the winter to spawn off southern California (Benson et al., 2002). The northern and southern limit of their migrations appears to be related to oceanic conditions (Ware and McFarlane, 1989) that fluctuate under climate forcing. Changes in population abundance have been observed in connection with changes in distribution patterns. For example, sardine are more productive when their spawning habitat shifts north and/or their population inhabits much wider geographic areas (Smith, 1990; McFarlane et al., 2002).

This dissertation is divided into five chapters. Chapter One summarizes the oceanography of the California Current, and the ecology of sardine and hake, reviews existing hypotheses explaining the link between productivity of the species and environmental variability, and outlines a conceptual model to explain the different response of sardine and hake to climate forcing. Chapters Two through Four describe patterns of sardine and hake habitat distribution, and explore mechanisms that generate and maintain those patterns. Realizing the broad and complex nature of subject, I do not provide a comprehensive analysis of mechanisms involved but rather a set of examples that help shed some light on the subject. Chapter Two focuses on sardine spawning habitat off the coast of southern California, examining the relationship between climate, spawning habitat characteristics and recruitment. Lack of data precludes a comparable discussion of the hake spawning habitat. Chapter Three focuses on hake adult habitat, outlining the mechanisms underlying variability in migration behavior and a model to quantify adult hake habitat. Chapter Four focuses on sardine adult habitat, outlining the temporal changes in the geographical distribution of this species and its relationship to climate, quantifying sardine adult habitat and exploring different scenarios of climate forcing effects. Finally, in Chapter Five I discuss the consequences of patterns observed in the previous chapters on the dynamics of sardine and hake populations and their implications for both single species and ecosystem management.



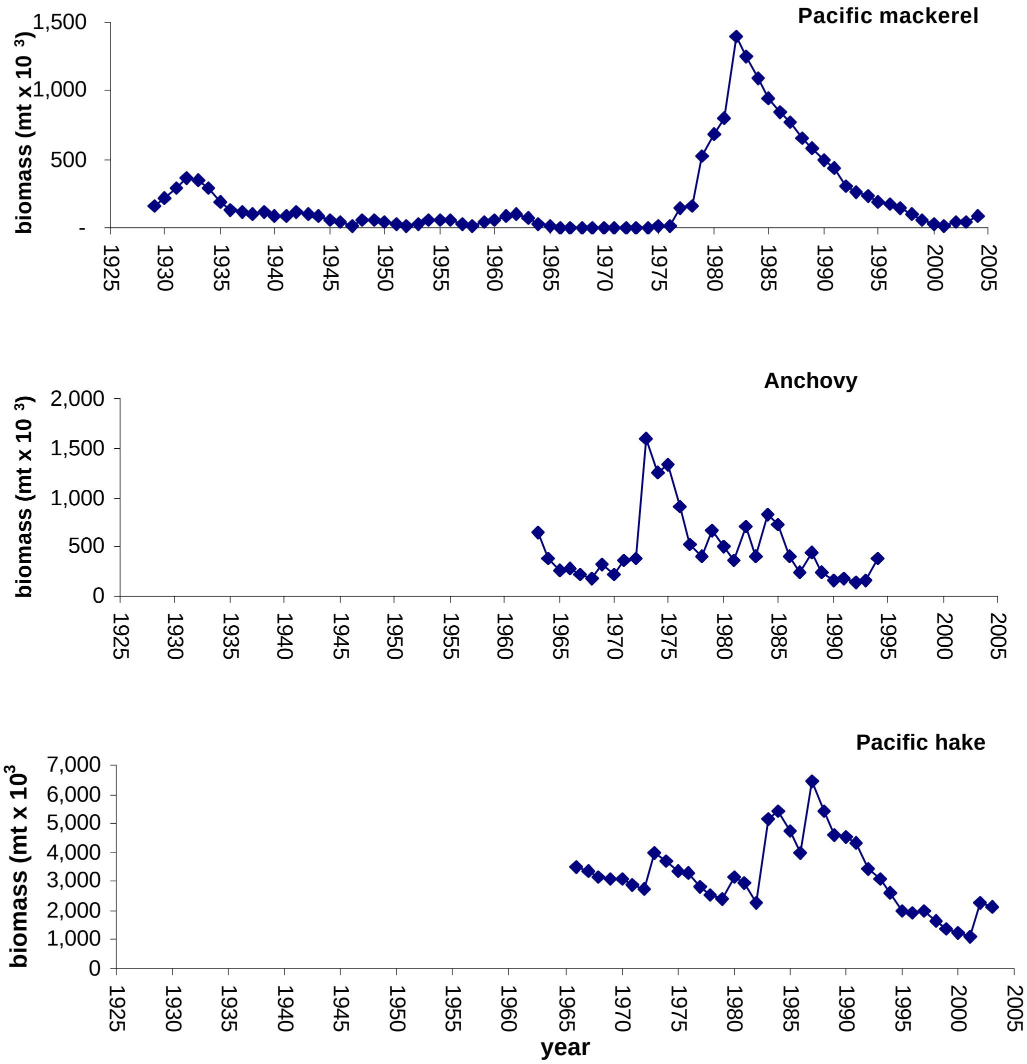


Figure 0.1: Time series of coastal pelagic adult biomass. Data for Pacific sardine, from 1935-1964 for age 2+, from Jacobson and MacCall (1995). For 1983-2003 for age 1+ from PFMC (2004). Data for Pacific mackerel, for age 1+ from PFMC (2004). Data for Pacific hake for age 3+ from Helser, 2003.

CHAPTER 1. Exploring the links between climate and the ecology and production of Pacific hake and sardine: a conceptual model.

1.1 INTRODUCTION

Climate forcing of the California Current (CC) has been identified as one of the main drivers of large fluctuation in the physical and biological conditions of this system (Logerwell et al., 2001; Francis et al., 1998; McGowan et al., 1998; Roemmich and McGowan, 1995; Chelton, 1981). Three dominant modes of climate variability have been identified: the El Niño Southern Oscillation (ENSO-interannual scale), the Pacific Decadal Oscillation (PDO-interdecadal scale), and the 'Victoria Pattern'. A growing body of literature exists describing these events and their impacts on the structure and functioning of marine ecosystems (Wooster and Zhang, 2004; Mantua and Hare, 2002; Hare and Mantua, 2000; McFarlane et al., 2000; Mantua et al., 1997; Trenberth, 1997; Bond et al., 2003; Peterson and Schwing, 2003).

Pacific hake (*Merluccius productus*) and Pacific sardine (*Sardinop sagax*) are two coastal pelagic species dominating the CC system. Both species spawn off the coasts of California and northern Mexico and exhibit large-scale migrations to feed in regions off Oregon, Washington and British Columbia (figure 1.1). Pacific hake abundance increases rapidly due to single large year classes (figure 1.2a), while the sardine population slowly increases in response to a series of strong year classes (Figure 1.2b).

This chapter provides a summary of the physics of the CC system, and the ecology of Pacific sardine and hake. I also evaluate hypotheses regarding factors controlling the annual production and spatial distribution of these two species and formulate a conceptual model linking climate and production variability of Pacific hake and sardine. I base my model on the following hypotheses:

- Production signatures of pelagic fish are a result of life history strategies (including choice of habitat) unique to each species.

- Climate impacts population dynamics of pelagic species primarily by forcing changes in pelagic habitat.

This chapter is divided into three sections. First I describe the physical environment and the ecology of Pacific sardine and hake. Next I outline existing hypotheses formulated to explain sardine and hake abundance variability in the CC system. I examine these hypotheses in the context of life history characteristics and habitats occupied by these two species. Finally, I discuss how a comparison of life histories and ecosystem constraints leads to the development of a conceptual model. Implications for the study of CC Ecosystem variability and management are briefly considered and will be revisited in chapter 5.

1.2 THE PHYSICAL ENVIRONMENT

In this section I provide an overview of the physical environment of Pacific sardine and hake. The following three references provide the basis for the description that follows: Lynn and Simpson (1987), Strub et al. (1990), Hickey (1998).

1.2.1 Large-scale currents

Pacific hake and Pacific sardine inhabit the CC Ecosystem. The CC Ecosystem is associated with the CC, an equatorward eastern boundary current in the North Pacific. The CC links the eastward flowing West Wind Drift in the north (approximately 45-50^0) to the westward flowing North Equatorial Current in the south (approximately 20^0 N). The CC, the North Equatorial Current and the West Wind Drift are part of the Central Pacific Gyre (generally termed Subtropical Gyre), located south of the Alaska Gyre (generally termed Subarctic Gyre) (Figure 1.3). The latitude at which part of the West Wind Drift turns south and becomes the CC varies from year to year, as does the location of the Subarctic Boundary (Fulton & LaBrasseur, 1983), the border between the Alaska Gyre and Central Pacific Gyre.

The CC consists of a slow, broad (from 50 to 1000 km offshore), shallow (upper 500m) year round flow carrying a mixture of Subarctic and Subtropical Gyre water equatorward along the coast. South of Pt.Conception (~35^{0}N) a portion of the current turns north to become the Southern California Countercurrent; at times this flow does not make it north and it recirculates in the Southern California Bight to become the Southern California Eddy. This poleward flowing current is matched at depth by the California Undercurrent (CU) which flows along the slope carrying saltier warm water from Baja, California to Vancouver Island, BC (~50^{0}N). The CU is relatively narrow (ca. 10-40 km) and strongest at depths of 100-300m. Additional surface poleward flow originates close to Pt. Conception in the winter as the Davidson Current and travels north to at least Vancouver Island. In comparison with the CU, the Davidson Current is generally broader (ca. 100km), stronger and it extends seaward of the slope. Figure 1.4 shows a simplified schematic of the seasonal large-scale flow in the CC system, developed by Femia (2003) and based on Hickey (1998). On average, the CC is strongest in spring and summer when it moves inshore, closer to the shelf-break. The CU develops in the spring and persists through late fall. The Davidson Current dominates the flow over the shelf and beyond the shelf brake through winter.

1.2.2 Forcing mechanisms

Ocean circulation in this area varies on seasonal, interannual and interdecadal base.
Two dominant atmospheric pressure regimes drive most of the seasonal as well as the interdecadal variability: the Aleutian Low Pressure system (ALP) during winter, and the North Pacific High Pressure system during summer (Emery and Hamilton, 1985; Mantua et al., 1997). Winds associated with these regimes drive the large scale surface flow, as well as the local coastal surface currents and onshore and offshore Ekman transport (Tabata, 1975; Hickey, 1979). Superimposed on this is the equatorially generated El Niño Southern Oscillation (ENSO), an anomalous large scale ocean-atmosphere system associated with strong fluctuations in ocean currents and surface temperatures, which leads to changes on an interannual scale (for detailed description of the process see Bakun, 1996; Trenberth, 1997). A positive ENSO phase (or El

Niño) is characterized by warmer than average sea surface temperatures in the central and eastern equatorial Pacific Ocean, reduced strength of the easterly trade winds in the Tropical Pacific, and an eastward shift in the region of intense tropical rainfall. A negative ENSO phase (or La Niña) is characterized by the opposite – cooler than average sea surface temperatures in the central and eastern equatorial Pacific, stronger than normal easterly trade winds, and a westward shift in the region of intense tropical rainfall. Although ENSO is centered in the tropics, the changes associated with El Niño and La Niña events affect climate around the world including the west coast of North America.

All of the above sources of variability affect a suite of local ocean conditions (Chelton, 1981; Lynn and Simpson, 1987; Pares-Sierra and O'Brien, 1989; Strub et al., 1990). For example El Niño can cause warming of the upper waters off the California coast, a depression of the nearshore thermocline, weakening of the CC, weakening in upwelling intensity, and an intensification of poleward flow (Chelton et al., 1982; Simpson, 1992; Hollowed, 1992; Hickey, 1998). Changes in the position and strength of the ALP have also been linked to the PDO pattern and the 'Victoria pattern'. The PDO, defined as the leading principal component of monthly sea surface temperature anomalies in the North Pacific (above 20 ^{0}N) (Mantua and Hare, 2002), has shifted from a negative phase in 1976-1977 to a positive phase. Recent discussion has centered on whether there has been a shift to a negative phase in 1999 (Green, 2002; Peterson and Schwing, 2003). The 'Victoria pattern', defined as the second principal component of monthly sea surface temperature anomalies in the North Pacific (Bond et al., 2003), became persistently negative since 1989 and 1990, then shifted to strongly positive values between 1998 and 1999. Both of the above inter-decadal patterns of climate variability are characterized by changes in North Pacific sea surface temperature, sea level pressure, and wind patterns. For example, during negative PDO regimes coastal sea surface temperatures in the Gulf of Alaska and California Current tend to be cool, during positive PDO regimes they tend to be warm. Changes in the ALP have also been associated with displacements of the center of winter surface wind stress, which changes the mean direction of wind stress near the coast of North America. For example, during the most recent warm PDO phase (post 1977) the ALP deepened and moved eastward (Mantua et al., 1977), which generated stronger eastward winter wind stress

(Parrish et al., 2001). This can lead to changes in the relative strength of the CC (Smith and Moser, 2003) as well as variations in the bifurcation of the subarctic current (Chelton and Davis, 1982), and hence the position of the northern boundary of the CC and the amount of subarctic water entering the CC. There is some evidence (Logerwell et al., 2003; Gargett, 1997, Polovina et al., 1995) that the extent of spring/summer upwelling in the CC system is influenced by the ALP. The ALP influences winter water column stability (e.g. depth of mixed layer, strength of stratification) which can facilitate or inhibit coastal upwelling of nutrient rich waters.

Both local and remote forcing produces physical and biological variability in the CC system. Strub et al. (1990) describe four sources of remote oceanic forcing: 1) the inflow from the west of the West Wind Drift at the northern boundary of the CC system; 2) the onshore transport of central Pacific waters from the west; 3) Kelvin and coastally trapped waves propagating into the region from the south and 4) the oceanic component of El Niño from the south. Local forcing differs according to region (Strub et al., 1990). Local winds in the north (north of 48^0 N) are primarily poleward and strongest in winter, weak equatorward winds are observed in summer (Hickey, 1998). Local winds in the south (~$25\text{-}35^0$ N) are equatorward on average and reach a maximum in late spring. Local winds at mid-latitudes ($35\text{-}48\ ^0$N) have a strong seasonal cycle (persistent equatorward winds in summer and intermittent poleward winds in winter). Spring and summer equatorward winds drive offshore Ekman transport of surface waters, causing an upwelling of deeper cooler and more nutrient rich waters. As in other coastal upwelling systems around the world, this generates very productive areas supporting some of the largest fisheries in the world.

There are a number of topographic features that also influence flow in the coastal regions of the CC system (Hickey, 1998). For example, summer upwelling between the Strait of Juan de Fuca (North Washington) and Cape Blanco (eastern Oregon) leads to the development of an equatorward upwelling jet over the continental shelf (Pierce et al., 2000; Hickey, 1998; Barth et al., 2000). In the vicinity of Cape Blanco, the energy of this jet intensifies as the shelf narrows (Bateen, 1997; Barth et al., 2000). South of Cape Blanco the jet turns offshore, and interacts with the CC. This leads to the development of eddy fields and meanders, which distinguishes the region south of Cape Blanco from that to the north (Strub et al., 1991). The region between Point Conception and San Diego (the Southern California Bight) has a wide shelf (ca. 20km). (Hickey, 1998). Wind speed from summer to fall is reduced by an order of magnitude here compared to other areas of the CC, which considerably reduces forcing by wind stress during this time of year. Local upwelling in this region generally occurs in winter and early spring.

1.2.3 Spatial and temporal patterns of variability

The CC system exhibits great spatial diversity in physical and biological processes (Parrish et al., 1981; Strub et al., 1990; Mendelssohn et al., 2003) both latitudinally (north to south) and longitudinally (east to west). A number of researchers (Strub et al., 1990; Parrish et al., 1981) describe the characteristics of regions that make up this system. From their descriptions, the image of a heterogenous California Current Ecosystem clearly emerges. From a ‘latitudinal perspective’ this system can be divided into three sub-areas (4 if we include Baja): the region north of Cape Blanco (the Washington-Oregon area), the region between Cape Blanco and Cape Mendocino (the northern-central California area), and the regions south of Pt. Conception (the central-southern California area). Figure 1.5 outlines the unique suite of physical and biological characteristics that characterizes each one of these sub-areas.

From a ‘longitudinal perspective’ the equatorward flow of the CC and its interaction with coastal and off-shore waters define specific regions within the system. For example, Lynn and Simpson (1987) describe three domains in the southern region of the CC (30-35^0 N) as one proceeds west to east across-shelf, based on dynamic height amplitude and seasonal phasing: the oceanic, the transition and the coastal domain. The oceanic domain is mostly controlled by large-scale air-sea interaction processes and large-scale dynamics (>1000 km). The transition domain is dominated by non-seasonal events like offshore mesoscale eddies and meanders located in the high-speed core of the California Current. The coastal domain is dominated by alterations in the inshore surface and subsurface current structure.

The image of a heterogeneous system also emerges when one considers characteristics such as sea surface temperature (SST) and mixed layer depth (MLD). Mendelssohn et. al. (2003) analyzed the annual cycle of the thermocline in the CC system and revealed two areas: 1) the northern and coastal regions and 2) the southern and offshore regions. Northern and coastal regions experience considerable spring and summer cooling at depth due to seasonal upwelling and at the surface due to penetration of subarctic water into the northern and coastal regions (Peterson and Schwing, 2003). These regions can also experience penetration of northern subarctic waters (Peterson and Schwing, 2003), which might also contribute to cooling at depth. The southern and offshore regions, dominated by subtropical water and associated species, reveal very little annual variability and reduced summer and autumn stratification in the seasonal mixed layer.

Spatial patterns of temporal (interannual to interdecadal) variability in the CC system have been observed (Strub et al., 1990; Lluch-Cota, 2002; Mendhelssohn et al, 2003). Variability in the southern region of the CC (south of 35^0N) appears to be dominated by an inter-annual signal, while variability in the northern region of the CC (north of 35^0N) appears to be mostly dominated by a seasonal signal (Strub et al., 1990). Mendhelsson et al (2003) discuss responses to atmospheric forcing in different vertical layers of the CC system. They hypothesize that there might be times and regions where the mixed layer and the thermocline dynamics in and below the mixed layer are dominated by different processes, with the ENSO signal dominating variability below the mixed layer, and the PDO signal dominating variability in the mixed layer. Lluch-Cota (2002) describes the climate signal in the CC system to reflect the combined effects of both the PDO and ENSO at varying degrees in both time and latitude.

1.3 EXISTING HYPOTHESES REGARDING CLIMATE FORCING ON PACIFIC SARDINE AND HAKE ABUNDANCE

A number of researchers have discussed the importance of both local and large-scale physical forcing on the population dynamics of marine organisms in the Northeast Pacific (Francis et al., 1998; Hollowed et al., 1987; Hollowed and Wooster, 1991; Beamish, 1994). The production regimes of many species and their demonstrated relationships with climate (Logerwell et al., 2001; Hare and Mantua, 2000; Hare and Francis, 1995) suggest that there are strong linkages between climate and the oceanography and biology of the CC system. A number of hypotheses have been formulated for sardine and hake to try and explain these linkages (Bakun & Parrish, 1980; Bailey, 1981; Bailey et al., 1982; Hollowed & Bailey, 1989;Ware & McFarlane, 1989 Cury & Roy, 1989; Hollowed, 1992; Jacobson & MacCall; Dorn, 1995; Bakun, 1996; Sakuma & Ralston, 1997; Saunders & McFarlane, 1997; Checkley, 2000; Smith & Logerwell, 2000; Logerwell et al., 2001; MacCall, 2002). A comparison of these hypotheses reveals a remarkable overlap in processes invoked to explain the population variability observed (table 1.1). Given such overlap, one might expect two species inhabiting the same area to be subject to the same climate forcing mechanisms and thus exhibit similar production variability patterns. The production patterns for Pacific sardine and hake (figure 1.6) do not support this. The population dynamics of these two species are clearly different: hake population dynamics show evidence of an ‘interannual signal’ while sardine population dynamics show evidence of an ‘interdecadal signal’.

1.4 LIFE HISTORY AND ECOLOGY OF SARDINE AND HAKE

In this section I outline life history characteristics (summary provided in table 2a & 2b, Figure 1.6) as well as the ecology of sardine and hake.

1.4.1 Life history

Spawning

Pacific sardine can live up to 20 years, but most live less than 8 (Schwartzlose et al, 1998). They become sexually mature at age 2. Adults are batch spawners, with large fish producing up to 200,000 eggs per spawning season (Schweigert, 1988); they school and spawn in the upper 165m of the water column mostly in waters off the coast of southern California and the Baja peninsula as far offshore as 185 km from the coast (Schwartzlose et al, 1999). Spawning begins in January and peaks in April/May although it can extend into the summer (Hart, 1973). Spawning has also been reported to occasionally occur as far north as the mouth of the Columbia River, Oregon and close to Vancouver Island, Canada (Scofield, 1934; Ahlstrom, 1948; Smith, 1990; Hargreaves et al., 1994; McFarlane and Beamish, 2001; McFarlane et al., 2002).

Pacific hake can live up to 27 years, but only a small number of individuals older than 15 have been caught (Gustafson, 2000). Individuals become sexually mature at age 3 (Bailey et al., 1982). Adults are batch spawners, but the number of eggs released/adult are three times lower than the eggs released/adult by sardine (Smith, pers. comm.). The main hake spawning ground is located in the offshore waters of the southern California Bight up to 400 km offshore (Bailey et al., 1982). Spawning occurs as deep as 500m from January to April with January and February being the peak months (Bailey et al., 1982). Spawning has also been reported to occur in waters off the coast of Oregon and British Columbia (Hollowed, 1992; Horne & Smith, 1997).

Egg incubation and larval stages

Sardine eggs are released in dense aggregations close to the surface. The larvae live close to the surface and mostly feed on micro-zooplankton (Schwartzlose et al, 1998). The eggs and larvae inhabit frontal waters bordering the California Current up to 100km offshore (Checkley, 2000) and large offshore eddies (Logerwell & Smith, 2001; Loggerwell et al., 2001).

In contrast, Pacific hake eggs are mostly found in loose aggregations at the base of the thermocline (Bailey et al., 1982; Moser et al., 1997). The larvae are also mostly found at the base of the thermocline (Bailey et al., 1982; Hollowed, 1992; Matarese et al., 1989) between 25-75 meters (Cass-Calay, 2003), usually in waters over the shelf break and slope, on average 155 km offshore (Bailey, 1981). As with sardine, hake larvae are also sometime found in off-shore eddies (Logerwell et al., 2001). If no pycnocline exists, eggs and larvae may be distributed throughout the mixed layer (Bailey et al., 1982). The larvae feed on a large range of prey (70-200um), mostly copepod eggs, nauplii, copepodites and adults (Sumida and Moser, 1980).

In summary, the vertical dimensions of the sardine and hake larval habitat are different: sardine live above the thermocline in the mixed layer and hake live at the base of the thermocline, below the mixed layer (figure 1.6).

Juvenile feeding and distribution

Not much is known about juvenile hake and sardine, as it has been very difficult to sample this part of the populations (Paul Smith, pers. comm.). Juveniles of both species presumably share the same nursery areas, located throughout the coast of central and southern California, with younger fish located in the mixed layer inshore of the 400 m isobath (Bailey et al., 1982; Smith, pers. comm.). Juvenile hake mainly eat copepods and euphausiids (Buckely and Livingston, 1997), while juvenile sardine feed on micro-zooplankton (Smith, pers. comm..).

Adult feeding and distribution

Hake and sardine have been known to undertake seasonal migrations from spawning grounds in the south to feeding grounds in the north (figure 1.1) (Hollowed, 1992; Bailey et al., 1982; Schwartzlose, 1998). The migration of Pacific hake has been well studied, while that of sardine is not as well known. Both species have been documented to migrate as far north as British Columbia and southeast Alaska to feed (Jacobson & MacCall, 1995; Hollowed & Bailey, 1989). The age distribution of their population affects their migration, with older fish migrating further north (Dorn, 1995; Schweigert, 1988).

The average length of adult sardines is 15-22 cm. Adults form schools inshore (depths < 100m) but have occasionally been reported to be offshore as well (MacCall, pers. comm.). Sardine are filter feeders, their diet switching from being entirely carnivorous (zooplankton) in the juvenile stage to being omnivorous (phytoplankton, zooplankton) in the adult stage (Smith, pers. comm.).

The average length of adult hake is 34-40 cm (Bailey et al., 1982). They begin their seasonal northward feeding migration inshore (depths < 100 m) during late spring/ early summer; in late fall they move offshore and then return south to spawn (Bailey et al., 1982) (figure 1.1). Females have been reported to leave the spawning grounds and begin their migration north earlier than males, perhaps in synchrony with the spring onset of the poleward flowing California Undercurrent (Saunders & McFarlane, 1997). Hake feeding migrations are both horizontal (south to north seasonally) and vertical (surface to depth diurnally) (Bailey et al., 1982). In summer, feeding hake are concentrated in large mid-water aggregations centered on the shelf break from central Oregon to north Vancouver Island (Saunders & Mcfarlane, 1997). Their diet relies primarily on euphausiid in spring and summer and increases in piscivory with size (Bailey et al., 1982; Buckley & Livingston, 1997). Adult hake have been identified as potential predators of juvenile salmon (Emmett and Brodeur, 2000), and are known to be voracious predators of euphausiids, shrimp, herring and other forage fish (Field, 2004). Cannibalism has been observed on the hake feeding grounds, with older larger hake eating smaller younger hake (Dorn, 1995; Buckley & Livingston, 1997).

1.4.2 Ecology

Factors influencing mortality of early life history stages

Year class strength of sardine and hake has been related to conditions affecting mortality during their first year of life (Parrish, 1981; Hollowed, 1992; Bailey et al., 1982; Bailey, 1981; Smith et al., 1992). A synthesis of the literature reveals that both species on average share the same broad spawning area, centered in waters off southern/central California, as well as juvenile nursery area centered along the coast of California. The ecosystem challenges presented to hake and sardine young are multiple and range from food availability, to predation, to advection away from favorable habitats (Bailey and Francis, 1985; Hollowed and Bailey, 1989; Jacobson & MacCall, 1995; Logerwell & Smith, 2001).

The prevailing hydrographic conditions during the first year of life have often been related to recruitment success (Bailey, 1981; Bailey et al., 1982; Francis et al., 1989; Hollowed & Bailey, 1989; Hollowed, 1992). Table 1.1 outlines the major physical processes that are thought to influence early life history survival of Pacific hake and sardine. These processes can be grouped into two categories: 1) those that affect transport to and away from favorable nursery areas; 2) those that concentrate prey. Cold years with intense upwelling have been reported to be detrimental to larval survival of Pacific hake and sardine (Bailey, 1980; Bailey, 1981; Francis et al., 1989; Bailey & Francis, 1985; Hollowed & Bailey, 1989; Hollowed and Wooster, 1991; Jacobson & MacCall, 1995; Horne et al., 1997). These years present significant advection offshore and south away from favorable inshore juvenile nursery areas, which results in lower growth rates, lowered prey abundance and higher predation mortalities. During warmer years (e.g. El Niño), reduced upwelling intensity produces reduced offshore advection, which may favor larval survival (Hollowed & Bailey, 1989; Hollowed, 1992; Smith et al., 2001). Eddies (both offshore and nearshore), jets and meanders have also been shown to be areas of increased larval survival for sardine and hake, possibly due to increased prey availability and retention in favorable habitats (Logerwell & Smith, 2001).

Thus, while both species appear to be influenced by the same physical forcing variables, the processes underlying the response may differ between species because the vertical dimensions of their respective habitats were not taken into account.

Factors influencing spawning behavior

Sardine spawning behavior varies in both time and space. In cold years, spawning occurs mainly in late spring/early summer (figure 1.7a) and south to waters off northern Baja. In warm years, spawning peaks in April (figure 1.7b) and shifts north (extending to waters off central California, Oregon and British Columbia) (Smith, 1990; Checkley, pers. comm. 2001; McFarlane et al., 2002; Parrish, unpublished manuscript, 2002).

In contrast to sardine, hake spawning reveals that compared to sardine, hake spawning behavior varies in space, but not in time. Hake spawning activity is reported to occur mostly from January to April every year (figure 1.8) (Bailey and Francis, 1985; Bailey et al., 1982). Hake spawning activity, as inferred from larval abundance, has been observed to shift north extending to waters off northern California and central Oregon during warm periods, and to shift south extending to waters off Baja California during cold periods (Bailey and Francis, 1985; Horne & Smith, 1997; Saunders & McFarlane, 1997).

In summary, both hake and sardine spawning activity shifts in space: equatorward during cold periods and poleward during warm periods. Sardine spawning behavior also shifts in time, with the majority of spawning occurring in the spring and summer (April-July) during cold periods and the majority of spawning occurring in the spring (April) during warm periods (figures 1.7a & 1.7b).

Factors influencing migration behavior

Considerable variability exists in the migration behavior of both hake and sardine. Based on scale deposition data, hake seems to have inhabited northern waters more consistently then sardine during the last two centuries (figure 1.9) (Holmgren, 2001; Strom pers. comm.). The migratory behavior of hake is influenced by a number of physical processes. Overall, feeding grounds extend farther north during El Niño years (Dorn, 1995; Bailey et al., 1982). Generally speaking, in the CC system these are years of stronger poleward flow, decreased CC flow, weak upwelling, and warm coastal sea surface temperatures (Hollowed, 1992; Bograd et al., 2001; Lynn and Bograd, 2002; Bograd and Lynn, 2003). Warmer temperatures and weaker upwelling results in lower nutrient enrichment leading to low zooplankton availability in southern waters (Horne and Smith, 1997) especially for younger fish whose diets rely primarily on euphausiids (Grover et al., 2002; Roemmich and McGowan, 1995). Reduced prey availability may motivate older hake, who are able to migrate, to seek better conditions further north. Strong poleward flow might also aid migration by reducing energy expenditure. The location of the subarctic boundary could also potentially influence the extent of hake migration. The location of this boundary, and thus of the prey/predators associated with it, changes interannually (Fulton & LaBrasseur, 1983). As this boundary shifts north or south so might the northern extent of the hake migration. The physical conditions associated with this boundary may support particularly rich feeding grounds. Limited northern migration years result in higher spatial overlap between adult and juvenile hake. This degree of spatial overlap has implications for cannibalism, with higher overlap increasing the probability of cannibalism (Buckley and Livingston, 1997). The depletion of younger fish may have a significant effect on the cohort and ultimately on the population as a whole (Horne and Smith, 1997).

The migratory behavior of sardine is not well understood. During their second year of life fish migrate northward in the early summer to feed, and travel south in the fall to spawn (Schweigert, 1988). Similar to hake, warm temperatures have been reported to shift sardine distribution to the north (Jacobson & MacCall, 1995; Smith, 1990). Increased population size also shifts their distribution to the north (McFarlane et al., 2002; Parrish, unpublished manuscript). The causal mechanisms behind these shifts are not very clear. It is possible that mechanisms similar to the ones outlined for shifts in adult hake migrations are in place for sardine. However, it is important to remember that adult hake live deeper in the water column compared to sardine, and thus in habitats potentially subject to different physical constraints.

1.5 DISCUSSION

Existing hypotheses might lead us to believe that similar mechanisms are controlling production variability of sardine and hake. However, close examination of these hypotheses within the context of life history strategies of each species reveals both similarities and differences. A comparison of the strategies adopted by sardine and hake should allow us to gain insight on biological responses to climate.

Both hake and sardine aggregate at the time of spawning and release a large number of eggs (up to 200,000 eggs per individual during a spawning season). Under favorable conditions a large number of larvae are hatched. These individuals can then disperse effectively exploring a wide range of habitats. In comparison with hake sardine invest more energy in sampling the environment. Sardine release three times more eggs than hake do. Compared to hake, they can also spawn for a longer period of time (figure 1.10) and have more consistently done so over a wider geographic area compared to hake. This suggests that sardine's strategy is to be more opportunistic, to sample as much habitat as possible until the "right place" is found.

On the other hand hake, while still exploring a wide range of habitats seem to have developed a set of life history traits targeted to overcome specific constraints presented by the habitat. Both species, for example, have egg and larval nursery areas located in the offshore region of the southern California Bight. However, hake eggs and larvae are located at depth-below the mixed layer (figure 1.6) where advection via Ekman transport is minimal and mixed-layer turbulent diffusion is absent. Hake larvae are also equipped with large mouths, which help them find prey at depth where food is limited. The colder temperatures at these depths slow down metabolic requirements, possibly another strategy to deal with lower food availability. On the other hand, sardine are located in areas possibly richer in food concentrations (the mixed layer) (figure 1.6), but where advection is a major problem. By living in the mixed layer sardine are also more immediately susceptible to variability in both transport processes and in primary and secondary production, compared to hake living deeper in the water column.

The migratory behavior of hake also points to specific strategies developed to deal with a constantly changing environment. Both species probably migrate to sample a larger number of environments and overcome seasonal and interannual variability in food distribution in a specific area. However the timing of hake spawning is less variable than that of sardine (figure 1.10). The shorter spawning season allows females to leave the spawning grounds earlier taking advantage of the northward flowing California Undercurrent, which peaks during the spawning period. By ‘riding these currents’ they might be expending less energy in migration and have more available for feeding and spawning. Hake also seem to have more consistently migrated: both paleorecords and catch data attest to the regularity of their northward migration.

1.5.1 Conceptual model

Based on this review I offer a conceptual model to explain differences in production patterns of hake and sardine. I propose that sardine and hake do not have the same response to climate variability. Their responses are driven by 1) the life history strategies adopted by each species, and 2) the physical variability of the habitats they occupy. Sardine are capable of both planktivory and zooplanktivory. They are also able to sample habitats widely, and do so by investing energy in a number of different directions. This wide spread investment allows them to quickly adapt to and exploit favorable environmental conditions, but capitalization requires a sequence of good years as they are a short lived species and one good year class is not enough to produce a surge in biomass. As a result, the impact that a single strong year class has on the overall production of sardine is small (figure 1.11). One could hypothesize that sardine life history traits have evolved to seek out and immediately thrive on good habitats. These traits (diets, spawning behavior, age structure) and their associated plasticity allow them to do well during times when most other species are doing poorly (e.g. El Niño conditions). Once that good habitat is discovered, individuals are imprinted to return there (Cury, 1994). If that habitat remains favorable for more than just one year, this will produce a sequence of good year classes increasing the abundance of the population. If however the favorable habitat is not persistent, sardine will not be able to take advantage of it, and their productivity will suffer. This implies that a higher frequency of good years (e.g. El Niño years) within a given period would favor this population.

Hake life history traits point to strategies that focus more on overcoming multiple constraints posed by their environments, rather than ensuring wide sampling (in time and space) of their habitat. Like sardine they have evolved to efficiently exploit good conditions, but they have done so by developing very specific strategies. In order for hake to thrive, a specific sequence of conditions need to occur, and when this happens hake can quickly and effectively capitalize on the conditions. Their age structure (longer lived species), in contrast with the sardine, is such that one good year class has the potential to have large effects on the overall biomass of the population. The impact that a single strong year class has on the overall production of hake is large compared to sardine (figure 1.11).

In addition to behavioral strategies, I also consider physical conditions of the habitats the two species inhabit and how these might affect their responses to climate variability. Sardine live in waters above the thermocline that have been described as being primarily influenced by decadal variability (Mendelsohn et al., 2003). Hake live in waters below the mixed layer, described as mainly influenced by interannual variability (Mendelsohn et al., 2000). Thus, the physical conditions of their habitats vary at different time scales, and this ultimately results in different responses to climate variability.

1.6 CONCLUSIONS

The comparison between sardine and hake life histories points to two important aspects of the study of the CC system specifically, as well as of ecosystems in general. The first has to do with spatial patterns of variability in the CC system and links between them. We are presented with two species that broadly inhabit similar areas and are subject to similar constraints. Sardine and hake spend different stages of their life histories in habitats located at both extremes of the CC system and migrate across the entire latitudinal range to reach those habitats. The migratory behavior of hake and sardine provides a link between these two areas. Hake for example are very important predators in the northern region of the CC system (NCC) (north of Cape Mendocino, ~41^{o} N) (Field, 2004). Their migration into these waters has potentially large impacts on a number of fish and other organisms they prey upon, not to mention implications for the fishery that operates in these waters. Survival of their early life history stages, influenced by processes that occur in the southern region of the CC system (SCC) (south of Monterey Bay, ~38 ^{o}N), is an important determinant of their abundance and hence the numbers of individuals that migrate into the NCC. The presence of these migratory fish brings into the system a signal resulting from processes occurring outside the area.

The second has to do with approaches to the study of population dynamics. Life history strategies of species, including choice of habitat, are the result of past and present selective pressure (Cury and Fontana, 1988). These strategies represent a sub-set of many possible solutions adopted by species to cope with their environment and ensure survival. By considering the nature of these strategies we can gain new insight to the study of biological response to climate variability. This will also allow us to better analyze the responses of stocks to ecosystem constraints and thus provide a needed perspective to the study of population dynamics: an ecological/evolutionary perspective.

In the end one should ask the question: ‘how does all this fit into resource management?’ Managers and scientists alike are shifting their focus towards developing ecosystem approaches to management of natural resources. Developing management strategeis that address ecosystem efects of fishing will force us to consider the ecological consequence of a fishery on the target fish population, on multispecies fisheries, as well as on the habitat and prey of those populations. Fishing inevitably changes the natural relationship between the harvested fish and their ecosystem, whether it is their habitats, predators or prey. Life history traits have evolved so that each population performs optimally in relation to exigencies and possibilities of its specific habitat (Longhurst, 2002) and the associated variability. An uncontrolled fishery might force a species to depart from its natural life history traits and take on new ones. For example by fishing down the older age classes of a population, the age structure of a population might entirely change. These new traits may not be appropriate to the habitat they have evolved to live in, or to cope with the variability associated with this habitat, and thus degrade their specific fitness. In order to prevent this from happening, a deeper understanding of the importance of life history strategies and their relationship with environmental constraints is necessary. This dissertation is an attempt to help move us in this direction.

Table 1.1: Processes invoked to explain variability in early life history.

PROCESS	PACIFIC SARDINE	PACIFIC HAKE
Eddies, Jets and meanders	Bakun, 1996; Smith & Logerwell, 2000; Logerwell et al., 2001; MacCall, 2002	Hollowed & Bailey, 1989; Sakuma & Ralston, 1997; Logerwell et al., 2001
Coastal upwelling	Bakun & Parrish, 1980; Jacobson & MacCall, 1995; Bakun, 1996	Hollowed & Bailey, 1989; Bailey, 1981
Alongshore advection	Bakun, 1996	Bailey et al., 1982; Hollowed, 1992; Dorn, 1995; Saunders & McFarlane, 1997
Frontal zones	Bakun, 1996; Checkley, 2000	Hollowed, 1992
Zooplankton distribution and abundance	Ware & McFarlane, 1989	Ware & McFarlane, 1989
Vertical mixing	Cury & Roy, 1989; Bakun, 1996	

Table 1.2a: Early life history characteristics.

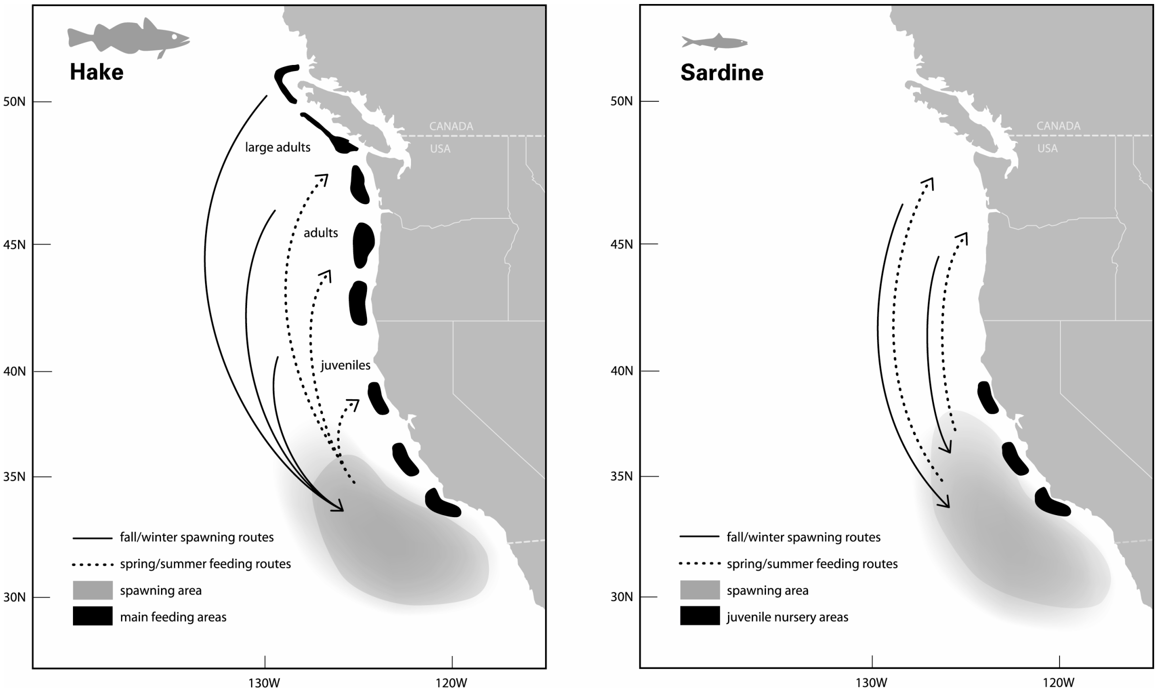
CHARACTERISTIC	PACIFIC HAKE	PACIFIC SARDINE	REFERENCE
Batch spawners	Yes	Yes	Schwartzlose et al., 1998 Smith, 1995
Days to hatch	4 to 5	3	Bailey et al., 1982
Hatch location	Below the mixed layer	Mixed layer	Bailey et al., 1982 Moser et al., 1997 Schwartzlose et al., 1998
Size at hatch	2.4mm	3.5mm	Bailey et al., 1983
Larval prey	Copepods	Copepods	Sumida & Moser, 1980
Larval predators	Invertebrates, marine mammals	Invertebrates, marine mammals, tuna, seabirds	Bailey et al., 1982 Bailey & Francis, 1985
Juvenile nursery location	Central California Shelf to shelf break	Central California Shelf to shelf break	Bailey et al., 1982 Schwartzlose et al., 1998
Juvenile prey	Copepods, euphausiids	Micro-zooplankton	Buckley and Livingston, 1997 Smith, pers. comm..
Juvenile predators	Tuna, sharks, dogfish marine mammals	Tuna, marine mammals, seabirds	Buckley and Livingston, 1997 Smith, pers. comm..

Table 1.2b: Adult characteristics.

CHARACTERISTIC	PACIFIC HAKE	PACIFIC SARDINE	REFERENCE
Average length	34-40cm	15-22cm	Bailey et al., 1982 Schwartzlose et al., 1998
Maximum age	27(12)*	20 (8)*	Matarese et al.,1989 Methot & Dorn, 1995 Gustafson, 2000
Age of 50% mature	3	2	Bailey et al., 1982
Batch spawners	Yes	Yes	Schwartzlose et al., 1998 Smith, 1995
Number of eggs released per individual	Up to ~ 70,000/spawning season	Up to ~200,000/spawning season	Schweigert, 1988; Smith, pers. comm.
Spawning depth	Below 200m	Above 165m	Smith, pers. comm. .
Spawning season	Jan.-April (Jan., Feb.**)	Jan.-August (Ap., May**)	Schwartzlose et al., 1998 Bailey et al., 1982
Spawning location	Outer shelf/slope up to 400 km offshore; offshore eddies	Shelf/outer shelf; offshore eddies	Smith, 1995 Logerwell et al., 2001 Bailey et al. 1982
Adult prey	Euphausiids, fish, shrimp	Euphausiids, diatoms	Schweigert, 1988 Bailey et al., 1982 Buckley and Livingston, 1997
Adult predators	Sablefish, tuna, sharks, dogfish	Tuna, marine mammals, seabirds	Gustafson, 2000
Age at maturity	3 to 4	2	Hart, 1973 Gustafson, 2000
Feeding distribution	Slope and outer shelf break	Coastal to mid-shelf with occasional offshore observation	Bailey et al., 1982
Migration factors	Larger fish migrate further north	Larger fish migrate further north	Dorn, 1995; Schwartzlose et al, 1999
	Females begin migration earlier		Saunders & McFarlane, 1997
	Females time migration with intensification of poleward currents		Saunders & McFarlane, 1997

*number in parenthesis indicates age mostly caught

** majority of spawning observed during this period



a **b**

Figure 1.1: Generalized representation of hake (a) and sardine (b) habitats in the CCS. Distances from shore of habitats represented are not drawn to scale.

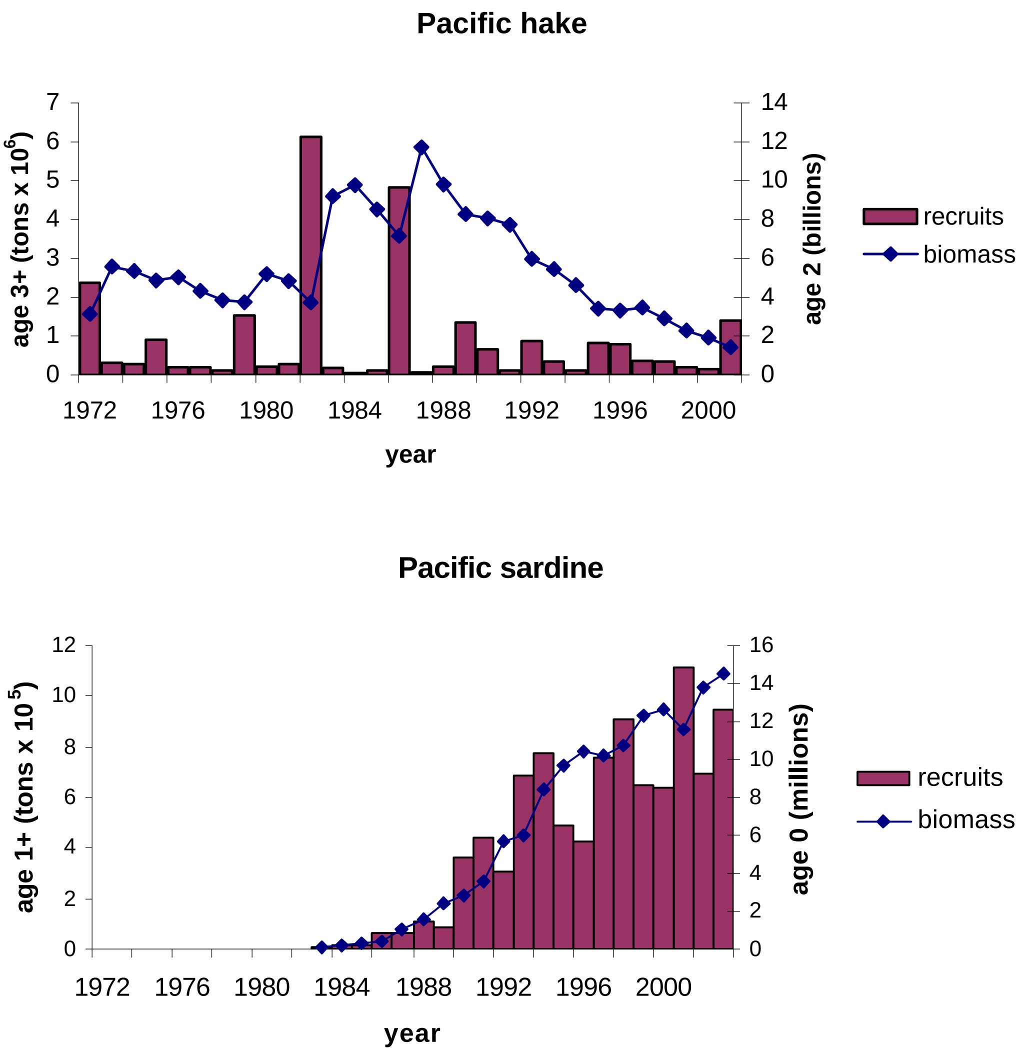


Figure 1.2: Time series of Pacific hake biomass and recruitment (data from Helser, 2002) (upper panel) and.Pacific sardine biomass and recruitment (data from Conser et al., 2002) (lower panel).

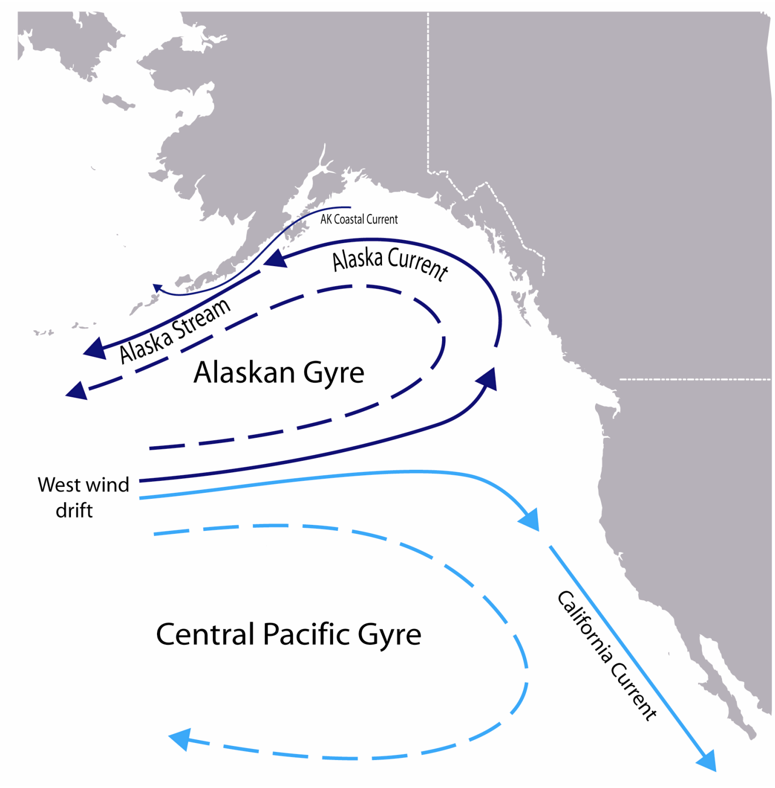


Figure 1.3: Generalized representation of circulation in the North Pacific.

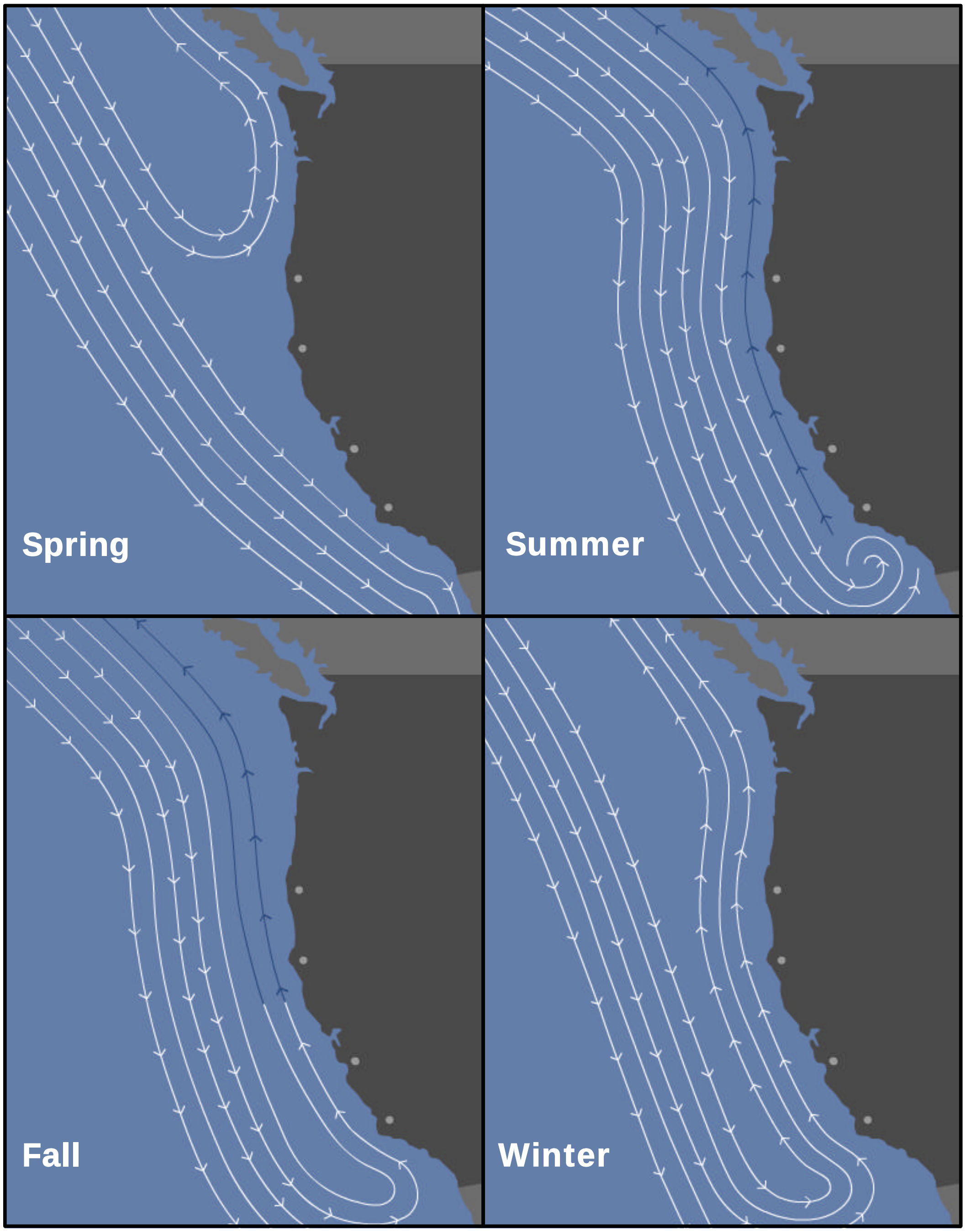


Figure 1.4: Schematic diagram illustrating mean seasonal circulation of large-scale boundary currents off the U.S west coast. Surface currents in white, subsurface in blue (Femia 2003, based on Hickey 1998).

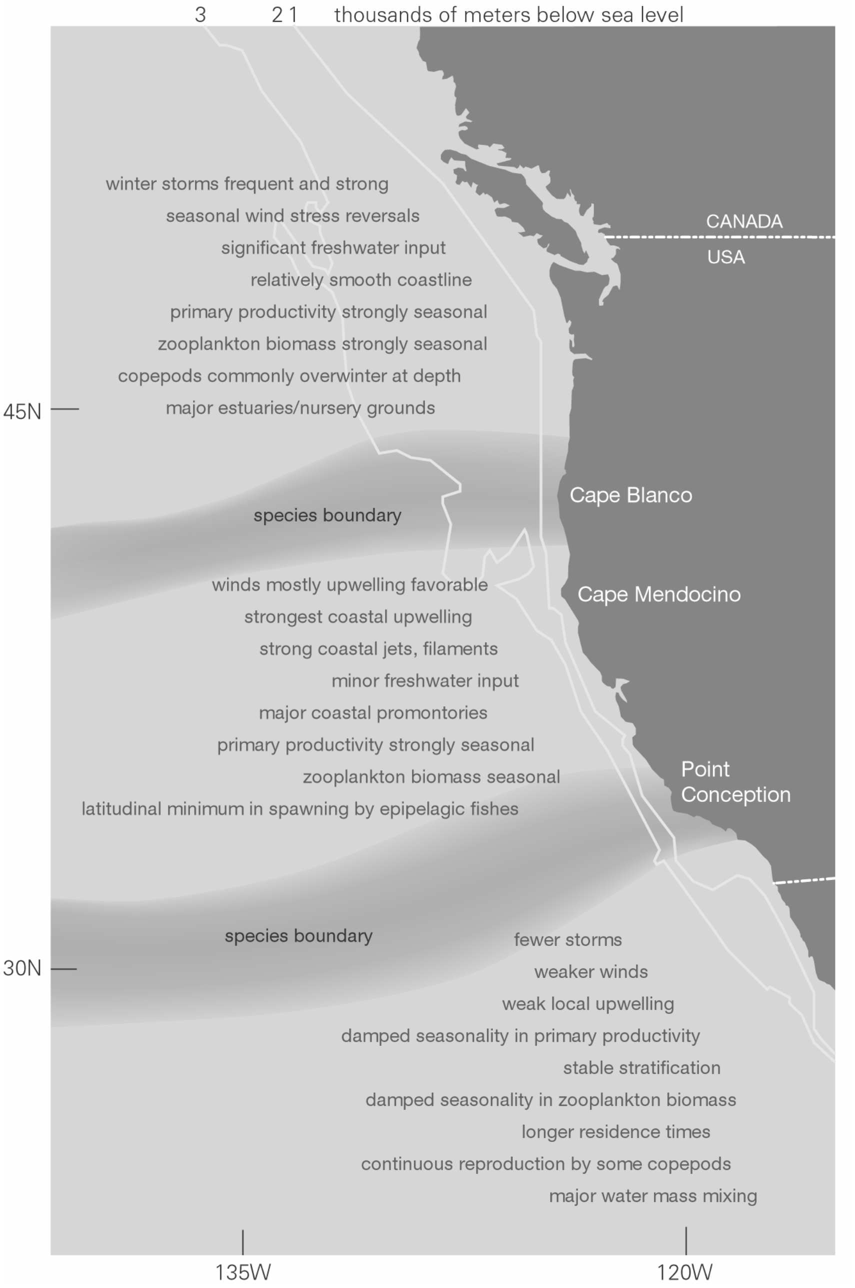


Figure 1.5: Generalized regional variations in physical and biological processes within the California Current System. The boundaries between regions are only approximate and vary over time (redrawn from http://www.cbl.umces.edu/fogarty/usglobec/reports/ebcccs/ebcccs.wg1.html).

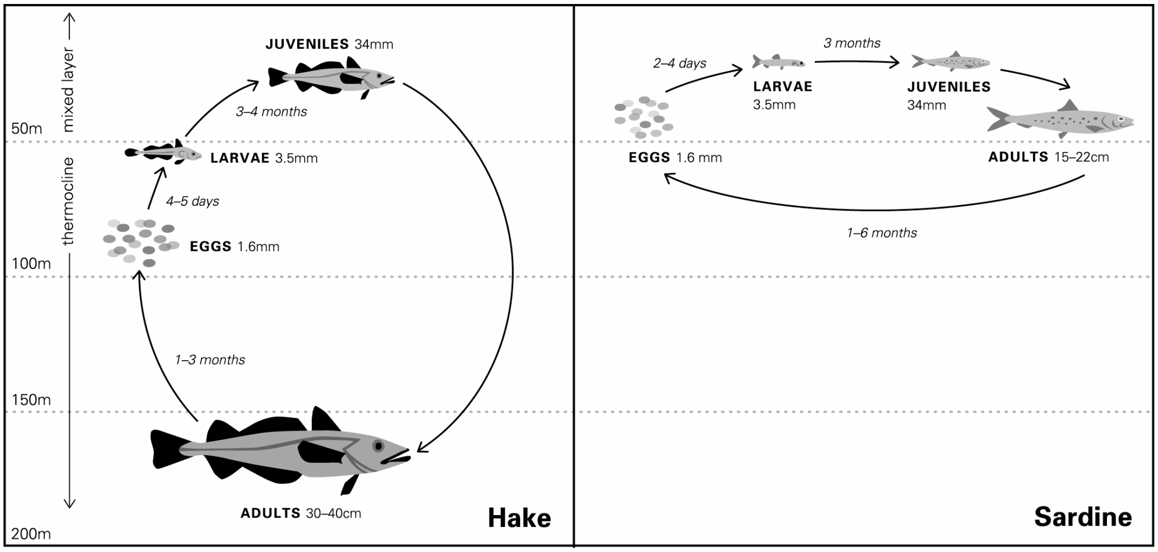


Figure 1.6: Generalized representation of hake and sardine life cycles with respect to depth.

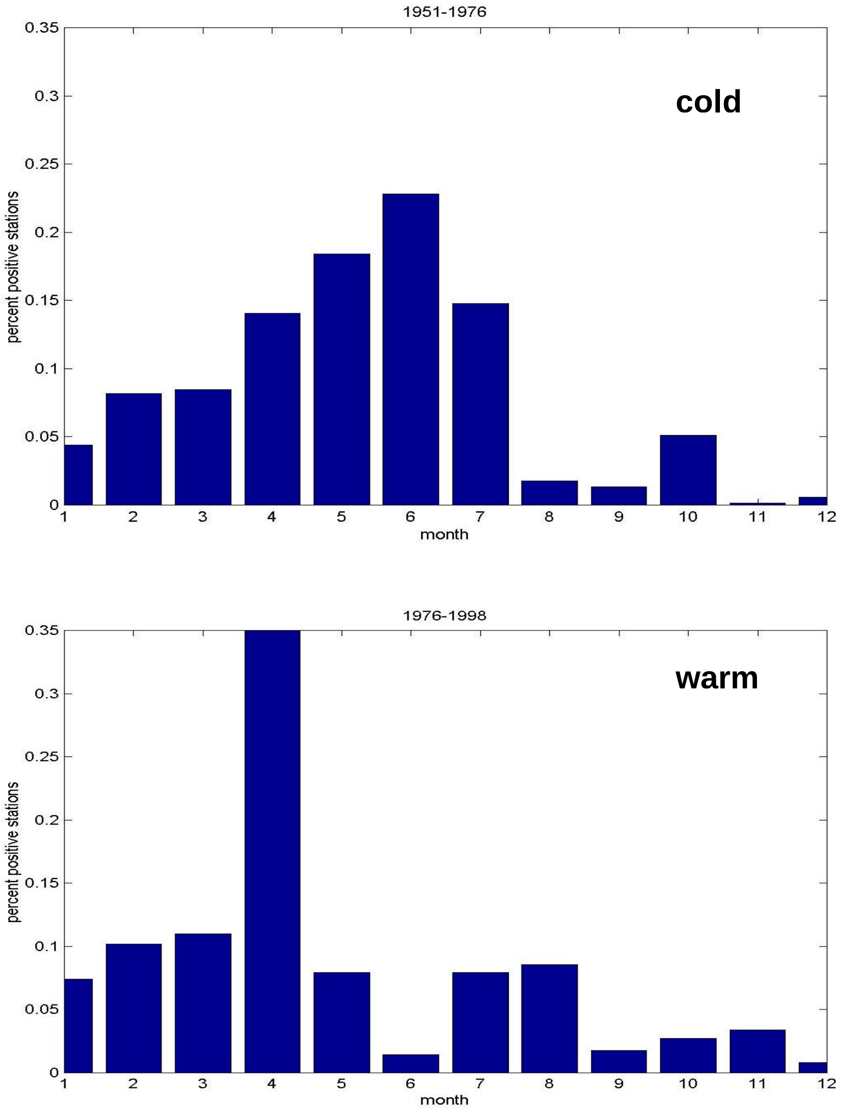


Figure 1.7: Seasonal distribution of sardine spawning (represented here by number of CalCOFI stations with larvae) in the CCS during a cold period (upper panel) and warm period (lower panel).

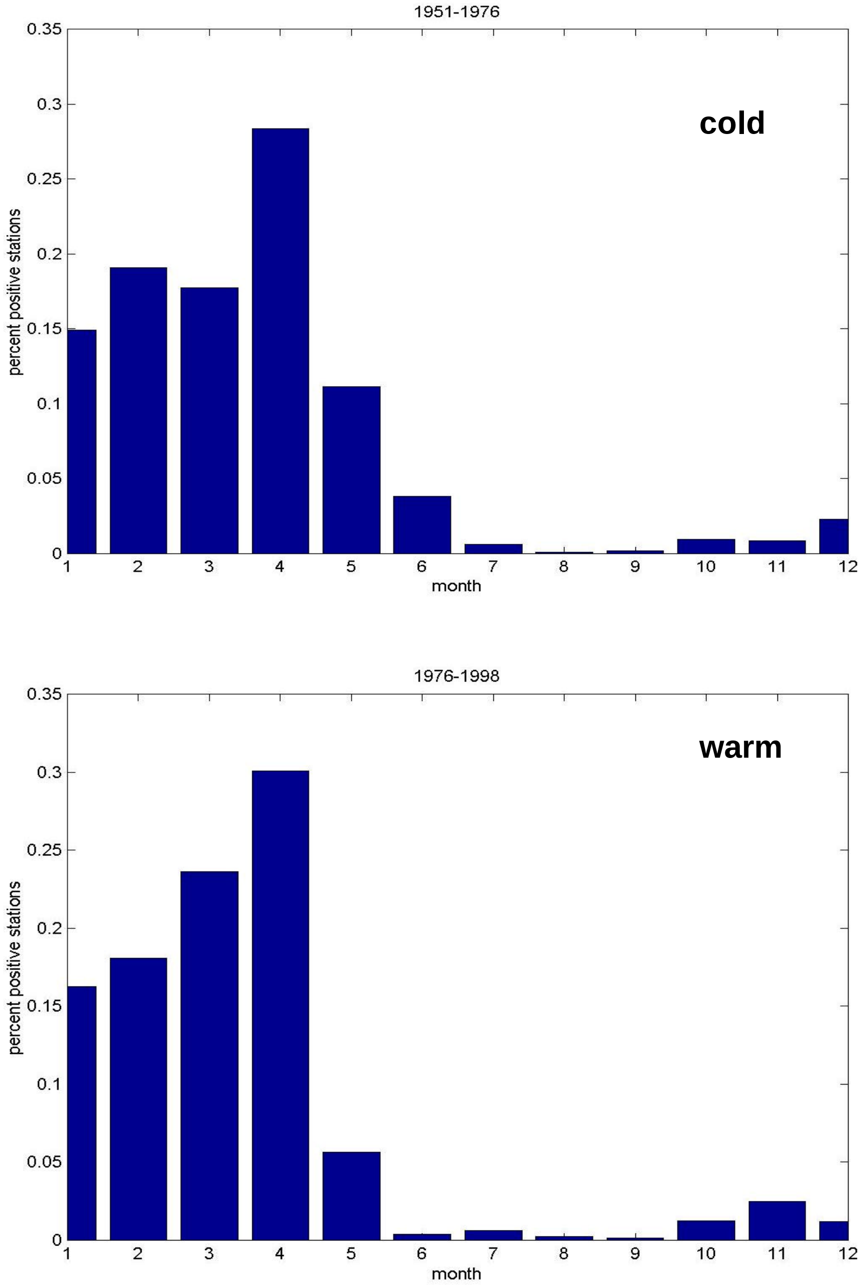


Figure 1.8: Seasonal distribution of hake spawning (represented here by number of CalCOFI stations with larvae) in the CCS during (a) cold period (b) warm period.

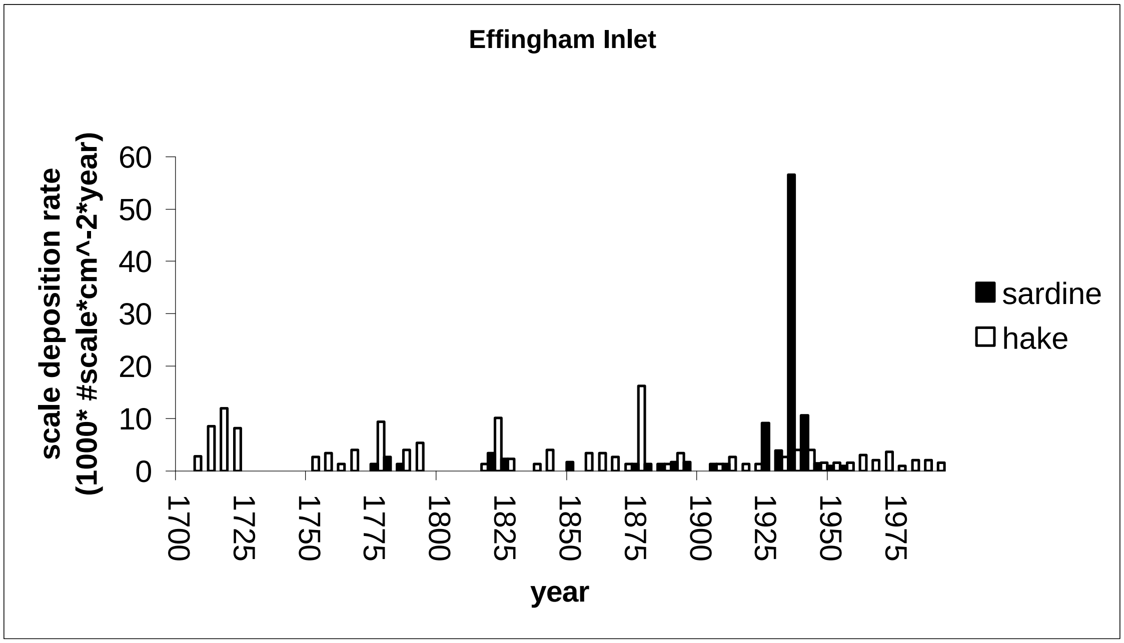


Figure 1.9: Scale deposition rate in Effingham Inlet (British Columbia) of hake and sardine. (Data from Holmgren, 2001)

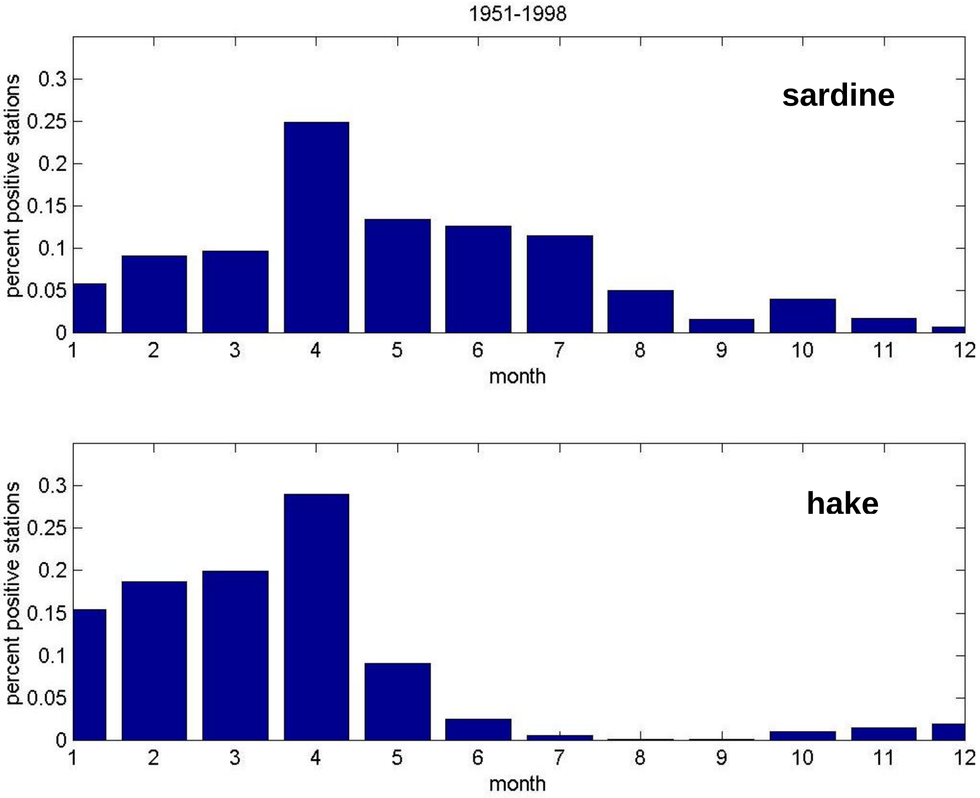


Figure 1.10: Seasonal distribution of spawning (represented here by number of CalCOFI stations with larvae) habitats in the CCS from 1951-1998. (month 1=Jan., month 2=Feb. etc.).

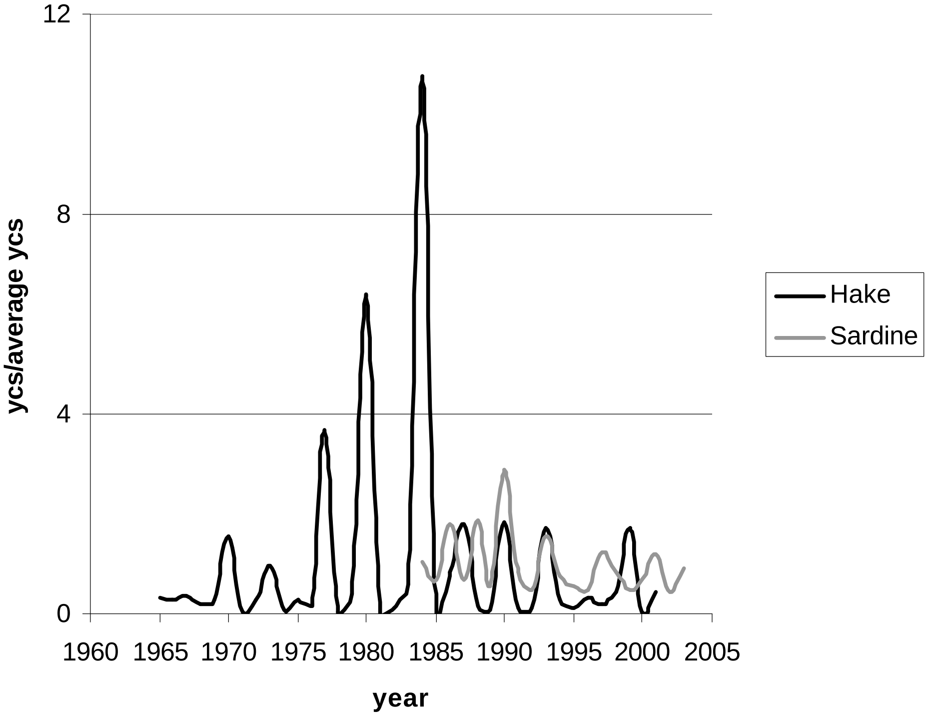


Figure 1.11: Time series of year class strength/average year class strength for Pacific sardine and hake.

CHAPTER 2. Larval stage controls on sardine recruitment variability: the balance between predation and food availability.

2.1 INTRODUCTION

Sardines (genera: *Sardinops* and *Sardina*) are a group of fishes that live in highly productive areas of the ocean: the coastal regions off Japan (Kuroshio Current), North America (California Current), South America (Humboldt Current), Southwestern (Benguela Current) and Western (Canary Current) Africa. Intensive sardine fisheries are conducted in these areas, and each one of these fisheries faces extremely variable population sizes. Pacific sardine (*Sardinops sagax*), for example, dominated the west coast fisheries of North America for much of the first half of the twentieth century. The population collapsed in the late 1940s, and remained at very low levels until the mid-1980s, when it began to rebuild (figure 2.1).

Although sardines have adapted to inhabit highly productive areas (boundary currents), they reportedly thrive, at least in the Eastern Pacific, during warm periods characterized by decreased primary productivity. Their reproductive success is reported to improve during warm years (e.g. El Niños) (Lluch-Belda, Lluch-Cota, Hernandez Vasquez, and Salinas Zavala, 1991; Jacobson and MacCall, 1995; Arntz and Fahrbach, 1996; Bakun and Broad, 2003; Niquen and Bouchon, 2004) and population sizes have also generally increased during decadal periods of “heightened El Niño character” (Bakun and Broad, 2003). In warm periods the center of spawning has been reported to shift northward (Smith, 1990; McFarlane, Smith, Baumgartner and Hunter, 2002), where spawning habitat characteristics during these times must evidently be more favorable compared to southern areas (e.g. temperature range, adult food availability). There are two hypotheses that could potentially explain why sardine reproductive success improves when the reproductive habitat shifts northward: 1) larval and juvenile food concentration increases; 2) larval and juvenile predation pressure decreases. Both food (faster growth, reduced starvation) and predation (lower predator incidence) are two habitat characteristics that potentially influence larval and juvenile survival. While the impact of food availability on survival has been discussed at length (Hjiort, 1914; Cushing, 1974; Lasker, 1975), predation on fish eggs and larvae is "one of the most critical, but least understood factors affecting the recruitment of marine fishes" (Hunter 1976, in Bailey and Yen, 1983).

Few data sets are available to empirically address these types of questions. Perhaps the longest regularly maintained time series of relevant observations covering a major portion of a population's habitat is the CalCOFI data series (figure 2.2). This sampling program includes a large number of net tow samples, taken fairly regularly and continuously over multiple decades, from which total zooplankton volumes have been measured and tabulated.

Bakun and Broad (2003) emphasize the role of the pervasive fields of predation faced by tiny organisms such as fish larvae. They hypothesize that opportune gaps that occasionally may open in these predation fields may in fact lead to remarkable reproductive success of a number of fish populations around the globe. Thus they explain the apparent success of Pacific sardine during warm years (e.g El Niño) to be the result of decreased predation pressure on early life history stages (i.e., low food concentrations characteristic of El Niño years are overcompensated by the reduced predation pressure on sardine larva, possibly leading to a burst in recruitment). Planktonic invertebrates are among the wide variety of predators that feed on fish larvae. Their predation impact has been documented for a number of egg and larval populations of clupeoid fish (Bailey and Houde, 1989; Bailey, 1994). For example, a number of authors have reported on predation by zooplankton on herring and anchovy (Alvarino, 1980; Purcell, 1985, 1989, 1990; Smith and Lasker, 1978; Theilacker , Huei Lo, and Townsend, 1993). However, little has been documented concerning predation on young sardine larvae by planktonic invertebrates. Planktonic invertebrates may also increase predation pressure on sardine larvae by attracting nektonic zooplanktivores. These may consume fish eggs and larvae along with more abundant zooplanktonic prey, or may spawn voraciously predatory early life stages that prey on sardine larvae (see Discussion section).

Thus the CalCOFI zooplankton volume data set may be both an index of larval food for sardines (i.e., copepod naplii and other suitable larval food items may be expected to be relatively abundant in situations where samples yield relatively high zooplankton volume) and an index of predation (both due to direct predation by zooplankton and by zooplanktivores attracted by abundant zooplankton that may also prey on fish larvae). But the two effects act oppositely with respect to reproductive success. That is, a positive relationship of annual recruitment to zooplankton abundance in the larval habitat of the year-class in question would indicate a predominant effect of food availability, while a negative (inverse) relationship would indicate predominance of predation over larval food availability in determining net annual reproductive success. A significant result one way or the other would yield important insight into the apparent paradox of improved reproductive success during warm years which, on regional scales at least, are known to be characterized by reduced primary productivity in the eastern boundary regions of the Pacific (e.g., Barber and Chavez, 1983; Pearcy, 1992).

In this chapter I quantify the abundance of zooplankton in sardine larval habitat within the CALCOFI region, off the south-west coast of North America (figure 2.2). My objective is to explore how zooplankton communities may influence larval survival and, ultimately, recruitment success of Pacific sardine.

2.2 METHODS

The CalCOFI program is the source of zooplankton and temperature data used in this study. It is a coordinated physical and biological monitoring program which was established following the collapse of the sardine population and fishery in the late 1940s. The time series for this analysis is based on single tows taken at all stations within the CalCOFI sampling pattern (figure 2.2), representing 37,852 samples from which mesozooplankton volume and sea surface temperature values were extracted. Details of the CalCOFI methods for measuring mesozooplankton (>505 μm) volume, a measure of zooplankton abundance, are described by Smith (1971). The data were adjusted for changes in gear type during the CalCOFI program following the procedure described in Ohman and Smith (1995). In order to account for the potential effects of gaps in the geographic coverage of the sampling program over time, analysis was conducted with: 1) data from the entire sampling grid, 2) only data from the current sampling grid (consistently covered from 1951-1998).

Since California sardine are reported to spawn primarily between February and August in 13.5 to 16.5 ^{0}C water (Tibby, 1937; Ahlstrom, 1954; Ahlstrom, 1965; Lluch-Belda, Lluch-Cota, Hernandez Vasquez, and Salinas Zavala, 1991; Parrish et al., 1989; Bentley et al., 1996), sardine reproductive habitat (which we equate here to sardine larval habitat) was defined as limited to this temperature range within these months, and only samples falling within these criteria were used in the tests. Note that choosing a specific temperature window to determine which samples will be incorporated in the analysis enables the analysis to automatically allow for spatial movement of the spawning zone in response to changes in sea temperatures brought about by climatic events.

In order to gauge the possibility that the choice of sampling band specifics might significantly change the results, additional tests using slightly different reasonable choices of both seasonal and temperature windows (e.g., January-May, 13-17^{o}C) were also performed. Both laboratory and field observations report temperatures above 13 ^{o}C to be suitable for sardine egg and larval survival (Ahlstrom, 1954; Lasker, 1964; Smith, 1978; Parrish et al., 1989; Bentley, Emmett, Lo, and Moser 1996). The upper limit of spawning is less clear, but hovers around 16 ^{o}C for the California sardine stock (Lluch-Belda, Lluch-Cota, Hernandez Vasquez, and Salinas Zavala, 1991). Wider windows would probably be required for other sardine stocks because, for example, Pacific sardine in southern stocks off southern Baja California spawn at higher temperature with eggs and larvae found in waters up to 25^{o}C (Lluch-Belda, Lluch-Cota, Hernandez Vasquez, and Salinas Zavala, 1991; Hernandez-Vasquez, 1994; Lynn, 2003). The results remain quite robust to different choices of the sample selection criteria. All seemed to accomplish the task of moving the pattern of selected samples northward and southward in response to inter-annual temperature variability, and thus allowing a direct focus on the causative factors controlling reproductive success (food availability and predation). Thus zooplankton abundances from tows falling within the selected seasonal and temperature window were extracted from the data set, and yearly average values were computed for the years where recruitment estimates were available.

Zooplankton data were regressed against sardine recruitment (estimated number of age 0 fish) and recruitment/spawner biomass (estimated number of age 0 fish/ thousand mt of age 1^+ fish). Recruitment and spawner biomass time series were taken from Jacobson and MacCall (1995) for the period from 1952 to 1960, and from Conser et al. (2003) for the period from 1983 to 1998 (table 2.1). Reliable estimates of recruitment and spawner biomass for the period from 1962 to 1984 do not exist (Barnes et al., 1992). Since recent and historical spawner biomass and recruitment data for sardine were not immediately comparable (biomass is reported for age 1+ in the historical data and for age 2+ in the recent data and recruitment data is reported for age 0 in the most recent data and for age 2s in the historical data) two time periods were considered: 1952-1962 and 1983-1998. Zooplankton abundances were summarized for years of high (# of recruits/spawners > 5 billion) and low recruitment (# of recruits/spawners < 5 billion), as well as El Niño (EN), La Niña (LN) and neutral years. EN, LN and neutral years were assigned as outlined in Table 2.2, based on the winter classification (January, February and March) reported by the Center for Climate Prediction (www.ncep.noaa.gov). A time series of 'zooplankton three year ratio' (as per Smith, 2001) was computed as follows: $(\text{zooplankton volume})_t$ / $(\text{zooplankton volume})_{t-3.}$

2.3 RESULTS

My results indicate an inverse relationship between sardine recruitment and zooplankton abundance: recruitment decreases with increasing zooplankton abundance (recruits vs ln(zooplankton abundance) for period 1953-1961, r^2=0.02, F=0.17, for period 1983-1998, r^2=0.55, F=17.17; recruits/spawner biomass vs ln (zooplankton abundance) for period 1983-1998, r^2=0.43, F=10.70) (figures 2.3a-2.3d). Both the mean and variance of zooplankton abundance in the relevant larval habitat zone is lower during high recruitment years (mean=46.99 ml/m^3, variance=0.728), compared to the mean and variance of zooplankton abundance during low recruitment years (mean=86.49 ml/m^3, variance=0.933) (figure 2.4). The mean and variance of zooplankton abundance in the relevant zone was also lower during El Niño (EN) years (47.98 ml/ m^3, 0.86) compared to the mean of variance of zooplankton abundance during La Niña (LN) years (110.05 ml/m^3,1.02) and neutral years (83.10 ml/m^3, 0.85) (figure 2.5). Decreases in zooplankton abundances during EN years are also evident in a time series of the three year ratio of zooplankton abundances (figure 2.6). Differences in means and variances between high and low recruitment years, as well as EN, LN and neutral years were tested using two sample t-tests and F-tests (table 2.3). All means and variances reported above were significantly different ($p<0.05$).

The results I report above are based on data from all stations on the CalCOFI grid (figure 2.2) in sardine reproductive habitat defined as waters between 13.5 and 16.5 °C sampled between February-August of the years outlined in table 2.2. Analysis including only data from stations on the current grid (figure 2.2), or based on a slightly different definition of sardine habitat (January-May, 12.5-17.5 °C) generated similar results.

2.4 DISCUSSION

Warm conditions displace the temperature zone of favorable sardine habitat north (Smith, 1990; McFarlane et al., 2002), possibly contributing to the observed sardine success during these periods. One hypothesis that has been advanced to explain this success is that the northern shift in sardine habitat allows access to waters richer in food concentrations, compared to southern waters occupied during colder periods (PICES Symposia, La Paz, 2002 and Honolulu, 2004). If this were the case, however, one would expect higher zooplankton abundances within the sardine habitat during warm years compared to the abundances found during cold years. However my results indicate that successful sardine year classes are characterized by low zooplankton abundance, thus reproductive success of California sardine cannot be explained by increased food availability in the reproductive (i.e., larval) habitat.

Lynn (2003) reports high zooplankton biomass in sardine egg nursery areas during recent years. This suggests that adults are choosing spawning areas that are rich in food concentrations (i.e., the spawning adults appear to be congregating where they are feeding well). However reproductive success is determined by the survival rate of larvae and juveniles. While food availability is undoubtedly important to larval survival, my results suggest that the impact of predation may be more important in determining interannual variation in year class strength. This may not be surprising as the abundance of potential predators in the sea is much higher than the abundance of fish eggs and larvae (McGowan and Miller, 1980). Moreover there is little evidence to support a contention that large numbers of fish larvae are starving (Sissenwine, 1984).

In summary, I view habitat variability at early life history stages as having an additive impact on reproductive success. While processes (both feeding/growth and predation) occurring in the juvenile stages are also undoubtedly important, my results indicate that the effect of predation at the larval stage is a powerful enough factor to emerge empirically from the confounding "noise" related to other factors and mechanisms.

My analysis of the California sardine reproductive habitat shows that food concentrations are not elevated during periods of higher reproductive success. I find both the mean abundance and variance of zooplankton in sardine reproductive habitat to be lower during warm years. This suggests that not only are there fewer zooplankton, but that individuals are less aggregated during warm years compared to cold years. This decreased aggregation might reduce the probability of encounter between zooplankton predators and sardine. The negative predation-related effects associated with higher zooplankton abundance could have effectively overwhelmed the positive 'high food availability' effects, such that the net composite influence of increased zooplankton abundance on larval sardine survival is negative. The low zooplankton abundances that I observed during both high recruitment years and El Niño years, appear to support the "loopholes" hypothesis formulated by Bakun and Broad (2003), which was based on comparative reasoning entirely independent of the data and results reported here.

Population growth of sardine has been shown to be sensitive to changes in vital rates of egg and early larval stages. Based on stage-based models, Lo et al. (1995) and Smith et al. (1992) show that the largest changes in sardine population growth come from a relative change in mortality rate of egg and larval stages, concluding that mortality rates of these stages are important determinants of recruitment success. Reductions in mortality rates due to predation could occur during warm years and clearly have the potential to enhance recruitment success.

Superimposed on the interannual trends in zooplankton abundance is a general decrease in zooplankton abundance observed in the California Current System over the past 50 years (Roemmich and McGowan, 1995). Several authors report that the decrease in zooplankton is not uniform across species, and that important patterns emerge when considering individual species (Lavaniegos and Ohman, 2003; Rebstock, 2001, 2003; Brinton and Townsend, 2003). For example Lavaniegos and Ohman (2003) suggest that the decrease in zooplankton volume observed is primarily due to a decrease in abundance of tunicates (salps and doliolids). Many soft-bodied zooplankton have been known to consume fish eggs and larvae (reviewed in Alvarino, 1984; Purcell, 1985, 1989 and 1990). Alvarino (1980) lists 109 potential planktonic predators found in CalCOFI samples collected in 1954, 1956 and 1958. She finds an inverse relationship between abundance of anchovy larvae and abundance of siphonophores and medusae, as well as chaetognaths. In addition, anchovy larvae were never found in hauls dominated by pelagic prochordates (salps or pyrosomes). This leads me to believe that the decrease in tunicates described by Lavaniegos and Ohman (2003) could represent a decrease in predation pressure on sardine eggs and larvae. Brinton and Townsend (2003) find a decrease in euphasiid abundance during strong El Niño episodes, but no overall decrease during the last 50 years. Theilacker et al. (1993) evaluate northern anchovy egg and larval mortality due to predation by the euphasiid assemblage commonly found in the California Current. Standardized CalCOFI plankton collections were analyzed to estimate prey and predator abundance and apply an immunoassay technique to identify the predators. The authors confirm that predation by euphausiids is a significant source of mortality for the young stages of northern anchovy off California. During their study, 47% and 78% of the total natural mortality could be ascribed to euphausiid predation. Thus the decrease in euphausiids abundance reported by Brinton and Townsend (2003) during strong El Niño episodes may also represent a decrease in predation pressure on California sardine eggs and larvae during those time periods.

Evidence of zooplankton predation on clupeoid species has mainly been reported for anchovy and herring (Alvarino, 1980, 1984; Purcell, 1985, 1989 and 1990; Smith and Lasker, 1978; Theilacker, Huei Lo, and Townsend, 1993). A number of other important factors exist (e.g. presence of alternate prey, rate of encounter, passive versus active predation) that for the sake of brevity I do not discuss here. Nevertheless it seems clear that zooplankton predation represents a significant source of mortality for clupeoid fishes. In order to fully evaluate the importance of zooplankton predation on Pacific sardine, zooplankton predation studies need to be extended to this species.

The available data did not allow me to address changes in plankton species composition, although I do recognize their potential importance. A shift in zooplankton and/or phytoplankton communities could greatly influence year class success (McFarlane and Beamish, 2001). The information available on species composition over this time scale is limited, as the CalCOFI program does not systematically characterize species composition of zooplankton samples collected. Thus I cannot exclude the possibility that lower zooplankton abundance during 'high recruitment' years observed in this study could simply be an indirect indicator of a change in plankton species composition. Such shifts in planktonic species compositions have been discussed (McFarlane and Beamish, 2001) and could obviously be important. Sardine larvae might benefit from these shifts by suddenly gaining access to a preferred prey item. However the trends observed by Lavaniegos and Ohman (2003) do not support this, as they attributed the decrease in zooplankton to a decrease in tunicates, and not a change in the overall abundance of other species.

In summary, the single measure of zooplankton abundance (settling volume) used in this study inseparably includes both (1) abundance of potential food and (2) abundance of potential predators. Again, one limitation is not having access to a time series of species composition that would allow us discern between the two. The other is that, to the best of my knowledge, no studies exist to date on predation of zooplankton on sardine larvae; this only allows us to draw inferences based on studies conducted on other species. As I discussed above several authors document the impact of predation by planktonic invertebrates on a number of egg and larval populations of clupeoid fish. Murphy (1966) discusses the potential role of zooplankton as sardine predators, and suggests that zooplankton predation on sardine larvae may be higher during cold periods. More specifically, some of the species contained in CalCOFI zooplankton samples (e.g. copepods, euphasiids and chaetognaths) are known to be capable of feeding on larval fish (McGowan and Miller, 1980). These zooplankton species are also known to be prey for fish species such as Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*) and others. During years of high zooplankton abundance, these fish may copiously spawn and their early life stages represent yet another source of predation on sardine larvae. In addition, there may be a greater attraction for these mobile wide-ranging pelagic species to enter the sardine reproductive zone, feed and incidentally spawn, during years when potential food (zooplankton) may be particularly available in that habitat zone.

However I do feel confident that, although additional factors (e.g shifts in species composition, more specific knowledge of sardine predators/prey) could be considered, the low zooplankton abundances observed during ‘high recruitment years’ point to the importance that a release in predation pressure may have in determining recruitment success of Pacific sardine. I believe that as far as the effects on larval stages are concerned in determining net recruitment, the negative effect of increased predation could take precedence over the positive effect of increased food.

Abrupt changes in zooplankton abundance have been observed to coincide with changes in sardine abundances in other areas of the world. For example in Peru, the 1970s period of sardine increase occurred right after an abrupt collapse in zooplankton abundances (Carrasco and Lozano, 1989). The South African sardine collapsed during a period of greatly increasing zooplankton volume (Verheye, H.M., 2000; Verheye and Richardson, 1998; Verheye, Ruchardson, Hutchings, Marska, and Gianakouras, 1998). It seems clear that if food availability were the dominant factor determining recruitment success, we would not be observing the same negative relationship between zooplankton abundance and sardine recruitment in distant areas of the world.

The results of this study emphasize the need for a new view of how trophic energy is transferred through an ecosystem. The conventional view that energy is transferred up the food web in a rather linear manner may not be entirely appropriate. Fish species are generally modeled by representing trophic energy transfers among adult biomass, but population dynamics are in many cases determined at non-adult life history stages. For example in the case of sardine, what constitutes a predator during the larval stage (zooplankton) might later become prey during the adult stage. Taking into account earlier life stages and the potential non-linearities introduced in the food web by mortalities inflicted at these life history stages offers a more complete view of the dynamics of the ecosystems in question.

Table 2.1: Time series of sardine spawning biomass, recruitment and zooplankton abundance. Historical spawning biomass for 1952-1961 is sardine age 2 and older (Jacobson and MacCall, 1995). Recent spawning biomass for 1983-1998 is sardine age 1 and older (Conser et al., 2000). Reliable spawning biomass and recruitment estimates for sardine during 1964-1982 are not available (Barnes et al., 1992). Recruitment is the number of age 0 (millions) fish. Recruitment estimates from first period (1952-1961) are numbers of fish at age 2 (Jacobson and MacCall, 1995). Recent recruitment estimates (1983-1998) are numbers of fish at age 0 (Conser et al., 2001).

Year	Spawning biomass (10^3 t)	No. of recruits (10^6 fish)	ln of zoopl. volume (ml/m^3)
1952	793	1197	
1953	780	382	5.11
1954	277	264	4.70
1955	136	588	5.02
1956	202	1586	5.24
1957	239	905	5.67
1958	170	288	4.54
1959	108	111	4.22
1960	90	74	4.64
1961	177	56	4.26
1983	5	141	4.06
1984	13	226	4.64
1985	21	220	5.29
1986	30	846	4.11
1987	74	832	4.34
1988	107	1461	4.42
1989	162	1159	4.21
1990	177	4710	4.05
1991	226	5902	4.32
1992	353	4105	3.79
1993	335	8928	3.38
1994	495	10907	3.86
1995	508	6786	4.11
1996	532	5566	4.52
1997	483	8136	4.08
1998	457	19022	3.06

Table 2.2.: Year classification based on winter (January, February, March) Niño3.4 index as reported by the Center for Climate Prediction (www.ncep.noaa.gov)

El Niño	Neutral	La Niña
1958	1953	1955
1959	1954	1956
1983	1957	1984
1987	1960	1985
1988	1961	1989
1991	1986	1996
1992	1990	
1993	1994	
1995	1997	
1998		

Table 2.3: Results of two sample t-tests and F-tests for differences in means and variances of zooplankton abundances during high and low recruitment years, as well as El Niño, La Niña and neutral years (see methods section for definitions).

Group tested	Mean var. 1*	Mean var. 2*	Variance var. 1*	Variance var. 2*	d.o.f	p-value (two tail) for differences in means	p-value differences in variances
high recr. (*var 1*) and low recr. (*var2*)	3.85	4.46	0.728	0.93	1125	3.26 x 10-43	0.0001
EN years (*var.1*) and LN years (*var. 2*)	3.85	4.71	0.86	1.02	1129	1.75 x 10-45	0.025
EN years (*var.1*) and neutral years (*var. 2*)	3.85	4.42	0.86	0.85	1637	3.95 x 10-30	0.55

*Ln(zooplankton abundance) (ml/m^3)

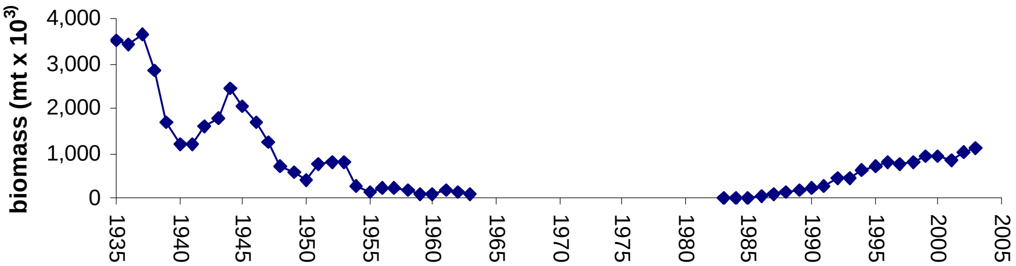


Figure 2.1: Time series of Pacific sardine adult biomass (age 2+ for first period, age 1+ for second period).

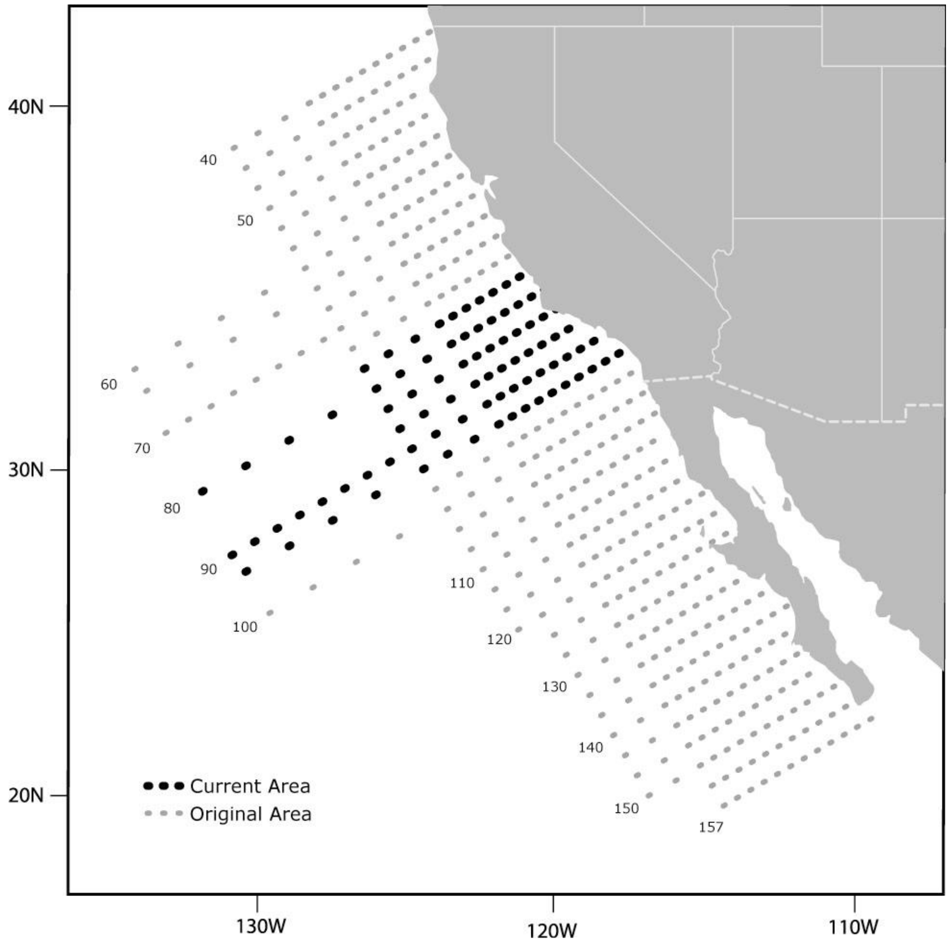


Figure 2.2: Stations sampled by the CalCOFI program from 1948 to present. Black dots identify stations sampled consistently throughout the time period (see methods for explanation).

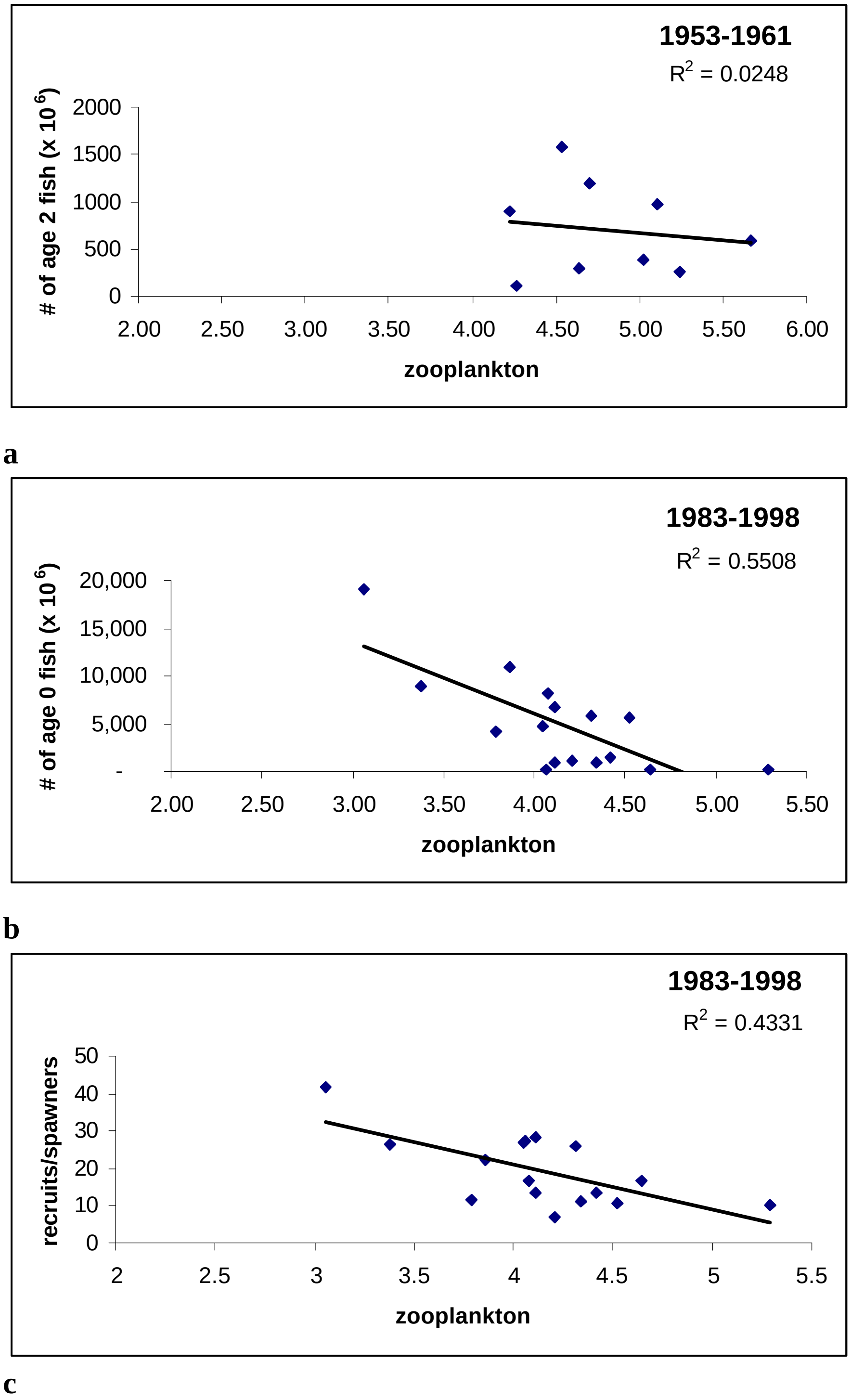


Figure 2.3: **a)** and **b)**: Log-linear relationship between estimated number of recruits and log of zooplankton abundance (ml/m^3) in preferred sardine spawning habitat (see methods section for definition); **c)** recruits/spawners and zooplankton abundance (ml/m^3) in preferred sardine spawning habitat (see methods section for definition).

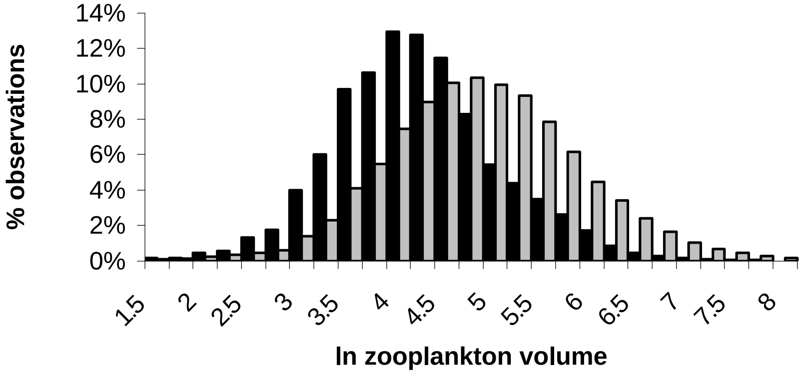


Figure 2.4. Distribution of zooplankton volume (ml/m^3) observations in sardine preferred spawning habitat (see methods section for definition) during high recruitment (black bars) and low recruitment (gray bars) years.

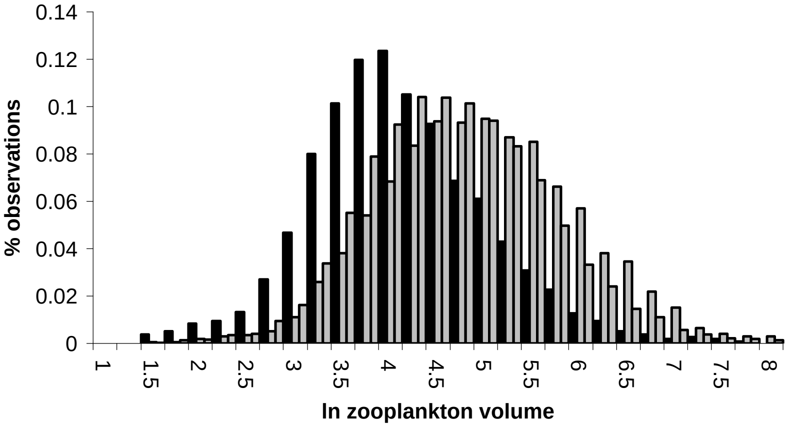


Figure 2.5. Distribution of zooplankton volume (ml/m^3) during EL Niño years (black bars) La Niña years (open bars) and neutral years (thatched bars).

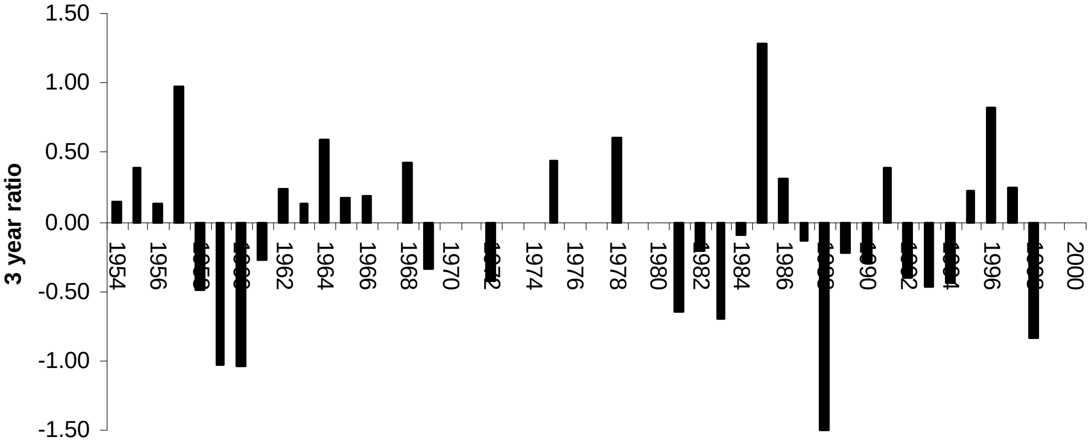


Figure 2.6: Time series of (zooplankton volume)$_t$ / (zooplankton volume)$_{t-3.}$ Shaded bars indicate El Niño years.

CHAPTER 3. Defining and quantifying hake habitat in the California Current.

3.1 INTRODUCTION

Climate induced variability in the CC system creates a dynamic range of habitat suitability. Chapter 1 described life history strategies adopted by sardine and hake to succeed in dynamic systems such as the CC. One of the principal characteristics of hake life history to emerge was migration (figure 3.1). Pacific hake travel long distances in their search of favorable habitat. The extent of migration varies and is related to oceanic conditions (Dorn, 1995; Saunders and McFarlane, 1997; Benson, 2002; Helser, 2004). In this chapter I define and quantify adult hake habitat in the CC based on physical properties of the system. I argue that while physical processes may not directly affect hake production, they may be the link between large scale ocean-atmosphere variability and hake distribution along the west coast.

The production variability of coastal pelagic species in the CC has been related to climate forcing (MacCall, 1996; Ware & McFarlane, 1995). Habitat variability is often invoked as the potential link between the two (MacCall, 1990; Ware and McFarlane, 1995; MacCall, 1996; Benson et al., 2002), but the mechanisms involved remain poorly understood (Beamish et al., 2000). The use of climate metrics (i.e. PDO, ENSO) to represent potential environmental forcing on fish populations and ecosystems (e.g Hare and Mantua, 2000) usually involves the aggregation of impacts across large spatial scales and range of species. Direct links are made between climate forcing and production variability. However, fluctuations in productivity are often the result of changes in physical habitat and food availability. In order to gain a complete understanding of the link between climate and production variability habitat changes should be addressed.

Habitat in terrestrial systems has long been interpreted as vegetation, sometimes with underlying gradients of moisture or soil chemistry (Rice, 2001). This definition seems to have been transferred to marine environments where classic definitions of marine habitat (e.g. rocky intertidal, kelp forests, coral reefs) usually involve vegetation or substrate type, all static features.

While this is appropriate for benthic communities it is not appropriate for pelagic communities. For pelagic species habitat is often a dynamic entity, its boundaries changing according to changes in time and space of the physical variables defining it.

Understanding how habitats are distributed in space and how their characteristics vary will contribute to our understanding of ecosystem processes and the sustainability of fish populations (Kracker, 1999). Lately, researchers have placed more emphasis on recognizing the importance of spatial patterns in ecological processes (Petitgas, 1993; Horne and Schneider, 1996, Petitgas, 1998). Recent discussions regarding the long-term sustainability of ocean resources have focused on the need to understand the size as well as the spatial distribution of fish populations (Kracker, 1999). Quantifying these patterns has been recognized as an essential component of our research efforts to understand how harvest pressure and climate change impact the sustainability of fish stocks (Wiebe et al., 1996).

Fish species often position themselves in response to a particular feature of the marine environment (Maravelias et al., 1996). Their distribution is not random, either in space or time, rather organized in structures (schools, aggregations). Geostatistics is a branch of applied statistics that focuses on detecting, modeling and estimating spatial patterns (Rossi et al., 1992). This type of modeling approach assumes spatial dependence (the value at one location is similar to the values at neighboring locations) instead of spatial independence (values at one location are independent of values at neighboring locations).

Spatial dependence is very important in ecology, "the scientific study of the relationships between organisms and their environments" (McNaughton and Wolf, 1973), yet traditional statistics measures tend to not take spatial dependence into account (Rossi et al., 1992). During the last decade a number of studies have applied geostatistical techniques, initially developed for terrestrial applications, to marine systems (Petitgas, 2001). Their focus has been on a number of fishery problems, ranging from estimating abundances from survey data (Simard et al., 1992; Conan et al., 1994; Barange and Hampton, 1997; Fletcher and Summer, 1999) to quantifying relationships between environmental variables and fish distributions (Simard et al., 1993; Maravelias et al., 1996).

Pacific hake (*Merluccius productus*) account for 61% of the pelagic biomass in the California Current system (Ware and McFarlane, 1995). Although distinct populations of Pacific hake also exist in the Strait of Georgia (McFarlane and Beamish, 1985), Puget Sound (Pederson, 1985) and inlets of the west coast of Vancouver Island (McFarlane and Beamish, 1985), the offshore population is of greatest importance, as it contributes large biomass for fisheries in both Canadian and United States (US) waters (Francis et al., 1989; Smith et al., 1990; Helser et al., 2004). A great deal of controversy revolves around this fishery. The largest and most valuable fish migrate farther north (McFarlane and Beamish, 1985) and dramatic variability in year-class strength (Bailey and Francis, 1985) affects the interannual distribution of biomass and therefore yield of hake between Canada and the US (Swartzman et al., 1987).

The abundance of hake in Canadian waters has been attributed to temperature (Dorn, 1995; Ware and McFarlane, 1995; Benson et al., 2002). Hake have been located farther north during warm years (figure 3.2) (Dorn 1991 and 1995; Wilson and Guttorsmen, 1998). However, evidence for a relationship between hake distribution and temperature has been weak (Benson et al., 2002). Several authors have suggested that hake distribution may instead be related to poleward flow (undercurrent), with stronger flow aiding the migration of hake, and weaker flow impeding it (Smith et al., 1990; Dorn, 1995; Benson et al., 2002).

Changes in hake distribution have large implications for regional ecosystems. Hake have been identified as potential predators of juvenile salmon (Emmett and Brodeur, 2000), and are known to be voracious predators of euphausiids, shrimp, herring and other forage fish (Gotshall, 1969; Rexstad and Pikitch, 1986; Hannah, 1995; Field, 2004). All of these are also prey to other species (salmon, rockfish, and other groundfish) that compete with hake. The presence or absence of hake off the Pacific Northwest coast will have large implications for the local food web. For example Field (2004) found that during warm years when hake are more abundant in Northern CC waters, there is an increase of top down effects in regional food webs.

In this chapter I will first examine the distribution of adult hake in the CC system in relation to poleward flow and temperature. I test the hypothesis that hake distribution is related to poleward flow. I then use a geostatistical approach to quantify adult Pacific hake habitat during different climate regimes. I model changes in amount and distribution of hake adult habitat as defined by the poleward undercurrent and examine the possibility of using the undercurrent as a predictive index of adult hake habitat abundance. Finally I briefly discuss the potential role of hake habitat as a CC ecosystem indicator.

3.2 METHODS

3.2.1 Study area

Data on hake abundance and distribution along the west coast of North America have been collected starting in 1977 by the National Marine Fishery Services (NMFS) and starting in 1992 in collaboration with the Department of Fisheries and Oceans Canada (DFO). Echo-integration summer trawl surveys have been conducted on a triennial basis along the continental shelf from California to the northern limit of hake aggregations in British Columbia (figure 3.3). Details of the triennial surveys are available in Wilson et al. (2000). Surveys run from July 1 to September 1 off the west coast of North America. Transects are on average 52 km long and 18 km apart, generally running mid-shelf to mid-slope between the 50 and 1500m isobaths. In order to capture conditions during different climate regimes I analyze survey data from 1995 (a neutral year) and 1998 (an El Niño year). Although 2001(a La Niña year) would have provided a stronger contrast, I could not include this year in my analysis as I did not have access to the data. Biological data from surveys prior to 1995 was not available in electronic format. Transport data have not been collected prior to 1995.

3.2.2 Biological data

Abundance and distribution of adult hake were derived from acoustic data collected using a Simrad EK500 quantitative echosounding system (Simrad Inc., Lynwood Wash.) split-beam transducers (38 and 120 kHz; Simrad Inc.) mounted on the bottom of the vessel hull, 9m below the surface (Wilson et al., 2000). Data collected with the 38kHz transducer were used in this study. Standard target strength-length relationships were used to convert acoustic backscatter to fish density. The target strength relationship used was TS=20logL-68, where L represents fish length measured in centimeters.

3.2.3 Physical data

Distribution and intensity of alongshore (north/south) flow were derived from an RD instrument 153.6 kHz narrow-band, hull mounted shipboard acoustic doppler current profiler (ADCP). For detailed methods on doppler data processing see Pierce et al., 2000. Temperature information was derived from CTD casts made at two or three locations where large aggregations of hake were observed, along every second or third transect, down to water depths of about 500m.

3.2.4 Descriptive analysis

The following values were computed:

For J transects (j = 1, 2, 3,.., J), I_j stations in transect j (i=1,2,3, ………, I_j), K_{ij} depths at station i_j (k_{ij}=1, 2, 3, …. K_{ij}).

Depth of center of mass of poleward flow at station ‘i’ (as in Pierce, 2000), herein referred to as core current

$$(1) \qquad Zc_{ij} = \sum_{k=1}^{kij} v_{ijk}\, z_{ijk} \Big/ \sum_{k=1}^{kij} v_{ijk}$$

v_{ijk} = raw poleward velocity at depth k, station i, transect j

z = depth of current measurement at depth k, station i, transect j

Z_c units = m

Weighted mean depth of hake at each station ‘i’

(2) $$\mathrm{Zf}_{\mathrm{ij}} = \sum_{k=1}^{kij} f_{ijk}\, z_{ijk} \,/\, \sum_{k=1}^{kij} f_{ijk}$$

f = number of fish at depth k, station i, transect j

z = depth of fish measurement at depth k, station i, transect j

Z_{f} units = m

Fish index at each station ‘i’

(3) $$\mathrm{FI}_{\mathrm{ij}} = \sum_{k=1}^{kij} f_{ijk} \,/\, mf$$

f = number of fish at depth k, station i, transect j

mf = maximum number of fish over entire survey range

Weighted alongshore flow velocity at each station (referred to herein as hake waters) ‘i’

(4) $$v_{\mathrm{f}ij} = \sum_{k=1}^{kij} f_{ijk} v_{ijk} \,/\, \sum_{k=1}^{kij} f_{ijk}$$

f_{ijk} = number of fish at depth k, station i, transect j

v_{ijk} = raw north/south (N/S) flow velocity for bins where number of fish > 0 at depth k, station i, transect j

v_{f} units = cm/sec

Mean alongshore flow velocity at each station ‘i’

(5) $$v_{c\,ij} = \sum_{k=1}^{kij} v_{ijk} \,/\, n$$

$v_{c\,ijk}$ = raw N/S velocity at depth k, station i, transect j

n = number of depth bins

v_c units=cm/sec

Weighted temperature at station ‘i’:

(6) $$\mathrm{T}_{\mathrm{f}\,ij} = \sum_{k=1}^{kij} T_{ijk}\, f_{ijk} \,/ \sum f_{ijk}$$

T = temperature for bins where number of fish > 0 at depth k, station i, transect j

f = number of fish at depth k, station i, transect j

T units= ^{0}C

To aid in spatial analysis, values were averaged over each transect as well as over latitudinal blocks. The latitudinal blocks were chosen as they also coincide with important topographic features, such as capes and promontories, known to influence the oceanography of the region (Hickey, 1979). Data from 33-38^0 N was omitted as no significant fish densities were observed here. Also, in order to effectively isolate waters where sub-surface poleward flow usually occurs, the values above were computed two ways: 1) including measurements from all depths bins; 2) only including measurements from 120-330 m depth bins (referred to herein as sub-surface). Any values shallower than 120m are probably not sub-surface poleward flow (Pierce et al., 2000). Also, hake were usually not detected at depths shallower than 120m. Please note that I will refer to alongshsore flow (north/south) throughout this chapter as ‘flow’.

3.2.5 Modeling approach

Structural analysis

I describe how particular habitat variables are related to hake abundance at a particular location (station) by means of models that assume spatial dependence (geostatistical analysis). I incorporate models that assume spatial independence as subsets of models that assume spatial dependence. Values at each location represent measurements taken at that location over 48 10m depth bins (0-480m). In order to normalize for differences in overall fish abundance between years, I calculated a fish anomaly value at each location (fish anomaly at a particular location = average overall fish abundance -fish abundance at a particular location). The term ‘fish abundance’ used in this section (3.2.5) refers to this fish anomaly value.

The framework for the models I used is based on the geostatistics method presented by Diggle et al (1998). Assume that we can model the hake abundance Y_i (number of hake at location 'i'), by the model:

(1) $$Y_i = m_i + S(\mathbf{x_i}) + e_i$$

where m i is a mean effect, x_i the observation location, $S(\mathbf{x_i})$ is a stationary Gaussian process with expected value $E[S(x)] = 0$ and $\text{cov}[S(\mathbf{x}_i), S(\mathbf{x}_j)] = s^2 r(\mathbf{x}_i - \mathbf{x}_j)$ (s^2 =variance; r =correlation coefficient) and e are mutually independent Gaussian random variables with mean = 0, and variance = t^2 (Diggle et al. 1998). t^2 is measurement error that corresponds to variability in observations at small distances, while s^2 corresponds to variability in observations that are far apart.

I modeled the mean effect using a multiple linear regression model. A model without spatial dependence lacks the $S(\mathbf{x_i})$ term. This term represents the autocorrelation in space between data points (how similar neighboring points are). The level of autocorrelation provides useful information on the nature of the spatial structure and generally depends on the distance between two sampling points.

Variogram estimation

The analysis involved two steps. The first step was to use an experimental variogram to describe the spatial structures of the variables in question. This allowed me to quantify the spatial dependency and partition it along the various distance classes. The experimental variogram represents the semivariance between data points as a function of the spatial distance between them. The experimental variogram is calculated using:

(2) $$g^*(h) = \frac{1}{2n(h)} \sum_{i}^{n(h)} [f(x_i) - f(x_i + h)]^2$$

Where $g^{*}(h)$ represents the experimental variogram for distance h, n(h) is the number of points separated by displacement *h*, and f(x_i) is the value at data point x_i (Petitgas, 1996). All the grid samples in the data set were included in the variogram calculation. Displacement *h* represents direction and magnitude, also called lag.

Variograms can be computed as either an average over all directions in which case the lag measure is scalar (omnidirectional variograms), or specific to a particular direction in which case the lag measure is a vector (directional variograms) (Rossi et al., 1992). Here I assumed the variogram behavior to be the same in all directions, and the results I present correspond to omnidirectional variograms.

Variogram model fitting

The next step was obtaining a model variogram; this can be achieved by fitting one of a number of acceptable functions, including exponential, Gaussian, spherical and power functions to the experimental variogram. I used an exponential function (Cressie, 1993)

$$(3) \qquad g(\mathbf{x}-\mathbf{x}') = t^{2} + s^{2}\left\{1-\exp\left[-\frac{(\mathbf{x}-\mathbf{x}')}{f}\right]\right\}$$

where t^{2} is the variability at scales smaller than the distance between samples and variability due to measurement error (the nugget effect), f is the distance over which samples are spatially autocorrelated (range), and s^{2} is the background variability that occurs at distances greater than the range (sill) (figure 3.4). The functional form of the model is related to the spatial continuity of the studied variable.

I then estimated linear regression and variogram model parameters simultaneously using the geoR package (Ribeiro and Diggle 2001) in the R software (http://www.r-project.org/)

Model selection and validation

Akaike's Information Criterion (AIC) was used to rank variogram models. The AIC statistic, estimated with the addition of each new parameter to the model, accounts for degrees of freedom used and the goodness of fit such that more parsimonius models have a lower AIC (Chambers and Hastie, 1992). In order to validate the chosen model, I applied a cross-validation method to a sub-set of the data. This method has been used for optimal choices of variogram models (Simrad et al., 1992; Petitgas and Poulard, 1989). The procedure consists of deleting one datum and using the remaining data to predict the deleted value using the chosen model.

3.3 RESULTS

In order to explore the relationship between hake distribution and temperature, I computed average temperature ($\overline{T}$) of hake waters for each CTD station. A frequency histogram of these values reveals that hake occur in waters of a wide range of temperatures (from a minimum of 3.5 ^{o}C to a maximum of 17.5 ^{o}C) (figure 3.5). As expected, temperatures of hake waters were significantly higher during 1998, an El Niño year ($\overline{T}$=12.2 ^{o}C, s^2=12.1) compared to 1995 a neutral year ($\overline{T}$=5.3 ^{o}C, s^2=7.0) (p=1.1 x 10^{-17}, *df*= 81, t-test for difference between means).

In contrast, average sub-surface flow speed in hake waters (figure 3.6) shows fish in waters with a much narrower window of values (between -0.05 m/sec and 0.25 m/sec, negative values indicate equatorward flow and positive values indicate poleward flow) compared to the temperature values reported above, with most of the flow between 0.025 and 0.075 m/sec, speeds reported to be typical of the poleward flowing undercurrent (Pierce et al., 2000). Average sub-surface flow speed in hake waters was higher in 1995 ($\overline{x}$ =0.05 m/sec, s^2=0.004) compared to 1998 ($\overline{x}$ =0.03 m/sec, s^2=0.003) (p=0.04, *d.f.*= 160, t-test for difference between means). Similar results were found when considering flow at all depths.

Sections of flow overlaid with hake distribution and abundance data were plotted for each transect. These reveal a picture of ubiquitous core of poleward flow at depth, with its strength and location varying both inshore/offshore, at in depth for the two years sampled. Complex flow patterns were evident in each section. The view of geostrophic flow in any one section is confused by the presence of barotropic tidal currents, baroclinic tidal currents and intertial oscillations (Pierce et al., 2000). For sections where fish were present, concentrations were almost always observed on the edge of the core poleward flow (figure 3.7). Depth of fish and core current averaged over latitudinal blocks were similar (figure 3.8) during both 1995 and 1998, with average depths mostly ranging between 170 and 220 meters. Depth of core current values are consistent with results from Pierce et al. (2000), as well as historical estimates of undercurrent depth (Neyesha et al., 1989).

The alongshore sub-surface layer flow speeds show significant scatter during both years (figure 3.9) probably due to the presence of unresolved tidal, inertial and other phenomena. A statistically significant large-scale trend with latitude is evident in both plots, by classical least squares fit as in Pierce et al. (2000). The core velocities decrease poleward. Current vectors for the subsurface layer (120-330m) clearly show poleward flow during both years, but the presence of other oceanic phenomena is also obvious (figure 3.10, 3.11, 3.12). Fish index (FI) values computed for each transect show the distribution of hake is variable along the coast, but there is a shift of the population north in 1998 (figure 3.13); large amounts of hake were found north of 50^{o}N (FI between 0.4 and 1) during 1998 in comparison with small (FI < 0.1) to no amounts of hake found in this area during 1995.

A plot of alongshore sub-surface flow speed in hake waters averaged over each transect (figure 3.14) also clearly portray a picture of variable flow along the coast, mostly poleward during both 1995 and 1998. During 1995, northard flow was measured at 81% of the transects and southward flow at 19% of the transects; during 1998 northerly flow was measured at 85% of the transects and southerly flow at 15%. Interesting latitudinal patterns can also be observed. A transition point in undercurrent strength just north of Cape Blanco is evident (figure 3.14). Pierce et al. (2000) also find a similar transition point in their analysis of the undercurrent. My analysis shows that both 1995 and 1998 flow speed north of Cape Blanco diminishes, with sub-surface flow velocity in 1995 being more southward compared to sub-surface flow in 1998 (figure 3.14). The distance from the shelf of maximum alongshore sub-surface flow is highly variable in 1995 compared to 1998, and gets closer to the shelf north of 45°N with areas of on-shelf flow (figure 3.15). In 1998 maximum alongshore sub-surface flow in the southern portion of the survey area (south of 44°N) is significantly closer to the shelf ($\overline{X}$ = 15, s^2= 146) compared to 1995 ($\overline{X}$ = 19, s^2= 77, $p<0.05$), while it gets farther away and never migrates on the shelf north of 44°N ($\overline{X}$ = 28, s^2= 428) compared to 1995 ($\overline{X}$ = 11, s^2= 511, $p<<0.05$). Distances of maximum fish densities follows this pattern, with maximum fish densities south of 44 °N observed slightly (although not significantly) closer to the shelf break in 1998 ($\overline{X}$ = 10, s^2= 108), compared to 1995 ($\overline{X}$ = 12, s^2= 113). Overall maximum fish distances from the shelf break in 1998 are highly variable and increase northward along the coast (figure 3.16).

In order to quantify adult hake habitat, I built a geostatistical habitat model using data from 1995. Table 3.1 represents all the models that were fit to the data. Formulations were chosen as best models based on AIC values. The formulation identified as best model (AIC = 6014) was:

$$y = b_0 + b_1 current^2 + b_2 current + b_3 depth + S(\mathbf{x}) \tag{4}$$

y = number of fish

depth = bottom depth

current = sub-surface alongshore flow velocity (120-330m)

Table 3.2 illustrates parameter estimates and standard deviations for the model of choice. Parameter values indicate that the relationship between habitat and current is dome shaped, with intermediate current velocities leading to higher amount of favorable hake habitat.

The model variogram (figure 3.17) exhibited a range (average distance beyond which points are no longer correlated spatially) of 2.67 km. The sill of the variogram quantifies the maximum level of variability between points. The sill for the model was 39.28. Fits to a sub-set of the observed data illustrate that a model not including a spatial component (figure 3.18) does not perform as well as the model including a spatial component (figure 3.19); the fit of the model to 1995 data is superior compared to the fit to 1998 data (figures 3.19).

Predicted hake habitat was calculated by implementing the mean effect component of equation 1. Maps of predicted hake habitat in 1995 and 1998 are presented in figure 3.20. Maps were produced in ArcView. I arbitrarily defined hake habitat as favorable at location where fish densities were higher than 1100 individuals and less favorable at locations where fish densities were less than 1100 individuals. Amount of favorable hake habitat was lower in 1995 (16% of area considered in modeled) compared to 1998 (51% of area considered in model).

3.4 DISCUSSION

The results of my analysis suggest that Pacific hake habitat is associated with sub-surface poleward flow and not a specific temperature range. Temperature has been one of the most widespread indices used to relate environmental conditions to abundance and distribution of fish populations. Temperature is known to influence the physiology of some species (Durant et al., 2003; Hardewig et al., 1996), and can be useful as an index of oceanic conditions impacting fish abundance and/or distribution. However if a specific process associated with the index has not been identified, the relationship is not likely to hold during different climate regimes and will therefore not be useful to researchers and managers. For example Benson et al. (2002) looked at how sea surface temperature (SST) and upwelling relate to the presence of hake in Canadian waters. The relationship with SST only existed until a shift to a new climate regime occurred. Upwelling was found to be a better predictor of hake abundance in Canadian waters. The authors note that this type of index includes transport and winds more explicitly and may thus be a better predictor. The influence of transport processes on poleward hake migration was also observed by Smith et al. (1990) who looked at the relationship between a number of oceanographic parameters and the observed ‘length at age’ pattern for Pacific hake sampled off Vancouver Island. Sea-level height, commonly used as an index of transport, had the strongest relationship to interannual variability in hake mean lengths-at-age in Canadian waters. The authors find that years of stronger than normal poleward flow (or weaker than normal equatorward flow) result in more smaller hake arriving off southern Vancouver Island. This suggests that northward migration of hake is assisted in years of strong poleward flow.

Temporal and spatial patterns characterize both hake distribution and undercurrent characteristics during the two years of this study. The distribution of Pacific hake shifted north in 1998, with higher densities of fish observed north of 50^{o}N. This shift north can not be explained by a higher number of older fish in the population, as the estimated population's age distribution in 1995 and 1998 are similar (figure 3.21). Instead, favorable flow characteristics could have facilitated the migration of hake north in 1998. The flow in 1998 was more ubiquitous and coherent compared to 1995. The literature suggests stronger undercurrent during warm years (Bograd et al., 2001; Lynn and Bograd, 2002; Bograd and Lynn, 2003). Pierce and Kosro (unpublished in Swartzman and Hickey, 2003) report on higher average undercurrent volume transport (m^3/sec) during 1998, compared to both 1995 and 2001.

Flow geometry such as distance from the shelf and area covered also differs between the two years of this study. In 1998 sub-surface poleward flow was significantly closer to the shelf in the southern part of the survey area (south of 44^{o}N)) (figure 3.15) . Along specific sections of the coastline (e.g. from 44.5-46 ^{o}N) alongshore flow was mostly poleward in 1998, and mostly equatorward in 1995. Flow geometry as well as flow velocity are likely to affect hake distribution. There is evidence of a higher concentration of prey at shelf-edge environments (Mackas et al., 1980; Simard and Mackas, 1989; Mackas, 1992; Mackas et al, 1997). Being at the edge of a current closer to the shelf break (as was the case in 1998 in the southern portion of the survey) probably gives hake better access to prey usually found in higher concentrations along the shelf. This is particularly important for younger, thus smaller, hake typically found in the southern portion of the survey area. Thus, the proximity to the shelf break of the flow in the southern area of the survey during 1998 could have facilitated access that year to richer feeding grounds for the smaller younger fish in the population.

I also find differences in the amount of hake habitat between 1995 and 1998. The model results show that amount of adult hake habitat in 1998 (an El Niño year) was greater than adult hake habitat in 1995 (a neutral year) (figure 3.20). This suggests that during El Niño years, habitat expands possibly as a result of changes in location and intensity of the poleward undercurrent.

Based on the results of this analysis I hypothesize that one of the ways climate influences the population dynamics of hake is by affecting the physical structure of adult hake habitat, expanding and contracting the amount available. I suggest that poleward flow in this area defines adult hake habitat, with flow properties aiding or impeding the poleward migration of the population. This is especially true for the southern half of the hake distribution where smaller fish are closer to shore in the juvenile nursery grounds (see chapter 1) thus flow closer to the coast is probably easier for them to detect. Favorable current characteristics during warm years (e.g. coherent ubiquitous flow along the coast located close to the shelf break) may facilitate the hake feeding migration north to richer feeding grounds and access to prey along the way. These conditions may also facilitate migration of smaller younger fish that would otherwise have a hard time covering long distances. For example, Smith et al. (1990) as well as Benson et al. (2002), find evidence of a greater number of smaller hake present in Canadian waters during 1998. Wilson and Guttorsmen (1997, 1998) find 95% of hake caught off the coast of Washington in 1995 to be above 42 cm in fork length, while only 50% in 1998 were in this size category. The presence of smaller younger hake further north could also lead to an increased spatial overlap of age classes and potentially a higher rate of cannibalism during warm years. Field (2004) reports on differences in the amount of hake present in hake diets during warm and cold years, with up 70 % of hake prey being smaller hake during warmer years compared to the less than 1 % during cooler years.

My hypothesis that poleward flow defines amount and location of adult hake habitat might lead the reader to believe that I do not consider food availability to be important. This is not the case. Pacific hake migrations are first and foremost motivated by a search for food, and are therefore primarily governed by factors related to food availability. The physical structure of the water column is one of these factors, as it probably influences the distribution of hake prey (i.e. euphausiids) that for the most part are not as able to retain position in the water column in regions of strong flow (Swartzman and Hickey, 2003). Swartzman (2001) and Swartzman and Hickey (2003) investigate the relationship between the distribution of euphausiids and hake along the west coast of North America. They find a consistent overlap of large plankton patches and fish shoals near the shelf break, although the degree of clustering between years differed depending upon latitude. However, Mackas et al. (1997) point out that despite the apparent relationship between euphausiids, hake and bathymetry evident at a coarser scale (tens of kilometers), this relationship does not hold at a finer scale. Their analysis highlights the importance of cues provided by flow fields. They do not find an overlap in space between plankton and hake at a finer scale; hake patches are located either above or below euphausiid patches and both organisms seem to be associated with specific bathymetric contours. Sensory spheres of both zooplankton and fish are quite small (Mackas et al, 1997). Mackas et al (1997) suggest that hake are cued by their immediate surrounding flow field, rather than by the surrounding bathymetry or prey density (both at ranges >= 10m).

I propose that Pacific hake gain evolutionary benefits by positioning themselves relative to poleward flow. One advantage is that being at the edge of this current puts them in or close to a location where the food supply is likely to be high (the shelf break). The other advantage is reduced energy expenditure during their northward migration. What determines competitive advantage of a certain life history strategy over another is ultimately related to energy gain and expenditure. Food allows individuals to gain that energy, but migrating long distances contributes to expending it. Close examination of hake life history traits reveals that hake time their migration in relation to the seasonality of the current (see chapter 1). Females for example leave the spawning grounds earlier, beginning their migration when the poleward current intensity is at its peak (Saunders and McFarlane, 1997). This suggests that Pacific hake have evolved to take advantage of poleward flow during their feeding migrations. Hake are active swimmers and do not need the current to migrate north. Poleward flow simply allows them to complete their migrations expending less energy, and gain access to new energy by accessing richer northern feeding grounds. There is evidence of poleward flow facilitating hake migration in other areas of the world (Sanchez and Gil, 2000). The fact that distant populations are affected by similar environmental processes leads me to believe that an association with poleward flow must provide competitive advantage to this species.

A quantitative measure of hake habitat such as the one I develop here could potentially serve as an ecosystem indicator. Hake is one of the major predators in the northern CC system. The amount and distribution of adult hake habitat has large implications for the Pacific Northwest food web. For example Field (2004) found that during warm years during which hake are more abundant in northern CC waters (north of Cape Mendocino), there is an increase in predation (particularly on pandalid shrimp and small flatfish) and competition (for euphausiids, forage fish and other prey of resident groundfish). The absence or presence of hake in Pacific Northwest waters is likely related to habitat suitability along its range of distribution. Changes in the amount of adult hake habitat could serve as an indicator of changes in the structure/energy flow of the northern CC ecosystem, as changes in hake distribution could imply changes in the productivity of other commercially and ecologically important species. In chapter 5, I will use the ecosystem model developed by Field (2004) for the northern CC ecosystem to explore what ecosystem structure might look like under different scenarios of hake abundance.

The data set I used for this analysis was very large (information on flow characteristics and hake spanning 15^o of latitude, ~300,000 grid points/year). While this provided fine resolution in space, it also presented a number of challenges and limitations. Averaging sub-surface alongshore flow along transects (figure 3.14) provided me with a useful way to synthesize results for such a large geographical area, but results from the northern area (north of 48^{o}N) should be interpreted with caution. The higher flow speed observed in northern areas (figure 3.14) are probably a combination of tidal currents and poleward flow. Tidal currents are known to exist especially off the coast of Vancouver Island (49-51^{o}N) and to mix here with the undercurrent (Thomson, 1981; Thomson et al., 1989). Tidal flow can be much faster in this area than the poleward flow and is typically located on the shelf break (Thomson et al., 1989). Other areas along the survey area exist where reported flow characteristics are a combination of poleward undercurrent and other phenomenon. The Cape Blanco region is one of these areas. Researchers report on an upwelling jet on the shelf break north of Cape Blanco and off the shelf break south of Cape Blanco (Pierce et al., 2000; Smith, 1995). This jet is known to interact significantly with the undercurrent, probably confusing our picture of geostrophic flow. Another such area is in the northern section of the survey (north of 48^{o}N). Values reported as transect averages only consider north/south velocities; in areas where the coastline is roughly in a north/south direction (e.g. 42-48^{o}N) these values are a good representation of alongshore flow. However, this is not the case for the area north of 48^{o}N where the slope of the coastline changes. For this area flow representations such as the one used in figures 3.10-3.12 are more appropriate.

Because of the large nature of the data set (thus the computational power necessary to build a model based on data from the entire hake distribution range) I used a sub-set of the data. This allowed me to test approaches and methods that could in the future be applied to the entire data-set. However, using a sub-set of the data introduced some measurement and process error. The range of habitat considered in the model I built is located at the southern most edge of the adult hake distribution (38-43 ^{o}N). This area is occupied by a mixture of juveniles and adults. It is difficult to discrimate acoustic signal of smaller sizes (juveniles) from signal for other organisms (e.g. euphasiids). Measurement error is introduced here, as smaller sizes might not be fully reported. This could be one of the explanations for the inferior fit of the model to the 1998 data compared to the 1995 data, as in 1998 the population reportedly shifted north (Wilson, 2000; Helser, 2001) and fewer adults were observed in southern areas. As can be seen in figures 3.18 and 3.19 the model does not do well with predicting ‘0 values’ (process error). Because of the shift north in the population described above, the 98 data set had a higher number of locations with 0 fish. As a result, the 98 model predictions were not as accurate as the 95 model predictions. A model based on data from a section of the hake habitat located farther north (e.g. 43-48 ^{o}N), where the majority of the population sampled is older (fish size is bigger thus more accurately sampled) and the area consistently occupied in both 1995 and 1998, could be more informative.

The factors influencing hake year class strength are multiple and complex. Because of this, a linear relationship between what I have discussed here and the hake production time series will not be found. For example, conditions on the larval and juvenile nursery grounds are of primary importance, as is the impact that the fishery has on the population. Here I have formulated hypotheses to explain the variability in hake migration and adult hake habitat, which are a part of this puzzle. All of these factors come together to produce the observed production variability. Similar changes in migration patterns have been observed for the other CC pelagic species, like sardine and mackerel (Beamish et al., 2000). One thing seems clear: pelagic fish are good indicators of shifts in ocean conditions, as their life histories are so tightly related to atmosphere/ocean conditions. This leads me to believe that perhaps in the future pelagic fish distribution might be used as an indicator of climate change. We will however only be able to do so if we understand the processes that link climate and pelagic fish production and distribution. This dissertation is a step in that direction.

Table 3.1: Model formulations. Value in grey indicates model chosen based on AIC value. Please note that differences in AIC <=1 are not significant.

Models with autocorrelation term	**AIC**
$b_0 + b_1 depth + S(\mathbf{x})$	6016
$b_0 + b_1 current + S(\mathbf{x})$	6018
$b_0 + b_1 current + b_2 depth + S(\mathbf{x})$	6017
$b_0 + b_1 current + b_2 depth + b_3 current \bullet depth + S(\mathbf{x})$	6019
$b_0 + b_1 current^2 + b_2 current + b_3 depth + S(\mathbf{x})$	6014

Models without autocorrelation term	**AIC**
${}^{nac}b_0 + {}^{nac}b_1 depth$	7092
${}^{nac}b_0 + {}^{nac}b_1 current$	7153
${}^{nac}b_0 + {}^{nac}b_1 current + {}^{nac}b_2 depth$	7056
${}^{nac}b_0 + {}^{nac}b_1 current + {}^{nac}b_2 depth + {}^{nac}b_3 current \bullet depth$	7186
${}^{nac}b_0 + {}^{nac}b_1 current^2 + {}^{nac}b_2 current + {}^{nac}b_3 depth$	7057

Table 3.2: Model parameter estimates**.**

Parameter	Mean value	Standard deviation
Non autocorrelation model:		
b_0^{nac}	12.68	0.49
b_1^{nac}	-5.73	13.5
b_2^{nac}	2.90	2.92
b_3^{nac}	-0.006	0.0004
Autocorrelation model		
b_0	8.20	0.992
b_1	20.28	12.04
b_2	-3.75	3.009
b_3	-0.0025	0.00087
t^2 (nugget)	2.81	
f (range)	3.67 kilometers	
s^2 (sill)	39.28	

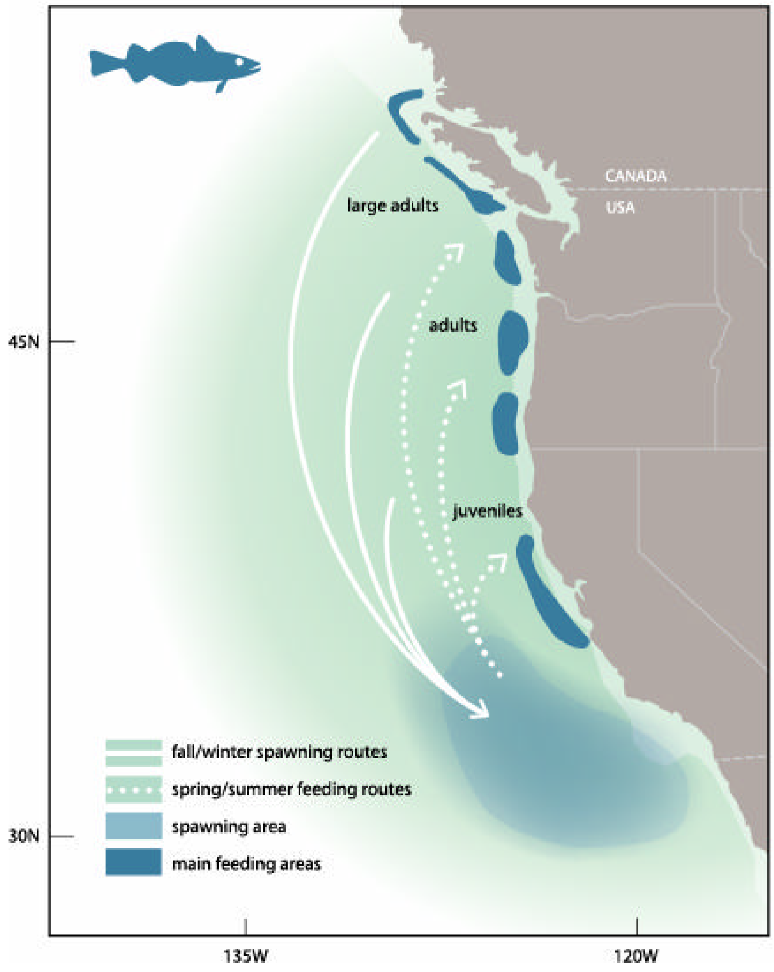


Figure 3.1: Schematic representations of Pacific hake migrations.

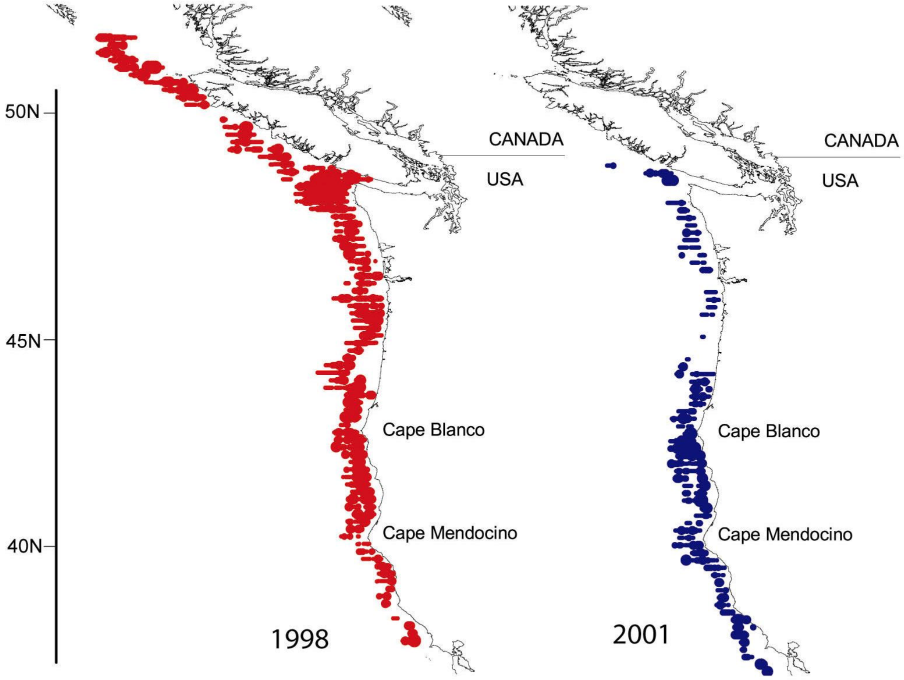


Figure 3.2: Acoustic backscatter signal representative of hake abundance during 1998 (warm year) and 2001 (cold year). Data from the National Marine Fisheries Service-Northwest Science Center (NMFS-NWSC).

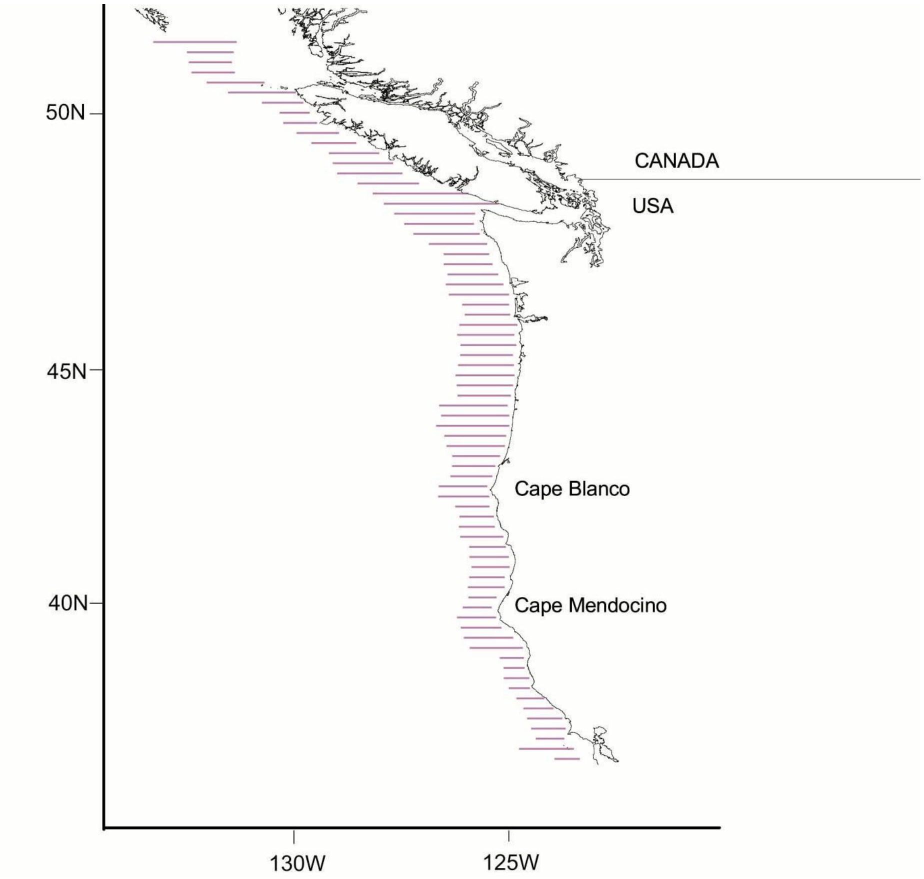


Figure 3.3: Distribution of joint NMFS/DFO triennial survey transects.

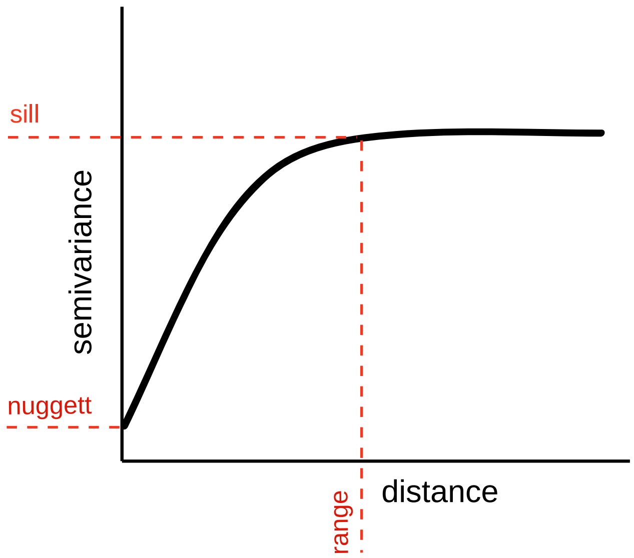


Figure 3.4: Sample variogram (semivariance between data points as a function of distance) illustrating the nuggett (variability due to measurement error), the range (distance over which samples are spatially autocorrelated) and the sill (background variability at distances grater than the range).

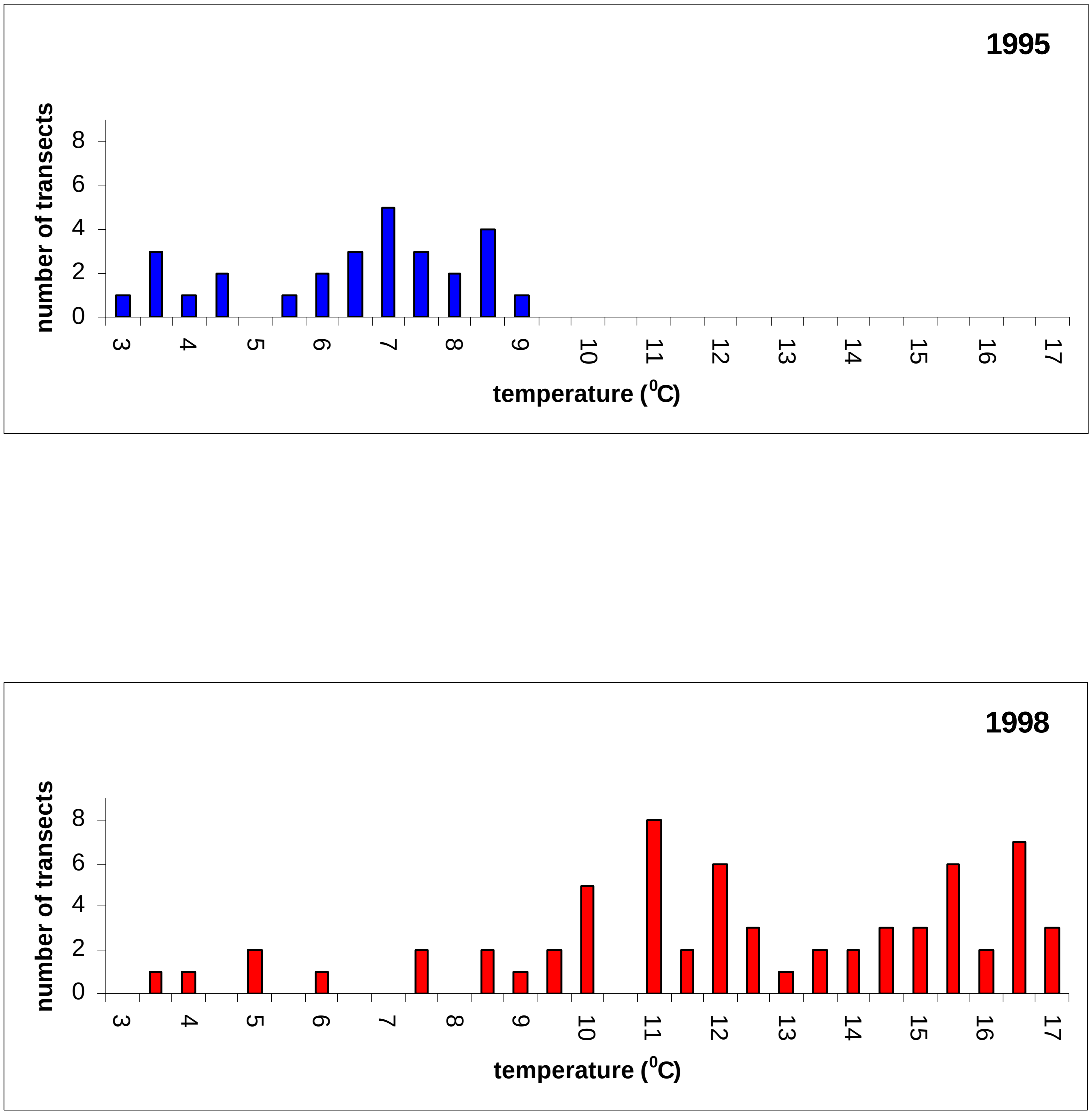


Figure 3.5: Frequency distribution of temperature values in hake waters at survey stations during 1995 (top panel) and 1998 (bottom panel).

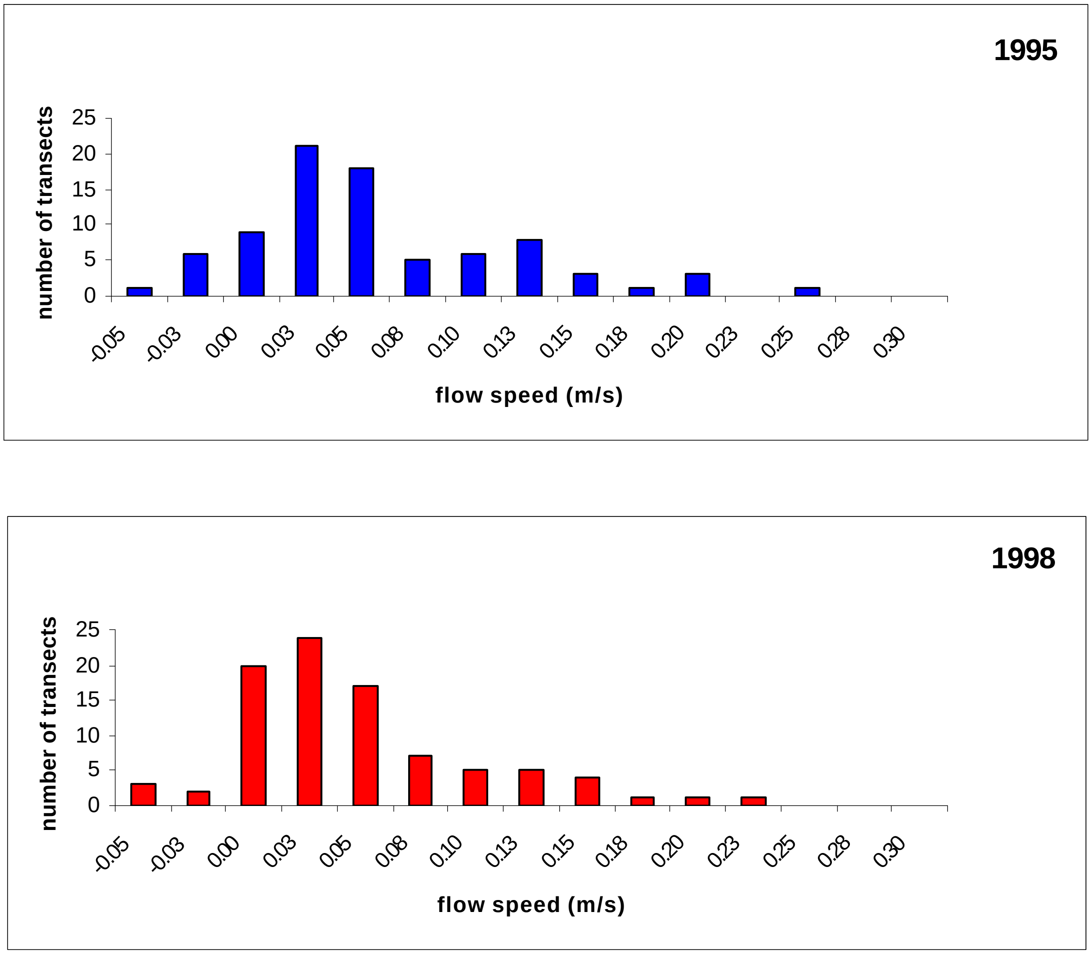


Figure 3.6: Frequency distribution of alongshore flow values in hake waters at survey transects during 1995 (top panel) and 1998 (bottom panel). Positive values indicate poleward flow, negative values indicate equtorward flow.

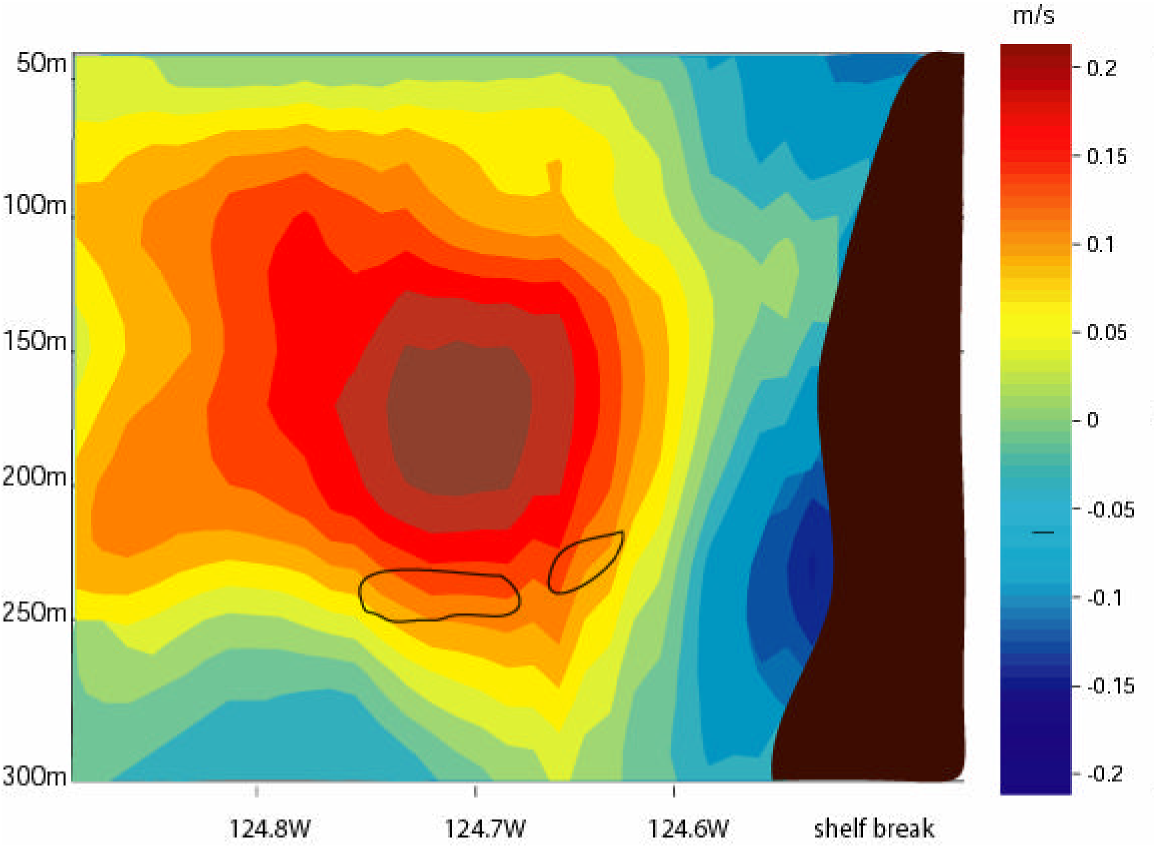


Figure 3.7: Distribution of alongshore flow (in color) and hake aggregations (in black-contours representing numbers of fish ≥ 2.83×10^2) for a transect located at 43 ^{0}N. The bottom contour is also shown (filled black area).

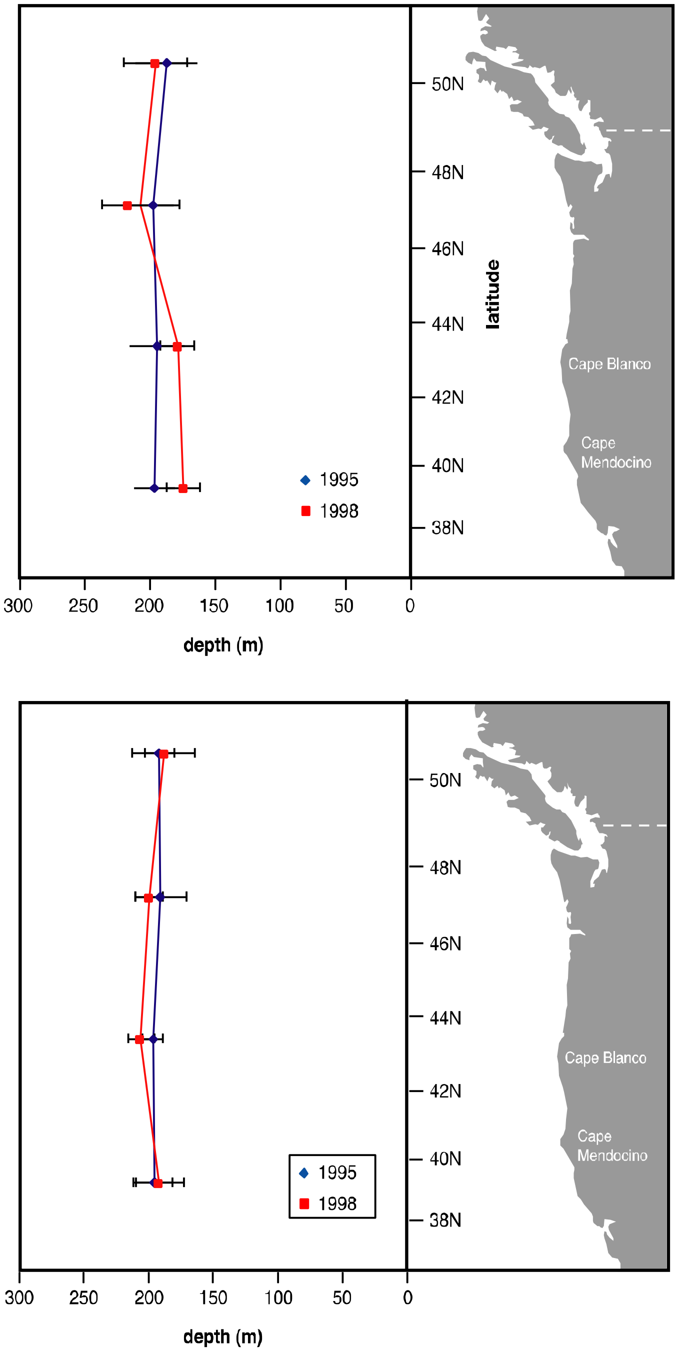
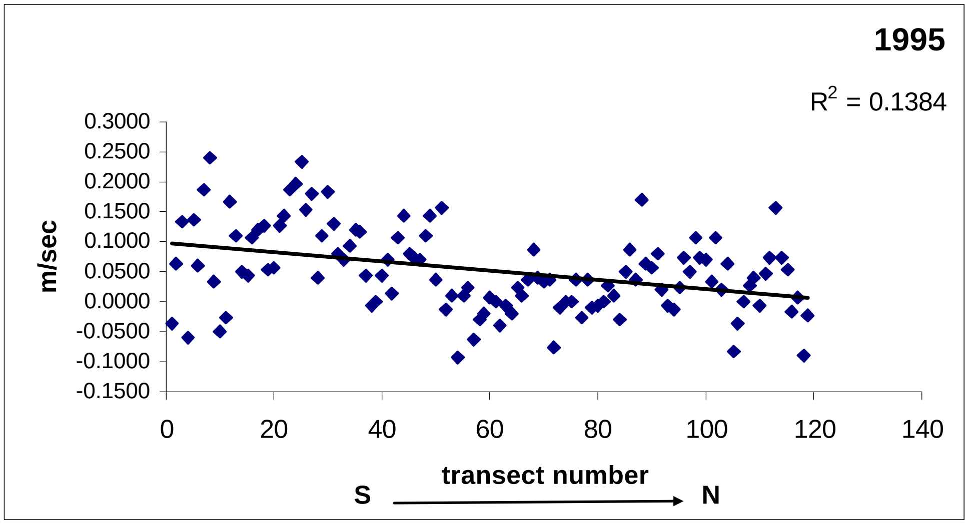


Figure 3.8: Depth of fish (top panel) and core current (bottom panel) averaged over 4 latitudinal blocks (37.5-42.5 ^{0}N, 42.5-47.5 ^{0}N , 47.5-52.5 ^{0}N).



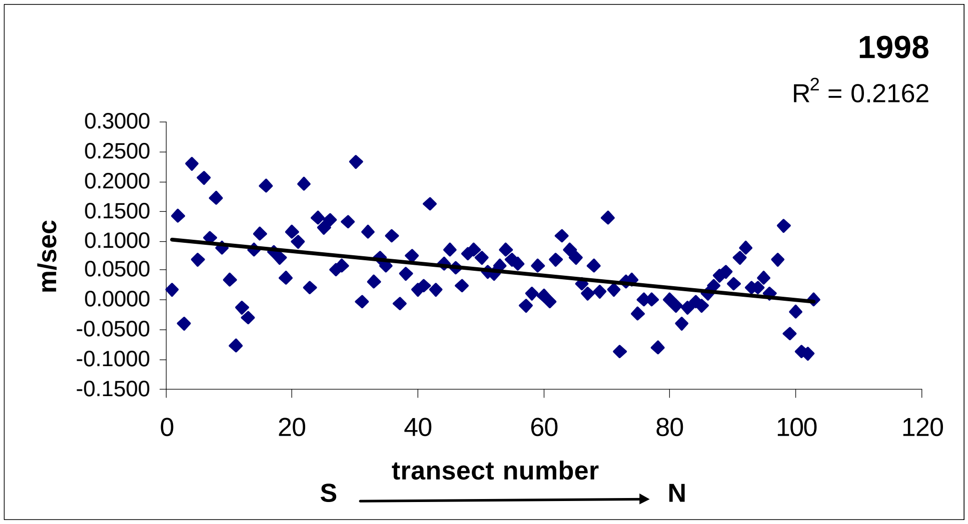


Figure 3.9: Average speed of sub-surface alongshore flow (negative values indicate equatorward flow, positive values indicate poleward flow) at each transect.

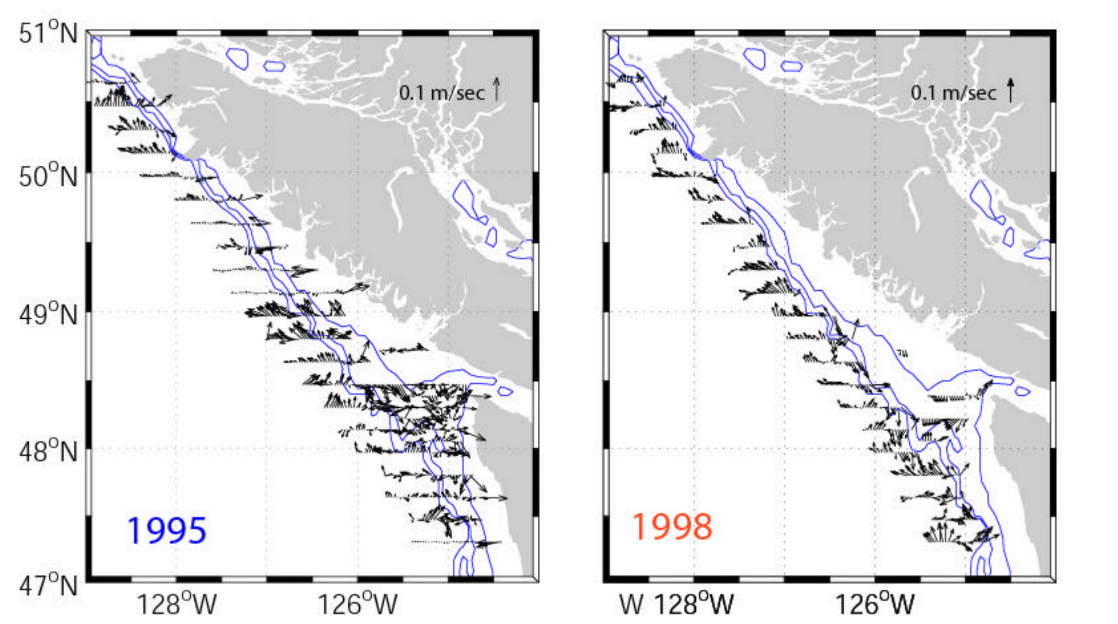


Figure 3.10: Velocity vectors from ADCP at each transect of a sub-section of the NMFS/DFO survey.

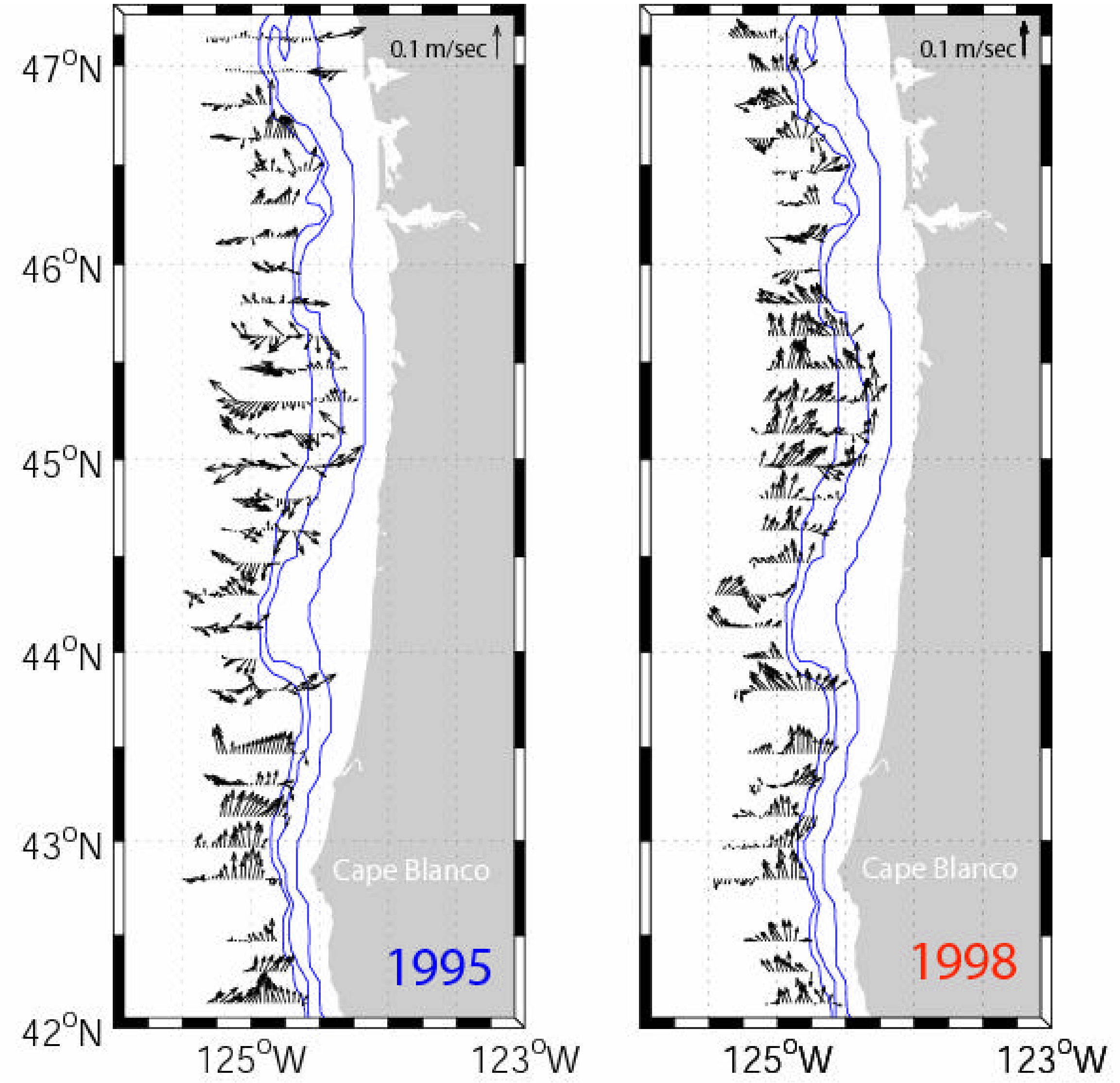


Figure 3.11: Velocity vectors from ADCP at each transect of a sub-section of the NMFS/DFO survey.

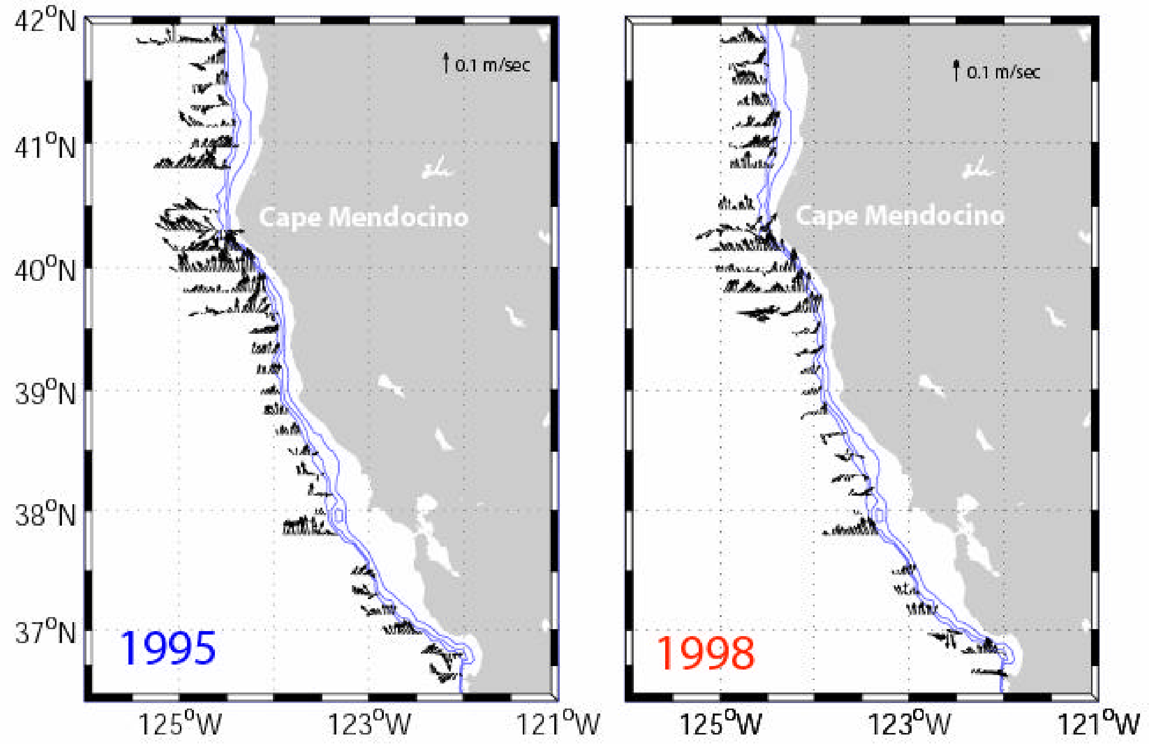


Figure 3.12: Velocity vectors from ADCP at each transect of a sub-section of the NMFS/DFO survey.

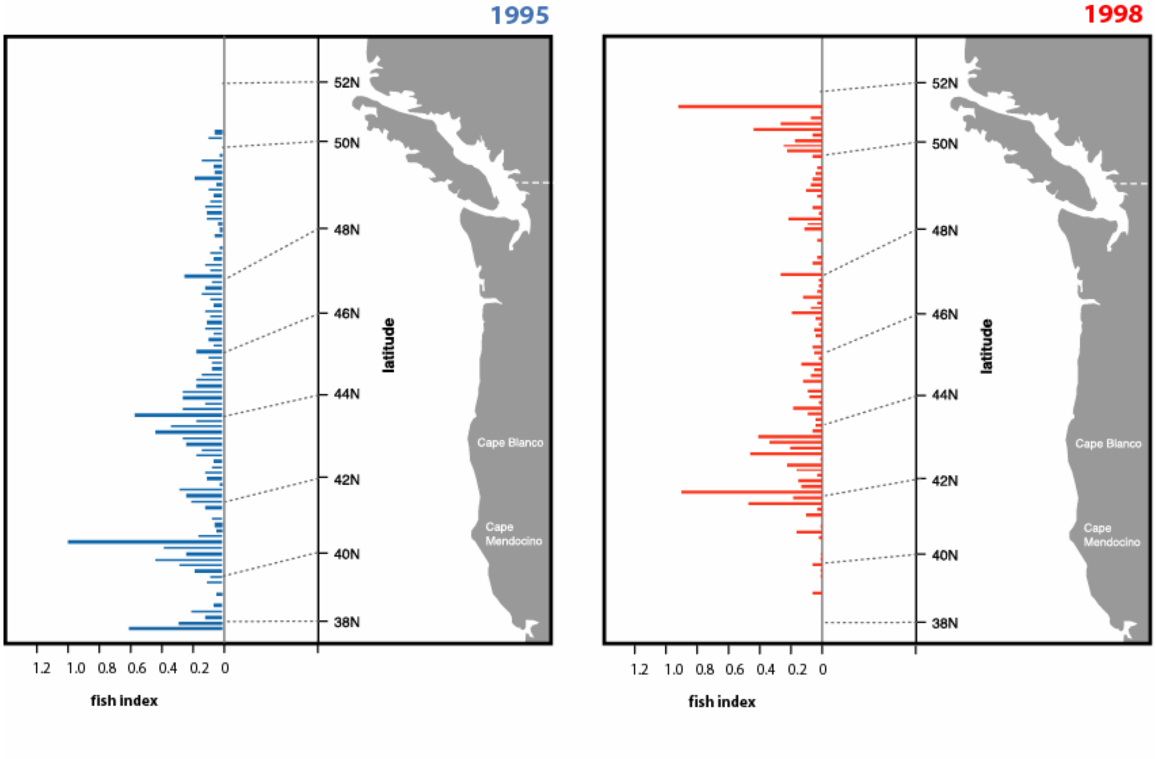


Figure 3.13: Fish index (number of fish per transect/maximum number of fish over survey area) by survey transect in 1995 and 1998.

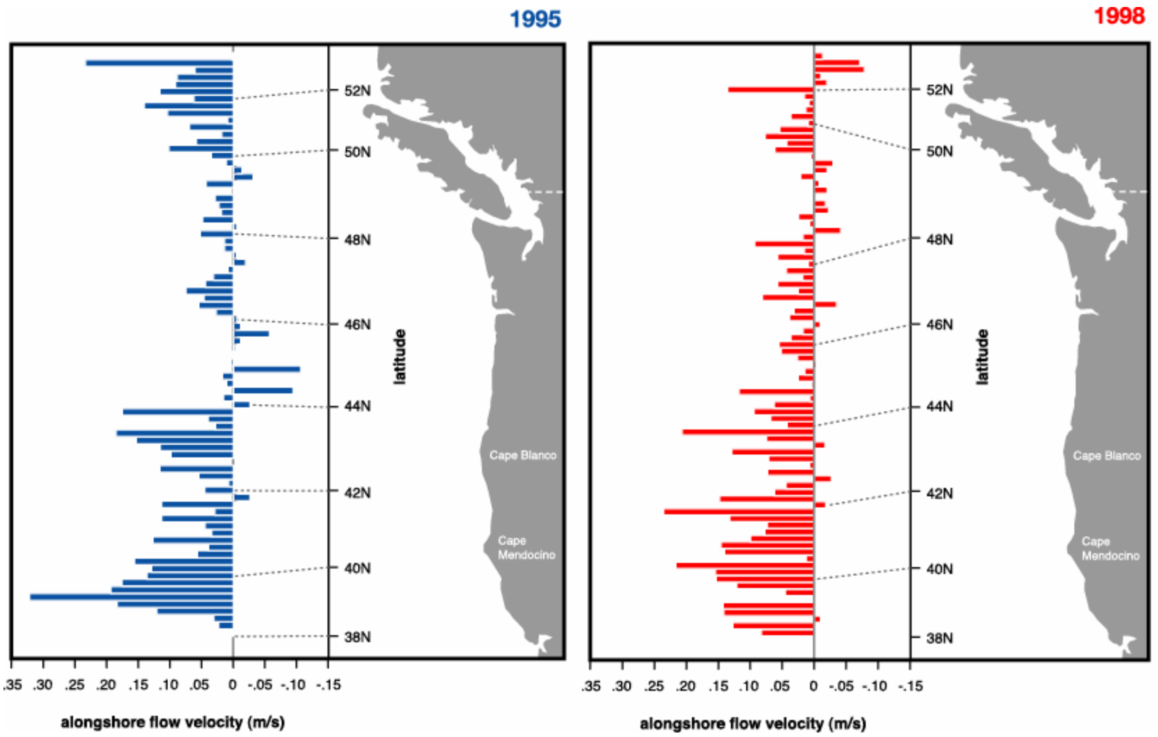


Figure 3.14: Sub-surface alongshore flow speed in hake waters for 1995 and 1998. Positive values indicate poleward flow, negative values indicate equatorward flow.

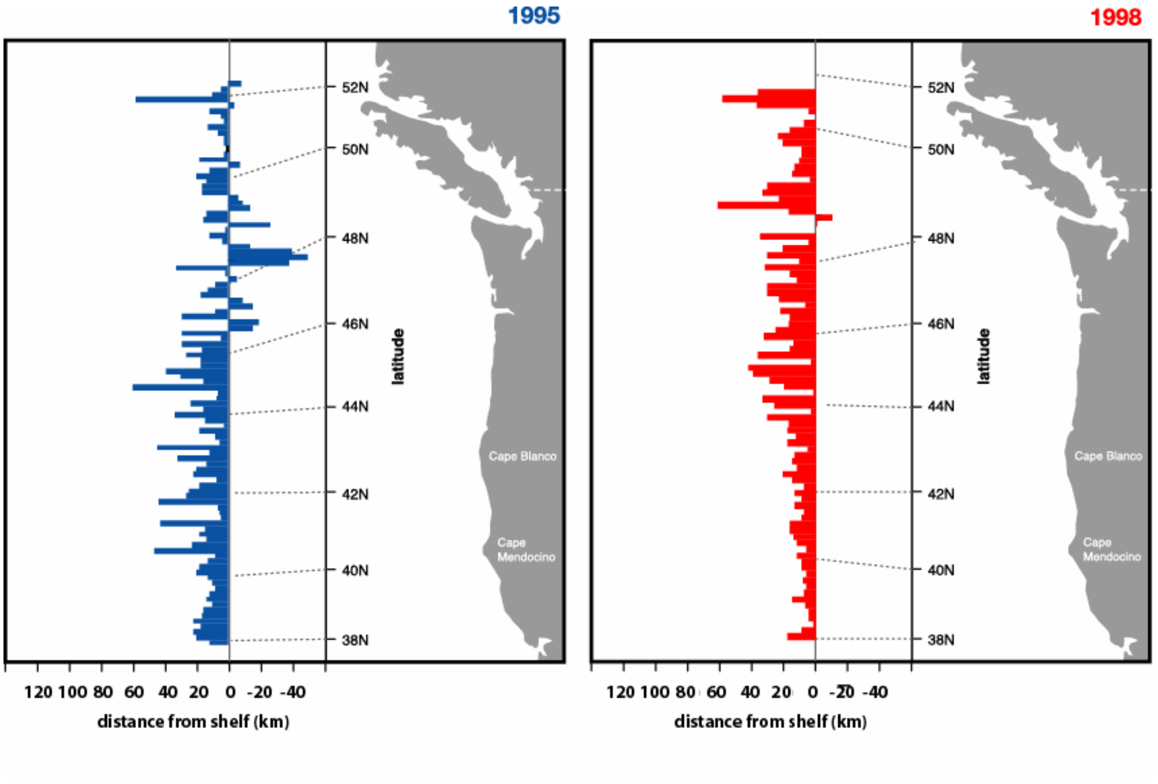


Figure 3.15: Distance from shelf (bottom depth=150m) of maximum sub-surface alongshore flow in 1995 and 1998. Negative values indicated on-shelf location, positive values indicate off-shelf location.

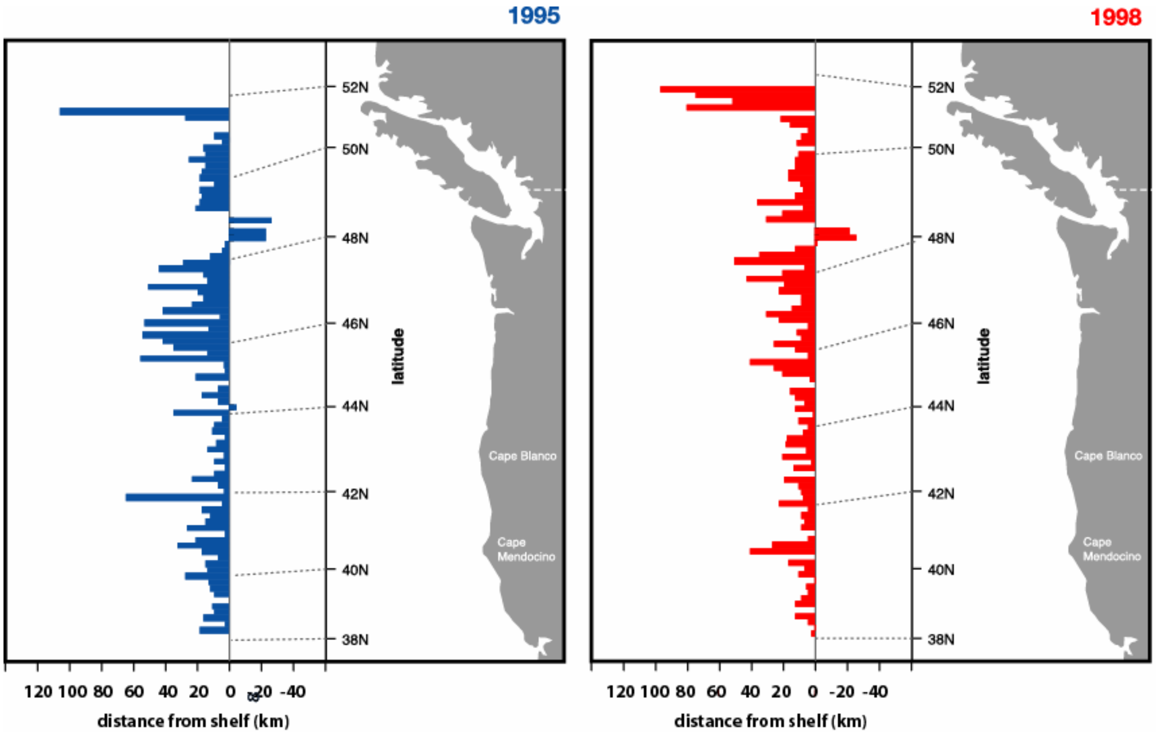


Figure 3.16: Distance from shelf (bottom depth=150m) of maximum fish concentrations in 1995 and 1998. Negative values indicated on-shelf location, positive values indicate off-shelf location.

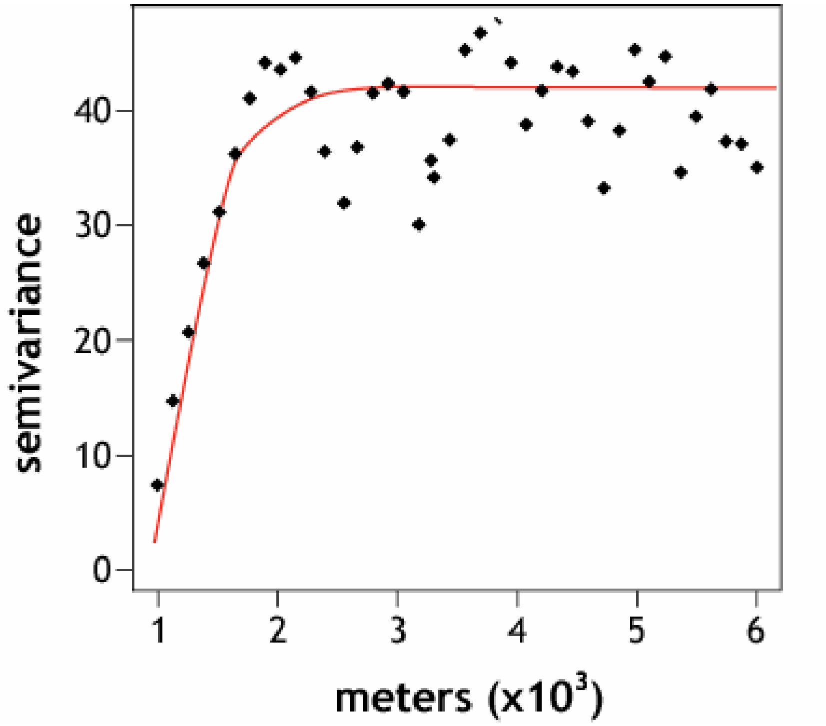


Figure 3.17: Experimental variogram (semivariance between data points as a function of distance) fitted to an exponential function (red line).

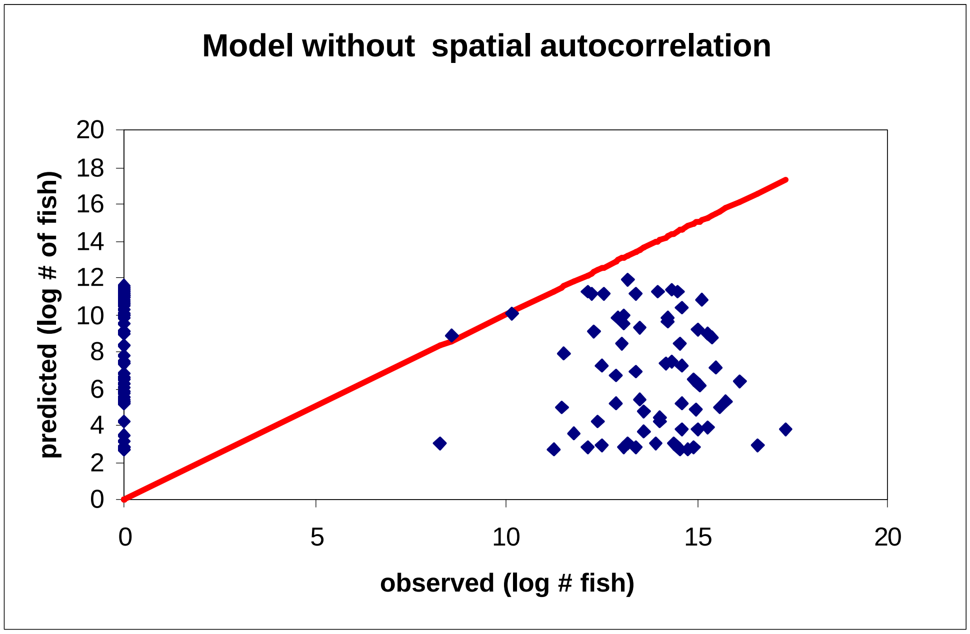


Figure 3.18: Fits of model without spatial autocorrelations predictions to a sub-set of the 1995 data.

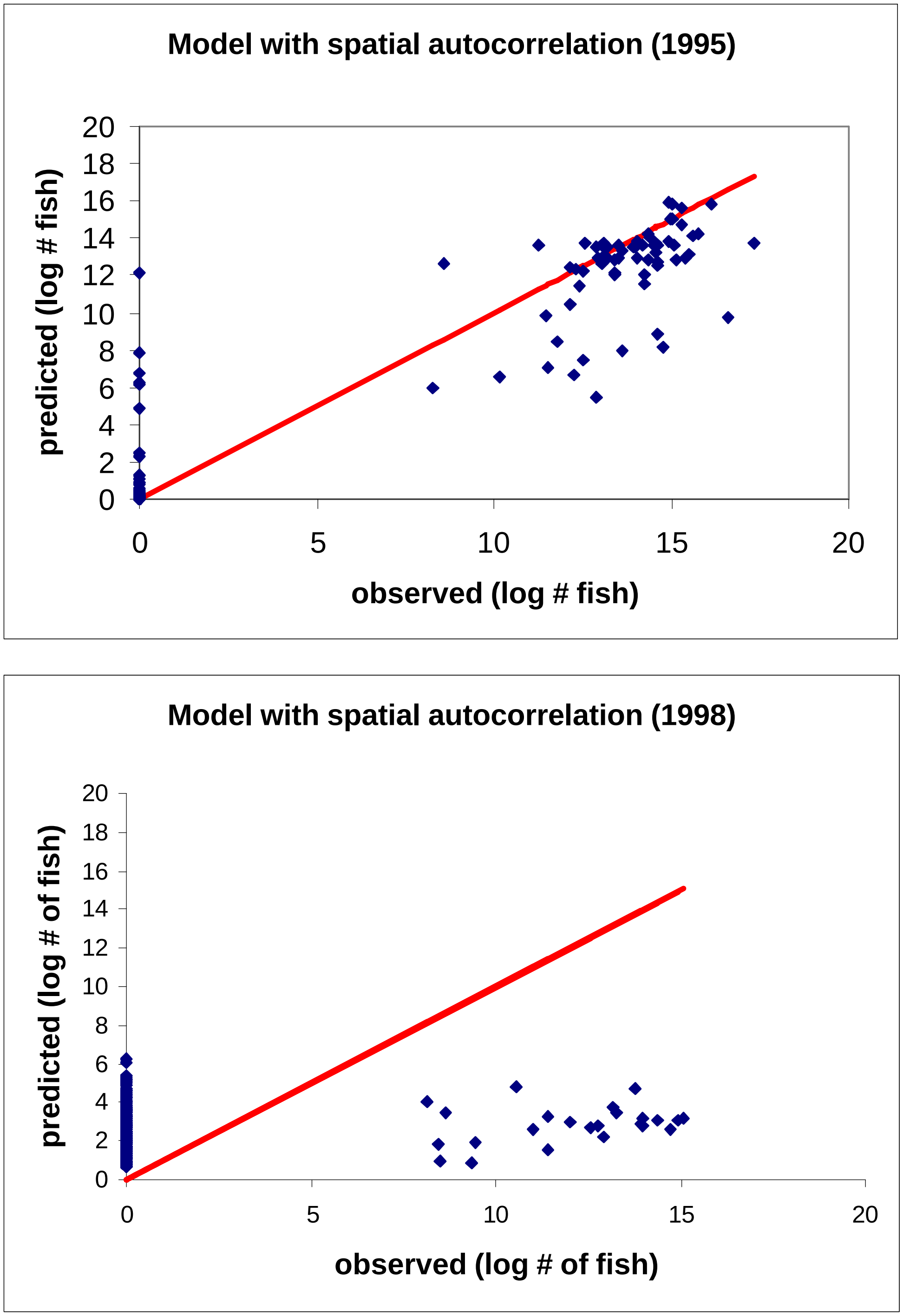


Figure 3.19: Fits of model predictions to a sub-set of observed data for 1995 (upper panel) and 1998 (lower panel).

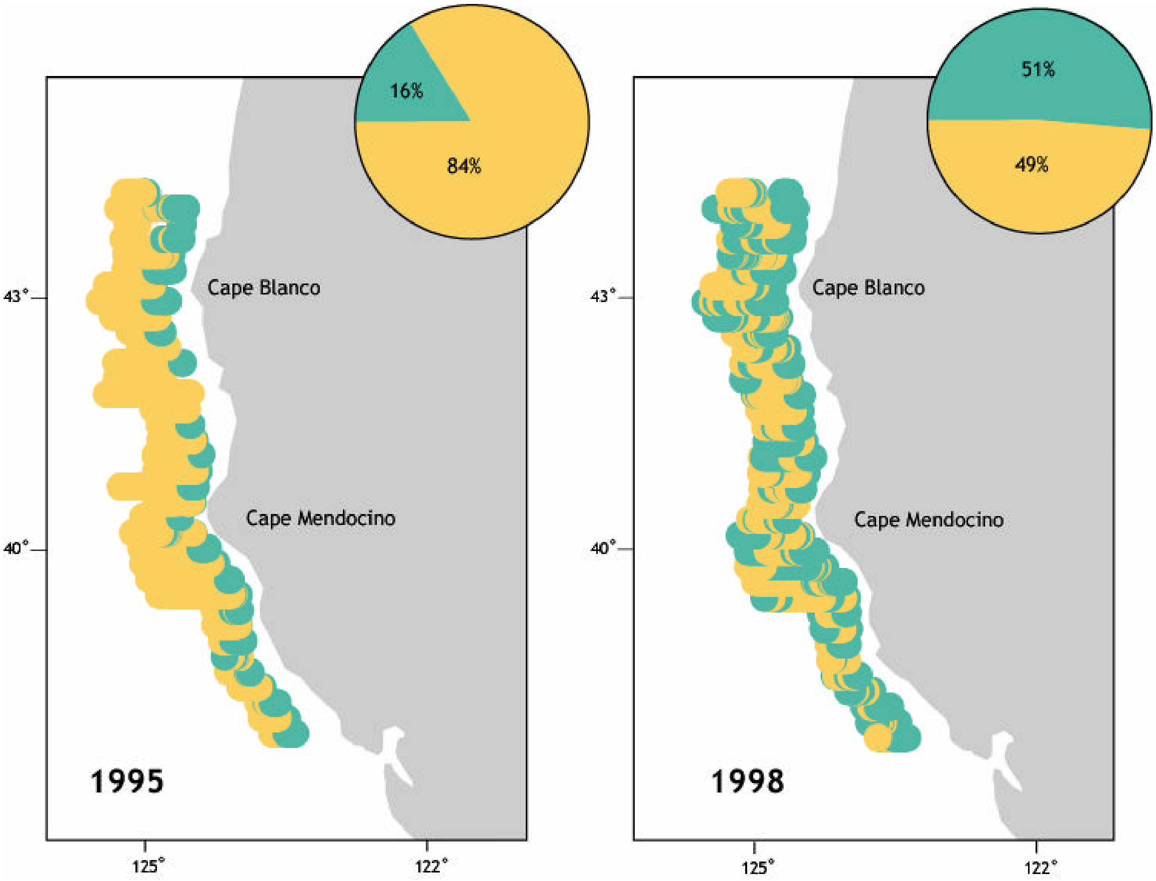
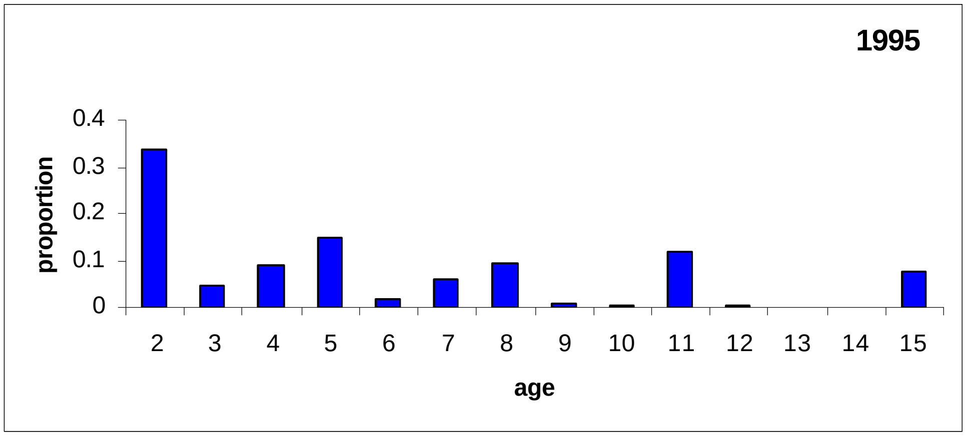


Figure 3.20: Predicted hake habitat given bottom depth and undercurrent velocities. Orange represents less suitable habitat (number of fish < 1100), green represents more suitable habitat (number of fish > 1100). Pie charts represent overall habitat distribution for 1995 and 1998.



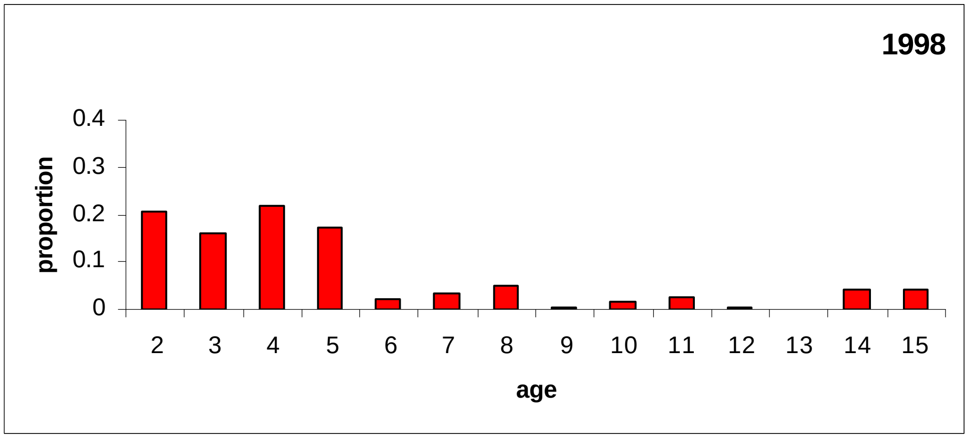


Figure 3.21: Estimates of proportions at age for the coastal stock of Pacific hake (Helser, 2004).

CHAPTER 4. Sardine habitat distribution and abundance patterns in the California Current.

4.1 INTRODUCTION

Sardines are fished in five of the world's coastal regions, off Japan, in the California, Humboldt, Benguela and Canary Current systems. Each of these populations has undergone wide fluctuations in both abundance and range. Except for the Bengulea, during warm periods, sardine spawning areas extend poleward as abundance increases (Lluch-Belda et al., 1989; Lluch-Belda et al., 1991; Rodriguez-Sanchez et al., 2001). In the Benguela, since waters in both the northern and southeastern extremities are relatively warm, sardine spawning during warm periods expands toward the centre of the system (Lluch-Belda et al., 1989).

The most northern stock of Pacific sardine (*Sardinops sagax*) the 'California sardine' supported the largest commercial fishery in the western hemisphere in the early 1900s (Wolf, 1992). At that time this species ranged from Baja California, Mexico, as far north as British Columbia, Canada. Spawning was reported to occur throughout most of its range (Emmett et al., 1994). Sardine biomass began to decline in the late 1940s (figure 4.1) and the stock was no longer observed off the coast of Oregon and British Columbia (Walford and Mosher, 1941; Ahlstrom, 1948). The population started increasing again in the early 1980s and since then fisheries off the Oregon, Washington and British Columbia coast have resumed.

California sardine are a migratory species. On average they are reported to spawn off the coast of southern and central California from January to June, and then move north and offshore in the summer towards feeding areas of high productivity (Ahlstrom 1960; Schweigert, 1988; Lluch-Belda et al., 1989; Schwartzlose et al., 1998) (figure 4.2). The migratory behavior of sardine is not well understood. Warm temperatures have been reported to shift their distribution to the north (Jacobson & MacCall, 1995; Smith, 1990). With increased population size their distribution also shifts to the north (McFarlane et al., 2002). During periods of low abundance their migratory behavior is greatly reduced (Ahlstrom 1960).

There has been considerable debate on the effects of overfishing, environmental factors and interspecific interactions on the sardine stock (Clark and Marr, 1955; Murphy, 1960; Murphy, 1966; Praeger and MacCall, 1993). Environmental conditions have long been thought to affect sardine population dynamics. Jacobson and MacCall (1995) empirically demonstrate that recruitment of sardine to habitat off northern Baja California and the Southern California Bight is related to sea surface temperature (SST) at Scripps pier before recruitment occurs. They hypothesize that this relationship is due to environmental effects on the distribution patterns of adults rather than survival of early life-history stages.

Sardine distribution patterns in the California Current (CC) system have been inferred from egg and larval surveys conducted both in the US (CalCOFI program) and Mexico (IMECOCAL program) (Figure 4.3). However, these surveys have not covered the entire portion of the sardine range as offshore and northern areas of their habitat have been sampled inconsistently. Information on distribution of adults in northern areas has been at most inferred by occasional surveys conducted by the National Marine Fisheries Service (NMFS) in the US and the Department of Fisheries and Ocean (DFO) in Canada. However, these surveys were not designed to directly target sardine. Perhaps due to the paucity of data, few attempts have been made to quantify sardine habitat and map its distribution over time.

I use SST as a proxy for larval, juvenile and adult habitat and construct a large scale view of potential sardine distribution. The purpose of this study is to test the hypothesis that sardine habitat area has fluctuated over time in the California Current (CC) system. I quantify changes in potential habitat from 1960 to 1997 over the entire range of California sardine. Finally I implement a linear regression model to explore effects of climate on habitat area.

4.2 METHODS

Habitat indices

This study considers waters between 13.5 ^{0}C and 16.5 ^{0}C to be potential larval, juvenile and adult sardine habitat. The temperature criterion was chosen since California sardine are reported to spawn primarily in 13.5 to 16.5 ^{0}C water (Tibby, 1937; Ahlstrom, 1954; Ahlstrom, 1965; Lluch-Belda et al., 1991; Parrish et al., 1989; Bentley et al., 1996). Also, there is evidence that food availability for sardine may be limited above 16.5 ^{0}C (Bentley, et al. 1996; Lo et al. 1996). SST data was extracted from the COADS database (measurements reported by ships of opportunity) (Woodruff et al. 1987; Mendelssohn and Roy, 1996) and used as a proxy for sardine habitat. Although California sardine are found throughout the upper mixed layer, a three dimensional analysis of sardine habitat was not possible here. Variability in mixed layer depth probably influences the volume of habitat occupied by sardine. Unfortunately time series on the vertical structure of the water column were not available at the geographic scale considered here. The analysis of sardine habitat in two dimensions allows the identification of temporal and spatial trends. Mixed layer depth data will be necessary to quantify sardine habitat in absolute terms.

SST data is reported in the COADS database as monthly means of 0.5 degree-longitude by 0.5 degree-latitude cells between 30-50°N during the 1932-1997 seasons (Woodruff et al. 1987; Mendelssohn and Roy 1996). Records from 1960 to 1997 were used, as observations prior to 1960 were scarce. Observations collected after 1997 were not available as they have not been quality controlled yet. In order to minimize potential problems with missing data, mean SST for larger 0.5 ^{0}W x 1 ^{0}N spatial blocks was calculated by averaging the original cell means (figure 4.4) (0.5 x 0.5 degrees). Area of potential sardine habitat was defined as percent of total number of spatial blocks with SST between 13.5-16.5 ^{0}C.

Habitat indices were derived for two seasonal periods: spawning period (January-June) and feeding period (July-December). For example, spawning habitat for a given area is the percent of total reported spatial blocks where mean January-June SST was between 13.5-16.5 ^{0}C. In order to examine latitudinal patterns, habitat indices were derived for the following sub-areas (each representing potential critical habitat for different sardine life history stages): a) 30-50 ^{0}N (the entire latitudinal range of California sardine); b) 30-34 ^{0}N, the spawning area (south of Pt. Conception); c) 35-39 ^{0}N, the spawning and juvenile nursery area (Pt. Conception to C.Mendocino); d) 40-43 ^{0}N, the juvenile nursery area and adult feeding grounds (C. Mendocino to C. Blanco); e) 44-50 ^{0}N adult feeding grounds (Pacific Northwest) (figure 4.5). Longitudinal patterns were examined by considering averages of the inner 4 longitudinal blocks (inshore areas) and the outer four longitudinal blocks (offshore areas) at each latitude (figure 4.4). Habitat data was averaged at each sub-area over two periods: a) 1960-1976, the period of dramatic decline in stock biomass and also a cool PDO phase; b) 1976-1997, the period of biomass increase and also a warm PDO phase.

Climate indices

In order to explore climate effects on habitat area, the following environmental processes were considered: transport, upwelling, wind stress, Pacific Decadal Oscillation (PDO), El Niño Southern Oscillation (ENSO). Indices of transport, upwelling, and wind stress were obtained from the Live Access Server maintained by the Pacific Fisheries Environmental Laboratory, National Oceanic and Atmospheric Administration (http://www.pfeg.noaa.gov/products/las.html). Measurements for each of these variables are reported for a number of positions along the west coast of North America.

Indices from latitudes within each habitat area under study were extracted. Yearly PDO and ENSO[1] values used in this analysis (figure 4.6) represent the average of monthly indices from July of the previous year to June of the next year (figure 4.7).

Modeling

I used both linear regression models and general additive models (GAMs) to examine the relationship between habitat amount and environmental variables. Using both modeling approaches allowed me to search for both linear and non-linear relationships. In order to quantify potential changes in habitat area generated by climate forcing, I incorporated the environmental variable most strongly related to habitat area (highest r^2 value) in the following linear regression model:

$$(1) \qquad H = a + bE + e$$

where H represents a sardine habitat index, E is an independent environmental variable, a is a constant, b is the slope parameter, and e is an additive error term.

I used the normal likelihood function to generate the best estimates of my parameters:

$$(2) \qquad L(H/a,b) = \frac{1}{\sqrt{2ps^{2}}}\exp\left[-\frac{((H\ )-(\hat{H}_{s}))^{2}}{2s^{2}}\right]$$

I generated likelihood profiles of H using equation 2. Rather than taking a traditional approach of statistical inference, i.e. significance or non significance of a particular variable (the value of the b parameter in equation (1)), I performed a likelihood profile analysis on H given each of the independent variables (Hilborn, 1997; Sharma and Hilborn, 2001). By using this approach I can

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[1] [1]The Multivariate ENSO index (MEI) was chosen to represent ENSO. This index takes into account six variables over the tropical Pacific: sea-level pressure, zonal (U) and meridional (V) components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky. For details on how the MEI and PDO indices are calculated see http://www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html and http://tao.atmos.washington.edu/pdo/.

quantify uncertainty around a point estimate of H and how likely a value of an estimate is with respect to another.

The following climate scenarios were implemented in the model: extreme warm years, represented by the mean of the highest five PDO and ENSO values of the time series (1.4 and 1.5 respectively), and extreme cold years, represented by the lowest five PDO and ENSO values of the time series (-1.2 and -1.2 respectively) (figure 4.6).

4.3 RESULTS

Figure 4.8 illustrates percent of the entire range of study (30-50 ^{0}N) identified as suitable spawning and feeding sardine habitat (areas with SST 13.5-16.5 ^{0}C) between 1960 and 1997. Habitat area during this period was highly variable. Feeding habitat was on average significantly larger (35%) than spawning habitat (16%). (t-test for difference in means, $p<<<0.05$). An increasing trend in feeding habitat can be observed for the period 1976-1997. El Niño (e.g. 1964, 1983, 1989, 1993) and La Niña events (e.g. 1985) are reflected in the habitat time series, although not all events generate changes in habitat area (e.g. 1974).

Analysis of habitat distribution by sub-area reveals both latitudinal and longitudinal patterns. On average, spawning habitat is located mostly south of Pt. Conception (30-34^{o}N) and between Pt. Conception and C. Mendocino (35-39 ^{0}N), while feeding habitat is mostly located between Pt. Conception and British Columbia (35-50 ^{0}N) (figure 4.9). Time series (1960-1997) of inshore and offshore habitat distributions at each sub-area are plotted in figures 4.10-4.11. Overall, inshore spawning habitat south of Pt. Conception (30-34 ^{0}N) is significantly more extensive and variable (mean=40%, CV=26%) than offshore spawning habitat area (mean=9%, CV=11%) (figure 4.10). Inshore feeding habitat off the Pacific Northwest coast (44-50 ^{0}N) is less extensive and more variable (mean=9%, CV=35%) compared to offshore habitat (mean=44%, CV=17%) (figure 4.11). Both interdecadal and interannual patterns are evident in the habitat time series. Habitat impacts of El Niño are not consistent throughout sub-areas. Interdecadal patterns in habitat distribution are consistently observed in most sub-areas. After 1976, inshore spawning habitat area south of Pt. Conception (30-34 ^{0}N) shows a significant ($p<0.05$) decreasing trend (figure 4.10), while offshore feeding habitat in the Pacific Northwest shows a significant ($p<0.05$) increasing trend (figure 4.11). Both inshore and offshore feeding habitat areas in the Pacific Northwest are less variable after 1976 ($CV_{inshore}$=24% and $CV_{offshore}$=12%) compared to the period preceding 1976 ($CV_{inshore}$=44% and $CV_{offshore}$=21%).

Differences in mean habitat area between 1960-1976 (the cold phase of the PDO and also a period of dramatic decreases in sardine stock biomass) and 1976-1997 (the warm phase of the PDO and also a period of significant stock increases) were detected (figures 4.12-4.13). After 1976, average spawning habitat was significantly higher in inshore and offshore waters between Pt. Conception and C. Mendocino (35-39 ^{0}N) ($p<<0.05$), and significantly lower in inshore waters south of Pt. Conception (30-34 ^{0}N) ($p<<0.05$) (figure 4.12). Significant increases in average feeding habitat after 1976 are also observed in both inshore and offshore waters off northern California and the Pacific Northwest (40-50 ^{0}N) (figure 4.13). Similar results were found for differences in mean habitat between 1976 and 1989, and 1989 and 1997 (‘Victoria pattern’ phases) (table 4.1).

Habitat area in offshore waters does not seem to be related to local climate conditions, except in waters between C. Mendocino and C. Blanco and in inshore waters south of Pt. Conception and off the Pacific Northwest coast, where significant relationships with local climate conditions were found. Basin scale climate indices (PDO and ENSO) were significantly related to sardine spawning and feeding habitat in all sub-areas, except for waters between C. Mendocino and C. Blanco (40-43 ^{0}N) (figures 4.14-4.16, table 4.2). In most areas, the highest r^2 values were found for linear relationships between habitat and PDO (figure 4.16). The relationship between habitat and ENSO appears to be stronger in inshore spawning habitat between Pt. Conception and C. Mendocino (35-39 ^{0}N) (r^2=.27 vs r^2=.20) and slightly stronger in inshore (r^2=.06 vs r^2=.04) and offshore (r^2=.13 vs r^2=.10) feeding habitat off the Pacific Northwest coast (44-50 ^{0}N). The results above were confirmed by GAM runs (table 4.2).

Figure 4.17 illustrates the possible effects of PDO climate scenarios on habitat area, and the uncertainty around them. These figures contain far more information than either a point estimate or a traditional p value. The biological significance can be judged by looking at the x-axis, in each case relating the amount of habitat in a particular sub-area to be expected given a specific climate scenario (e.g. a warm PDO year). A standard frequentist method would report on the predicted habitat value and confidence bounds. In contrast, the likelihood profile shows us the uncertainty around a point estimate of habitat area and how likely that value is with respect to another value. Thus, in the case of this analysis, I am able to look at effects of environmental indices that may not be considered statistically significant by the frequentist approach. The model predicted differences in habitat area during a warm and cold PDO year at all sub-areas except for offshore spawning habitat south of Pt. Conception (30-34 ^{0}N). The largest differences were predicted for inshore spawning habitat south of Pt. Conception (30-34 ^{0}N) and offshore feeding areas off the coast of the Pacific Northwest (44-50 ^{0}N) (figure 4.17).

4.4 DISCUSSION

My results show that sardine habitat distribution in the CC system has changed over time possibly as a result of climate forcing. Climate effects on sardine habitat are complex and show significant spatial patterns. El Niño effects on habitat are evident in most sub-areas considered, and generally seem to expand habitat into northern and offshore areas (figures 4.10-4.11). However, El Niño impacts on habitat are not consistent throughout sub-areas. This is not surprising, as El Niño events in the CC are discussed as having unique characteristics across latitudes (Chelton, 1981; Hayward, 1993; Lynn et al., 1998; Bograd and Lynn, 2003). PDO effects on habitat are observed. Significant interdecadal changes in both average amount and variability of sardine habitat occur at most sub-areas considered, with differences between inshore and offshore waters (figures 4.10-4.13). Both spawning and feeding habitat have expanded north and offshore during the period of dramatic sardine biomass increase (1976-1997): inshore spawning habitat south of Pt. Conception decreases (figures 4.10 and 4.12) while average inshore and offshore spawning habitat between Pt. Conception and C. Mendocino significantly increases (figure 4.12); offshore feeding habitat north of C. Blanco increases (figure

4.13) and remains high without varying much throughout the period (figure 4.11). Feeding habitat in offshore waters of the Pacific Northwest coast during this period is also less variable (thus more persistent) (CV 12%) compared to the period preceding 1976 (CV 21%). Model predictions reveal significant increases in habitat area during warm PDO conditions (1976-1997) at all sub-areas, except for offshore waters south of Pt. Conception. The largest changes in habitat area occur in inshore waters south of Pt. Conception and offshore waters off the Pacific Northwest coast (figure 4.17).

The spatial distribution of sardine habitat seems to be related to large scale climate process such as ENSO and PDO in all areas except for waters between C. Mendocino and C. Blanco (40-43 ^{0}N); here habitat is non-linearly related to local climate conditions (i.e. wind stress, upwelling and transport). The oceanography of this region is highly energetic, dominated by meanders and eddies whose dynamics are largely controlled by seasonal upwelling (Hickey, 1998). These features probably play a large role in defining sardine habitat, thus the relationship I find between habitat and local climate conditions. In all other sub-areas the relationship between habitat and ENSO appears to be weaker compared to the relationship with the PDO (figure 4.16), except for inshore waters between Pt. Conception and C. Mendocino and Pacific Northwest waters. The above results suggest that climate effects on sardine habitat in the CC system are spatially heterogeneous, with ENSO effects dominating some areas and PDO effects dominating others. However, conclusions based on relationships with these two indices should be made with caution. Clearly, basin scale level changes impact sardine habitat distribution in most sub-areas. The potential links between basin scale processes such as ENSO and PDO and sardine habitat variability are multiple and range from strength of stratification, to variability in major ocean currents. However, separating effects is rather challenging as these two climate phenomenon are clearly not independent of each other (Newman et al., 2003) each index incorporating a number of related phenomenon. For example, Lynn and Bograd (2003) acknowledge that characteristics attributed to regimes may be low frequency manifestation of interannual forcing (e.g. El Niño events.). While evaluating the extent of interaction between the PDO and the ENSO is beyond the scope of this dissertation, comparisons between their effects on habitat should be made with caution. My results could also be biased by the coarse resolution of my habitat index. By integrating SST information over 0.5 x 1 degree blocks I gain a large scale view of sardine habitat but I could also be loosing important signals of fine scale variability usually related to local processes; this might be especially true for inshore areas, where stronger links with local climate conditions are observed (Mantua, pers. comm.).

This study confirms the importance of spawning habitat south of P. Conception, and documents the shift north of spawning areas during warm years, to waters between Pt. Conception and C. Mendocino discussed in the literature (Smith, 1990; McFarlane et al., 2002; Lynn, 2003). It also highlights the importance of offshore and northern waters of the sardine range. Waters off the Pacific Northwest coast make a significant contribution to overall adult feeding habitat. The expansion of adult sardine feeding habitat into northern areas of the CC system I document here is consistent with reports in the literature of increased abundance of sardine in Pacific Northwest waters during the last two decades (Emmett and Brodeur, 2000; Hargreaves et al., 1994; Field et al., 2001). Sardine stocks disappeared from the Pacific Northwest in 1948-1949 (Schewigert, 1988). They reappeared in this area beginning in the late 1980s. Significant fishing for sardine has occurred off northern Mexico and California since the early 1980s and more recently (mid 1990's) off Oregon, Washington and British Columbia (Conser et al., 2003). Field et al (2001) report range expansions of sardine documented since the latter part of the eighteenth century. They find the reappearance of sardine in Pacific Northwest waters over the last 200 years to be consistent with periods of intense El Niño activity. My finding of increased sardine habitat in Pacific Northwest waters during the last two decades is consistent with this, as this has been a period of record El Niño activity (Bograd and Lynn, 2003) as well as a positive PDO regime.

I propose that the expansion north and offshore of adult sardine feeding habitat played a role in the recent increase in population abundance. I find adult sardine feeding habitat in Pacific Northwest waters to have increased and year to year variability to have declined over the last two decades (figures 4.11, 4.13). These waters are known to be productive feeding grounds for a number of coastal pelagic species. Changes in climate (i.e. a shift to warmer conditions) seem to have allowed for a significant increase in available sardine feeding habitat in waters off the coast of the Pacific Northwest. Increased and consistent access to particularly productive waters may have equipped sardine with more energy to spawn and produce viable eggs. Needless to say, my conclusions should be reconciled with a more detailed analysis to determine whether characteristics of newly available feeding habitat have potential to benefit reproduction, growth and survival of adult sardine. Changes in spawning habitat distribution also play a role in the recent increase in population abundance. Here I document a shift north and offshore of the spawning habitat during the latest warming period (1976-1997). Chapter Two explores how these shifts may have affected larval survival and, ultimately, recruitment success of Pacific sardine.

Data availability invariably influences the choice of scale of study (Steele, 1978). My attempts in this dissertation to define and quantify pelagic habitat (Chapter Three and Four), given two data sets with very different spatial and temporal scales, are a good example of this. With regards to space, my description of Pacific hake habitat addresses both small scale and large scale processes thanks to the rich data set available. Because of the lack of sardine information discussed above, I could only apply a large scale approach in my analysis of habitat for this species. With regards to time, the opposite is true. Pacific hake data were only available for two years. In contrast, my choice of proxy for sardine habitat allows me to consider almost 50 years. Although the overall lack of sardine data may seem limiting, analysis such as this one can help prioritize future data collection research efforts.

The temperature range used to define the sardine habitat index was mostly based on studies of adult spawners and larvae off the coast of southern California (Tibby, 1937; Ahlstrom, 1954; Ahlstrom, 1965; Lluch-Belda et al., 1991; Parrish et al., 1989; Bentley et al., 1996). Juveniles and adults from other areas in the CC may have different temperature requirements. For example, evidence exists that other sardine stocks spawn in waters as warm as 25 ^{0}C (Lluch-Belda et al., 1991; Hernandez-Vasquez, 1994). Although sardine may be able to tolerate warmer or colder temperatures, studies to date on the California sardine lead me to believe that the majority of this stock occupies waters between 13.5 and 16.5 ^{0}C. Until information on other sardine life history stages and areas in the CC becomes available, the assumption I make here enables us to derive large scale patterns of sardine habitat.

Variability of sardine habitat has implications for the productivity of both the species and the ecosystem. Sardine are prey to a number of fish, including commercially important fish species (e.g. yellowtail, barracuda, bonito, tuna, marlin, mackerel, hake, salmon and sharks) seabirds (pelicans, gulls and cormorants) and marine mammals (sea lions, seals, porpoises and whales) (Conser et al., 2003). Their importance as prey will probably increase as their abundance increases. For example Chapman (1936) reported sardine to be a major forage species for both coho and Chinook salmon off Washington during the 1930s when sardine were highly abundant. Sardine are also competitors to other zooplanktivouros species such as Pacific hake. Their increased abundance in Pacific Northwest waters has the potential to impact local ecosystem structure. Understanding habitat variability of migratory species in the CC is particularly challenging, as defining such a dynamic entity can be difficult. The approach I develop here will have to be refined as new data become available. However, my hope is that this analysis will begin to highlight important patterns of sardine habitat distribution, setting the stage for more detailed studies.

Table 4.1: Average sardine habitat during PDO and Victoria Pattern phases (asterisks indicate significant differences in means).

	Mean habitat (PDO)		**Mean habitat (' Victoria pattern ')**	
WINTER INSHORE	**1960-1976**	**1976-1997**	**1976-1989**	**1990-1997**
30-34 ^{0}N	47.6*	33.9*	36.3*	29.7*
35-39 ^{0}N	2.2*	4.5*	4.2	5.1
40-43 ^{0}N	0.1	0.5	0.4	0.4
44-50 ^{0}N	0.11	0.4	0.08*	0.4*
WINTER OFFSHORE	**1960-1976**	**1976-1997**	**1976-1989**	**1990-1997**
30-34 ^{0}N	9.4	9	9.1	8.7
35-39 ^{0}N	3.7*	6.4*	5.7*	7.7*
40-43 ^{0}N	0.3	0.9	0.5	1.7
44-50 ^{0}N	0.3	0.4	0.5	0.3
SUMMER INSHORE	**1960-1976**	**1976-1997**	**1976-1989**	**1990-1997**
30-34 ^{0}N	8.1	6.8	7.2	6.1
35-39 ^{0}N	17.4	17.5	18.1	16.6
40-43 ^{0}N	6.9*	8.9*	32.7*	27.3*
44-50 ^{0}N	7.5*	10*	9.3*	11.1*
SUMMER OFFSHORE	**1960-1976**	**1976-1997**	**1976-1989**	**1990-1997**
30-34 ^{0}N	2.2*	0.7*	0.86	0.51
35-39 ^{0}N	11*	8.9*	10.3*	6.3*
40-43 ^{0}N	29.6	30.7	8.4	9.7
44-50 ^{0}N	40.8*	47.4*	45.9*	50*

Table 4.2: Output from General Additive Model runs for significant relationships between climate variables and sardine habitat amount during winter (spawning) and summer (feeding) seasons. In parenthesis variables significantly related to habitat amount

	p values	**GCV**
WINTER INSHORE		
30-34 ^{0}N	.013 (PDO) .010 (upwell.)	74.648
35-39 ^{0}N	.00022 (ENSO)	7.3722
WINTER OFFSHORE		
30-34 ^{0}N	.032 (PDO)	1.045
35-39 ^{0}N	.020 (ENSO)	12.11
SUMMER INSHORE		
40-43 ^{0}N	.012 (wind stress) .06 (transport)	10.129
44-50 ^{0}N	.003 (wind stress)	7.70
SUMMER OFFSHORE		
40-43 ^{0}N	$<< 0.05$ (SST) .023 (upwell.) .015 (wind stress) .071 (transport)	18.334
44-50 ^{0}N	.017 (wind stress) .021 (ENSO)	41.62

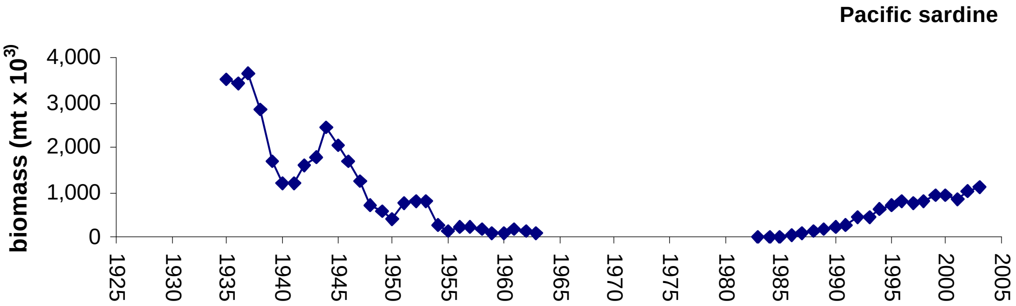


Figure 4.1: Time series of sardine adult biomass. Data for Pacific sardine, from 1935-1964 for age 2+, from Jacobson and MacCall (1995). For 1983-2003 for age 1+ from PFMC (2004).

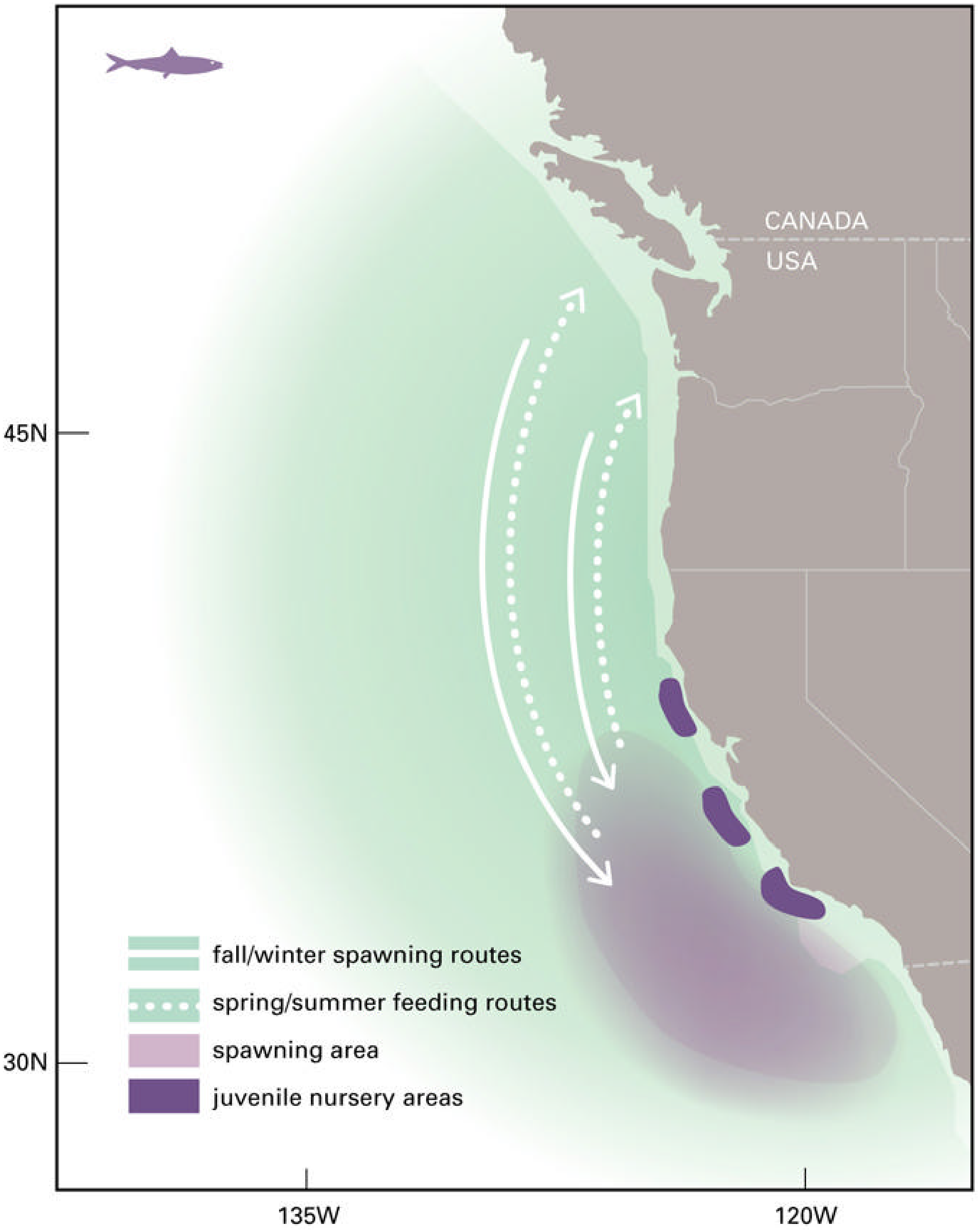


Figure 4.2: Schematic representation of sardine migration in the California Current.

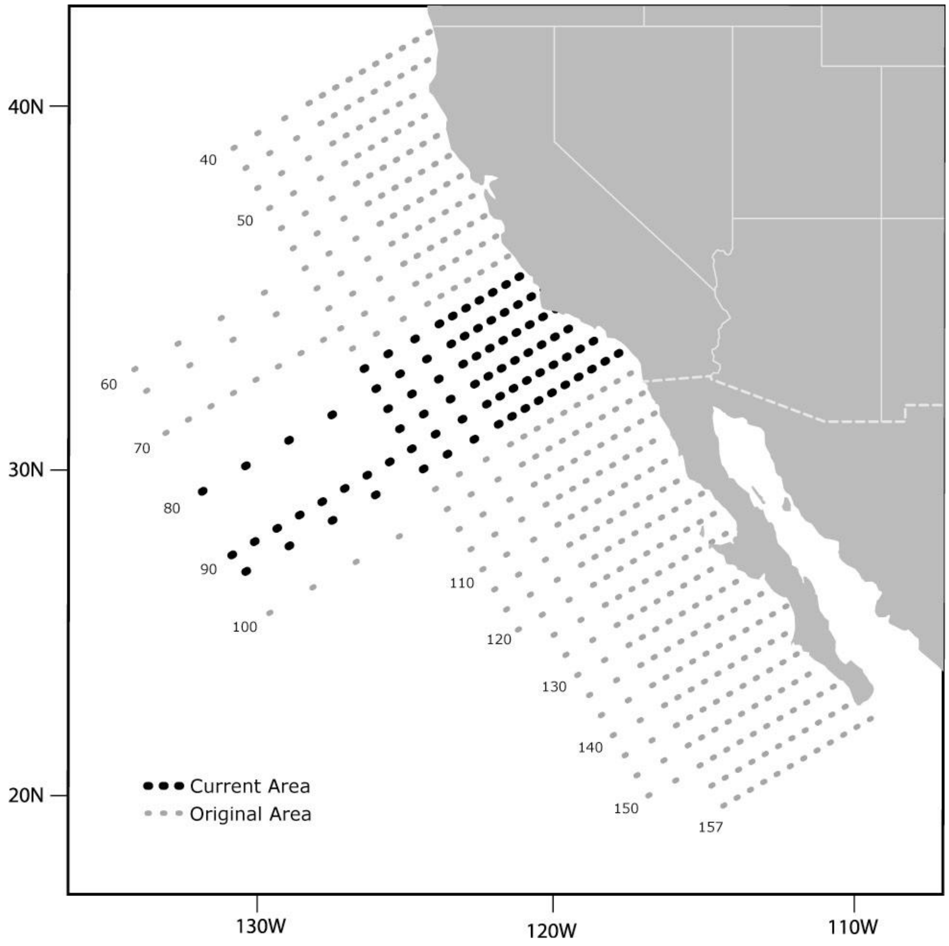


Figure 4.3: Stations sampled by the CalCOFI (U.S.) and IMECOCAL (Mexico) programs from 1948 to present. Black dots identify stations sampled consistently throughout the time period.

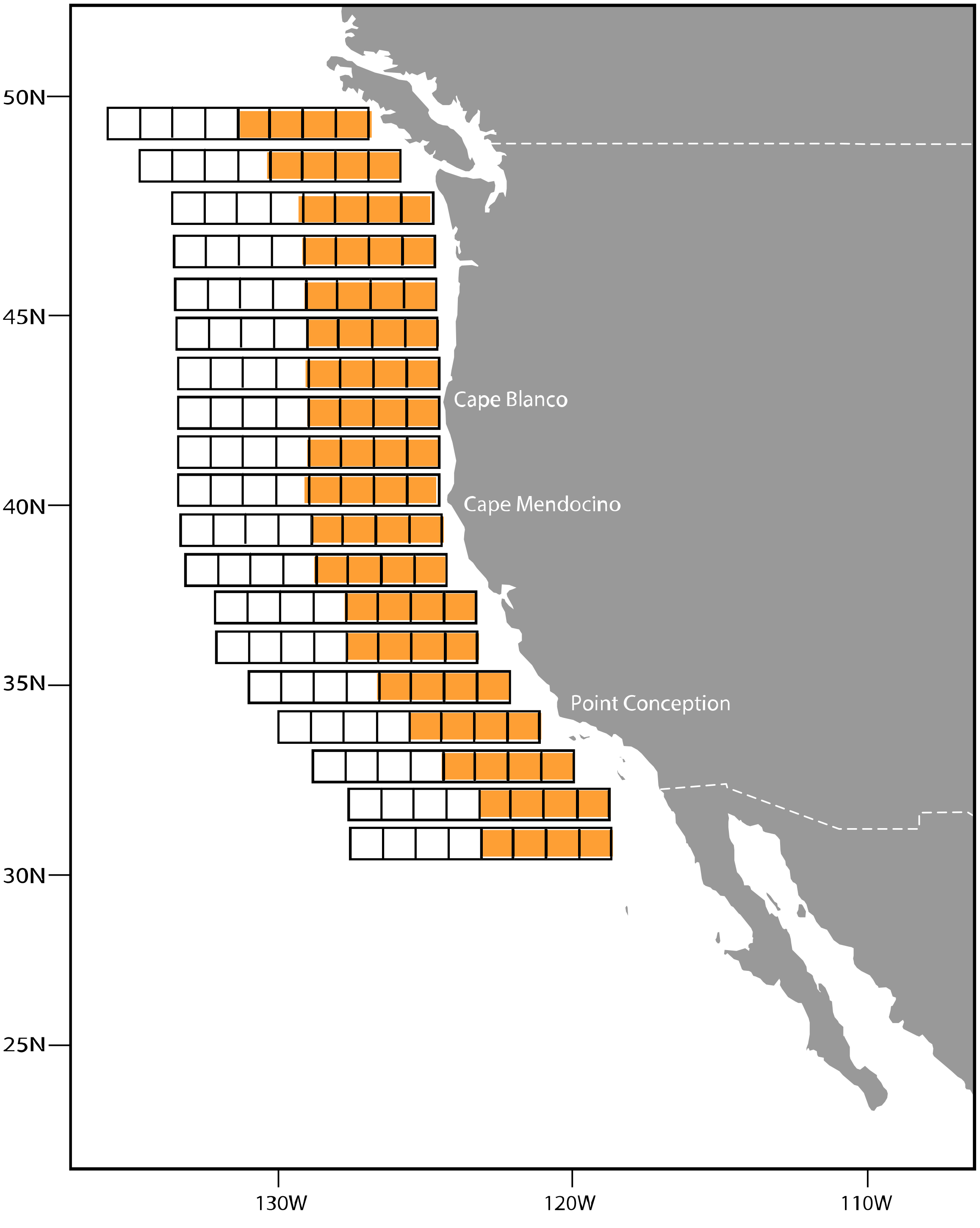


Figure 4.4: Location and distribution of spatial blocks (1^{o} N x 0.5^{o} E) used in the analysis. Blocks classified as 'inshore' are in orange, blocks classified as 'offshore' are in white. Figure is not drawn to scale.

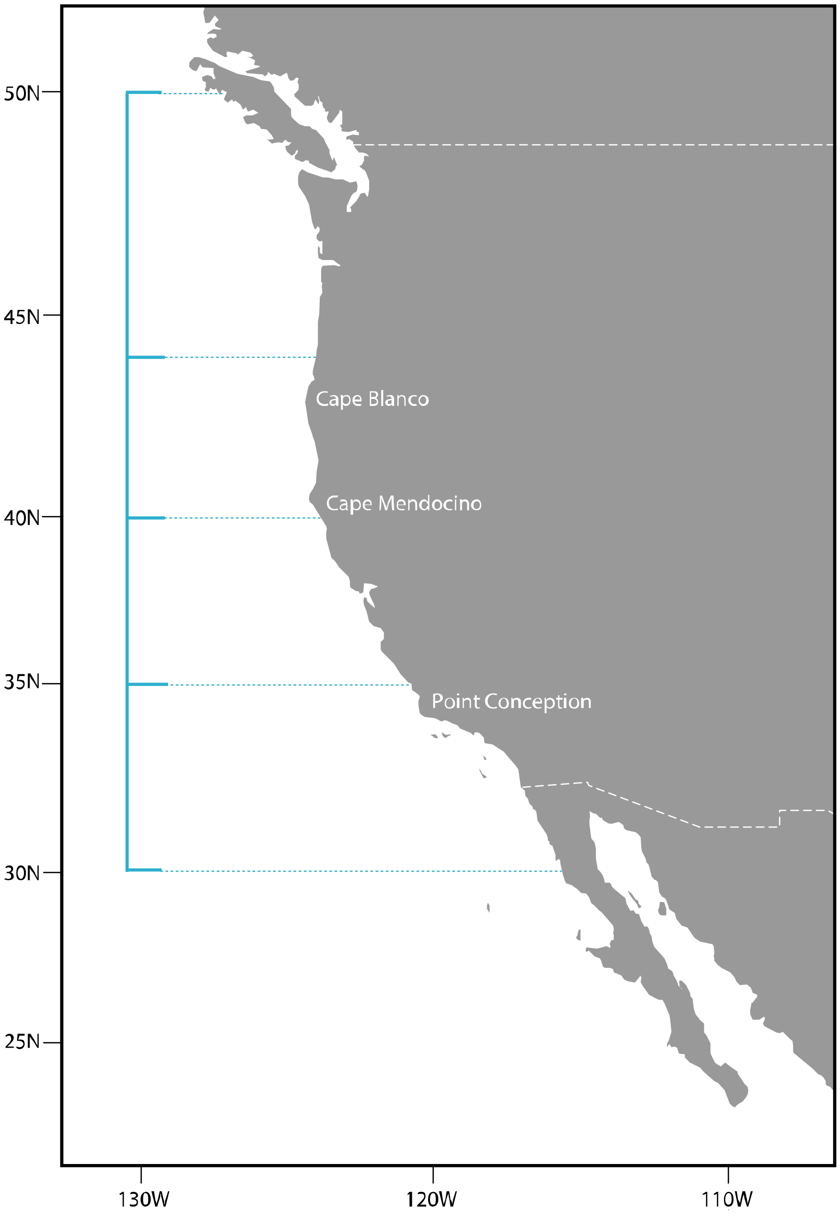


Figure 4.5: Boundaries of sub-areas considered in the analysis.

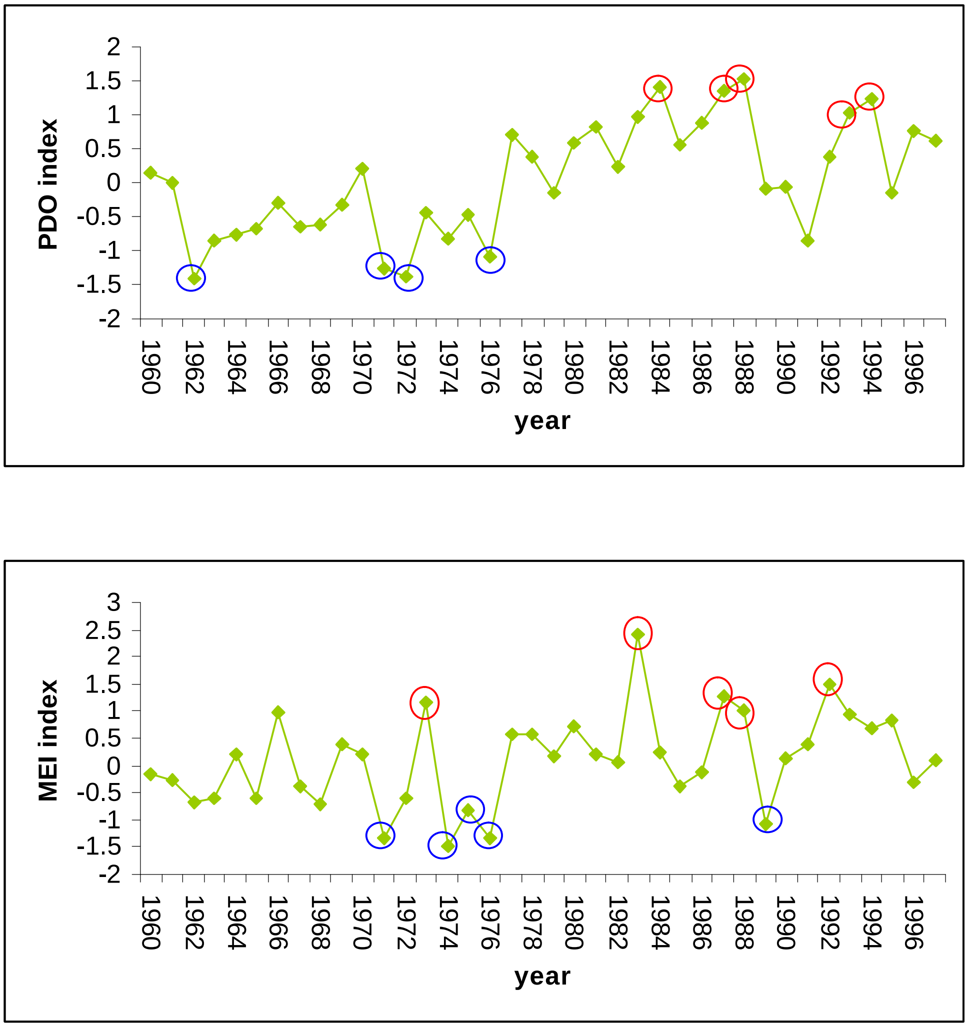


Figure 4.6: Time series of PDO (upper panel) and ENSO (lower panel) indices used in the analysis. Means of the highest 5 values for each time series (circled in red) represent warm year scenarios used in the analysis and means of the 5 lowest values (circled in blue) represent cold year scenarios (see methods section).

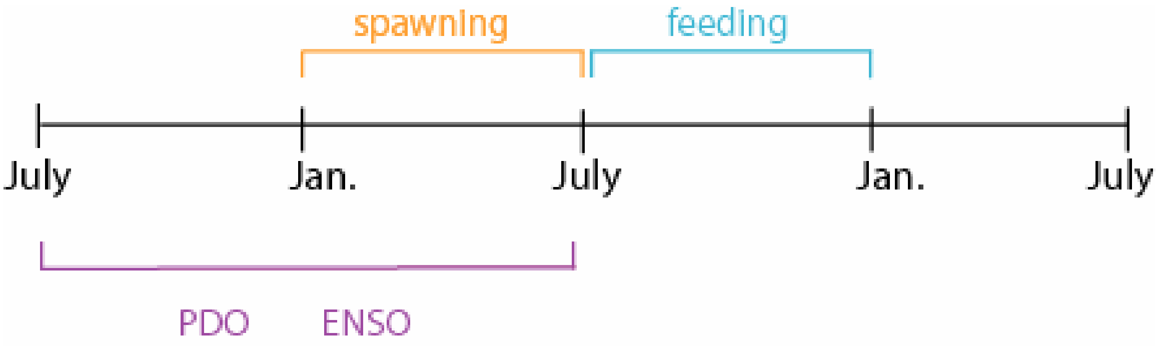


Figure 4.7: Schematic representation of time windows chosen for indices used in the analysis.

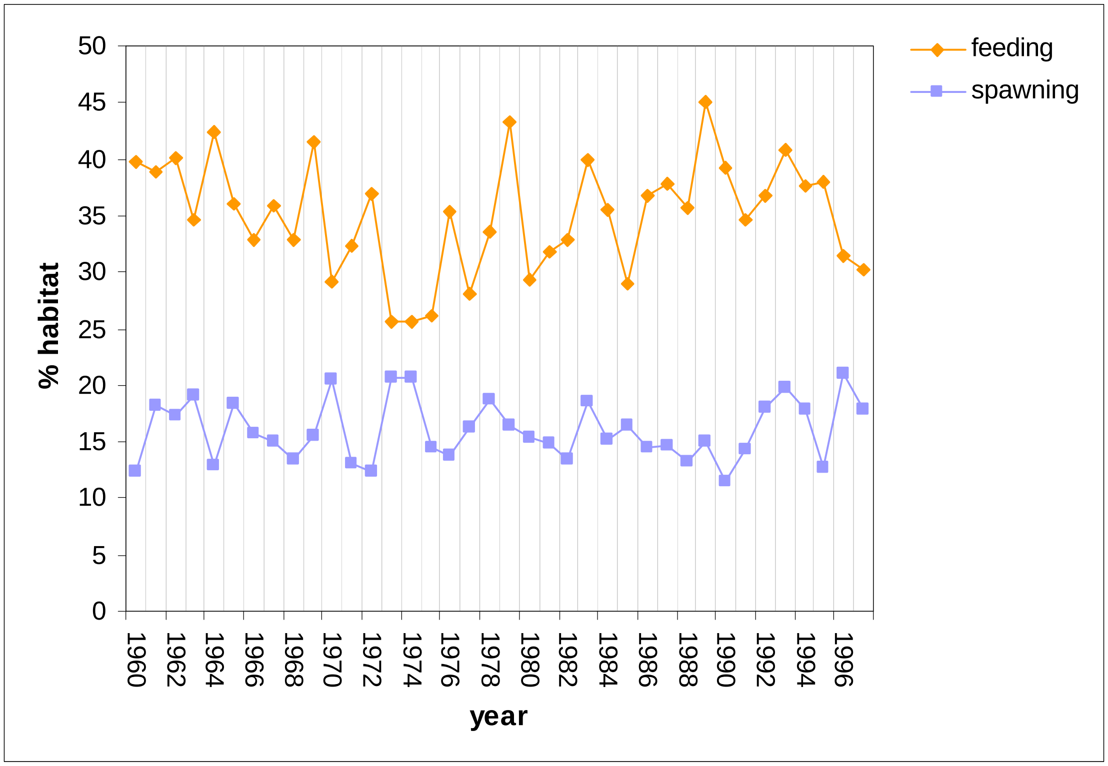


Figure 4.8: Percent sardine habitat for period 1960 to 1997 over range of study (30-50 ^{o}N).

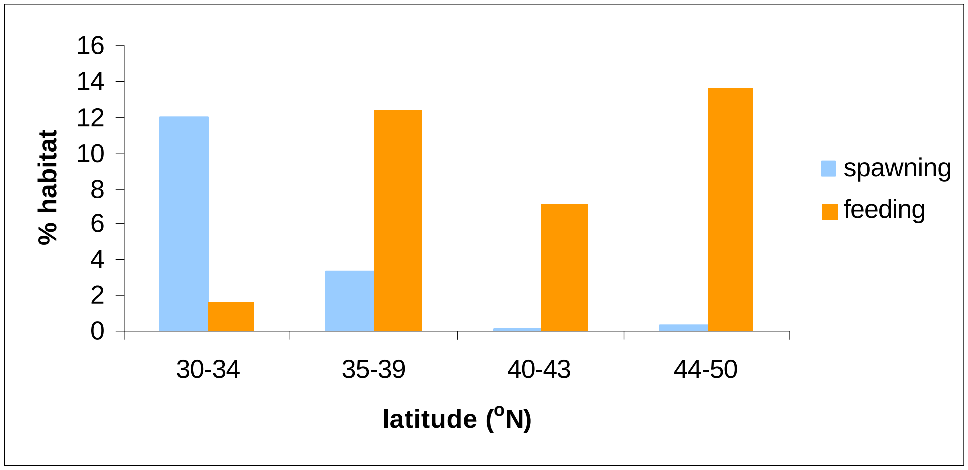
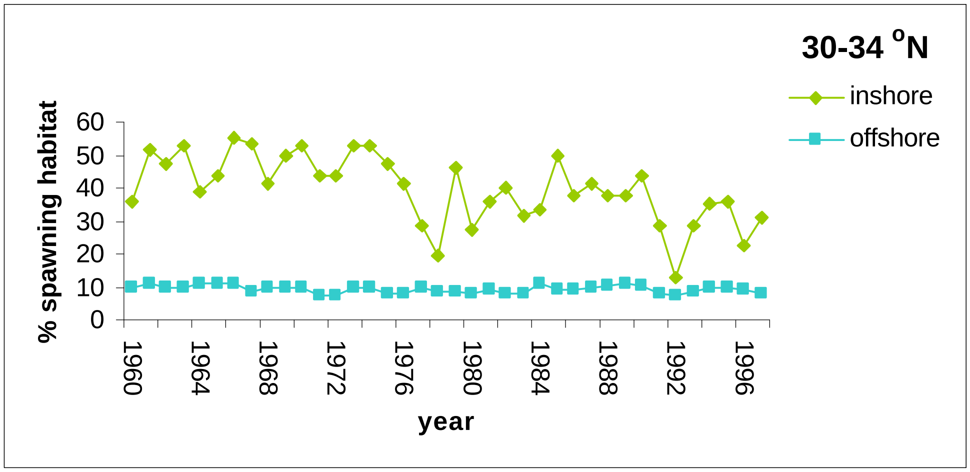


Figure 4.9: Average percent sardine habitat area for the period 1960-1997.



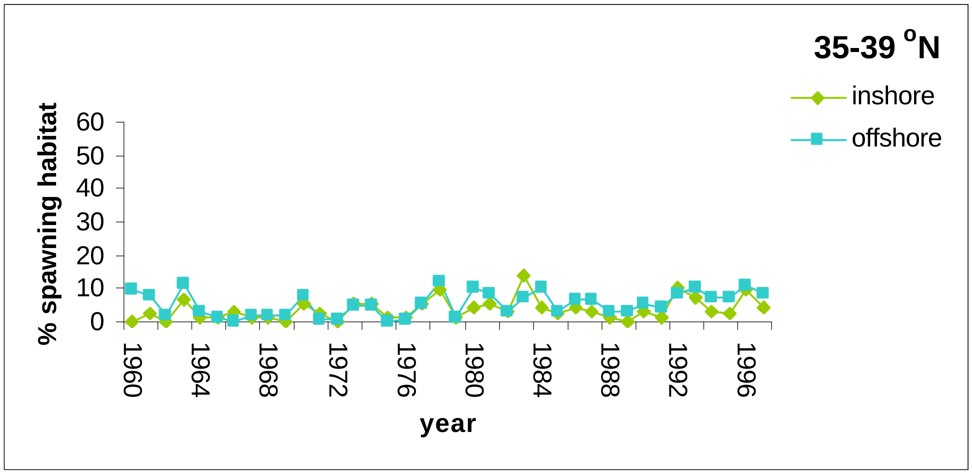


Figure 4.10: Percent spawning habitat area south of Pt. Conception (upper panel) and between Pt. Conception and C. Mendocino (lower panel).

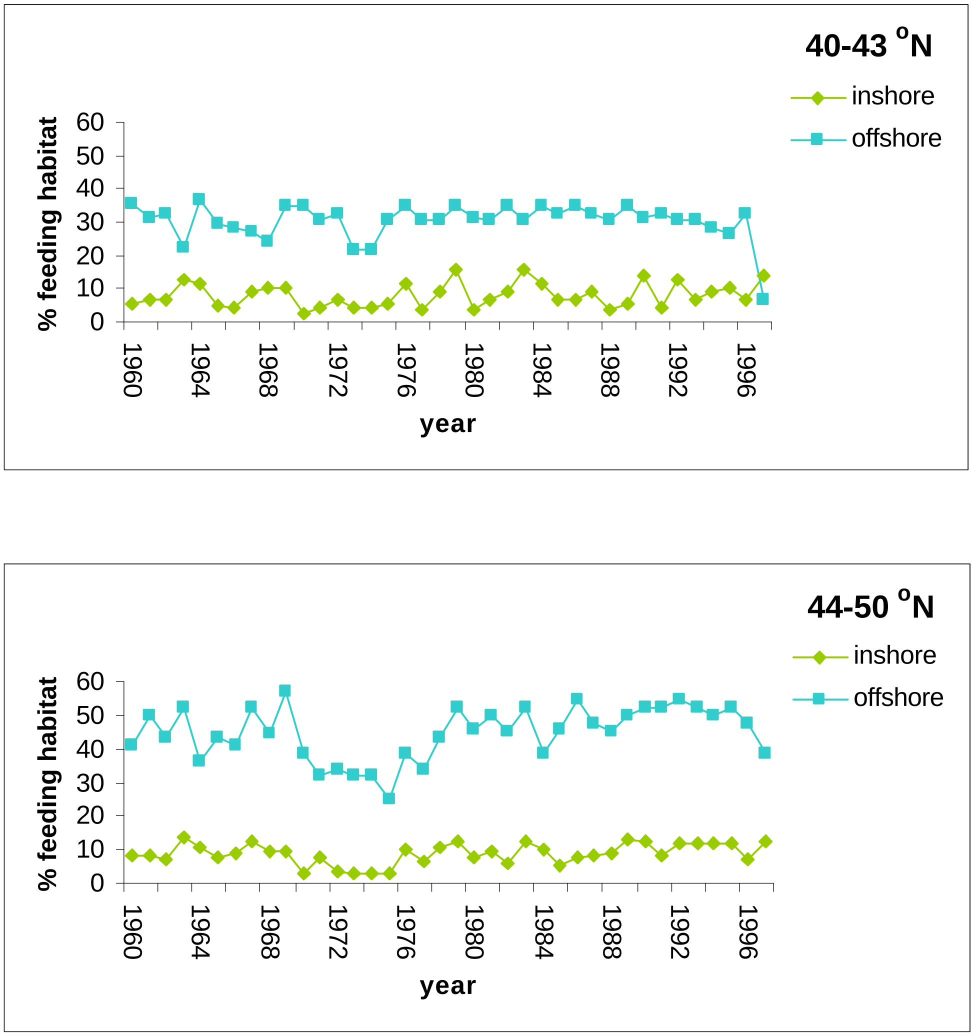


Figure 4.11: Percent feeding habitat area between C. Mendocino and C. Blanco (upper panel) and in Pacific Northwest waters (lower panel).

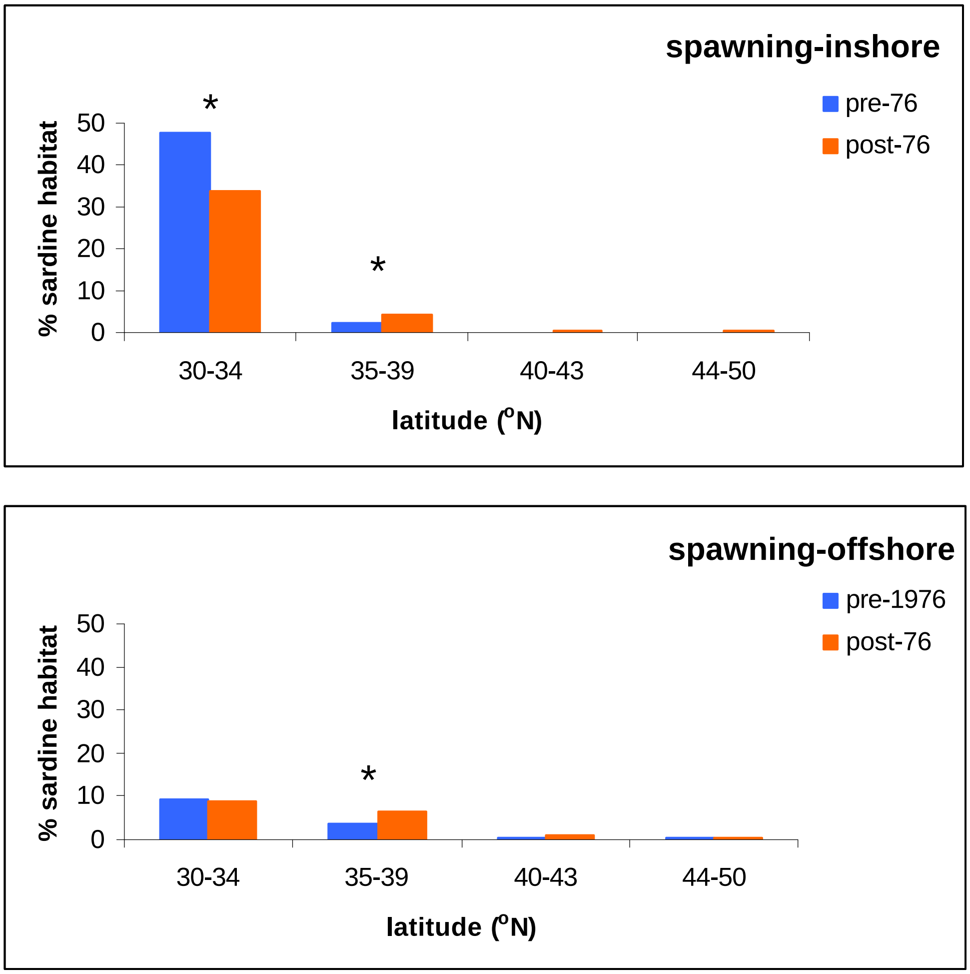


Figure 4.12: Percent sardine spawning habitat area for inshore and offshore areas for the period 1960-1976 (pre 1976 in legend) and between 1976 and 1997 (post-1976 in legend). Asterisk indicate significant differences in means (t-test, p<.05).

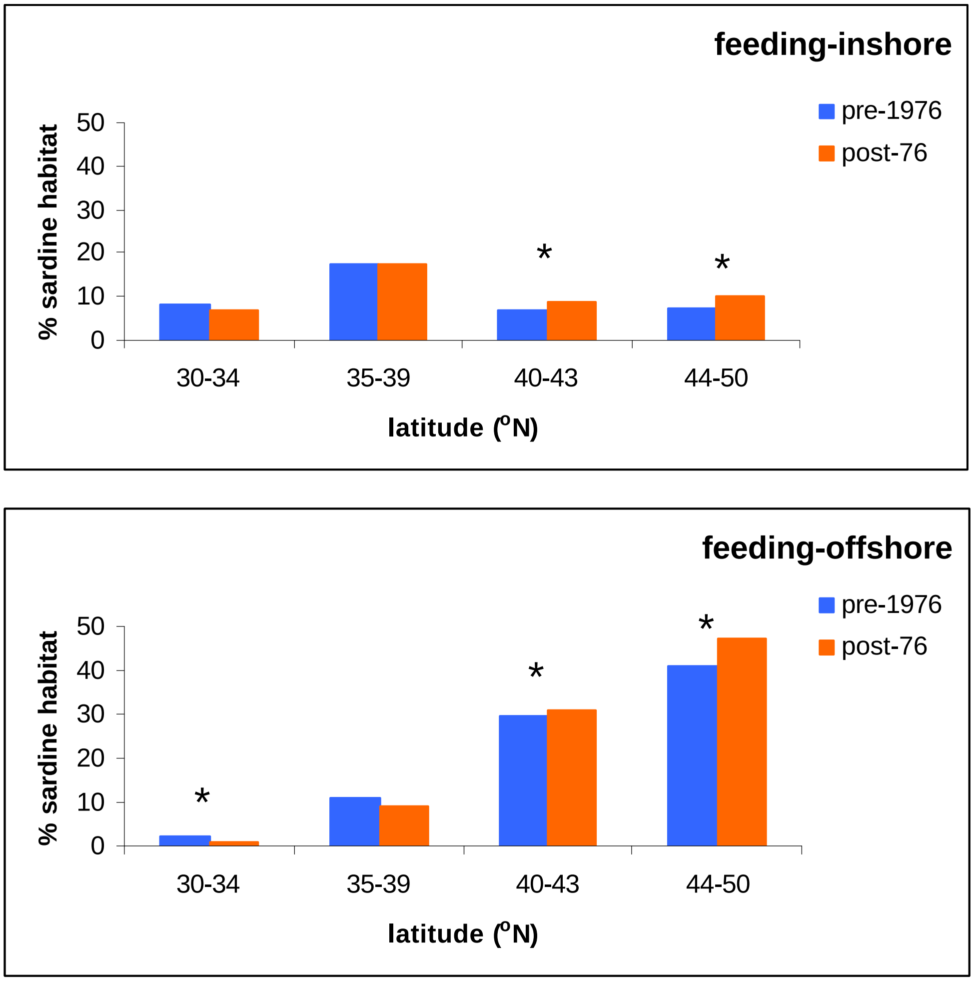


Figure 4.13: Percent sardine and between 1976 and 1997 (post-1976 in legend). Asterisk indicate significant feeding habitat area for inshore and offshore areas for the period 1960-1976 (pre 1976 in legend) differences in means (t-test, p<.05).

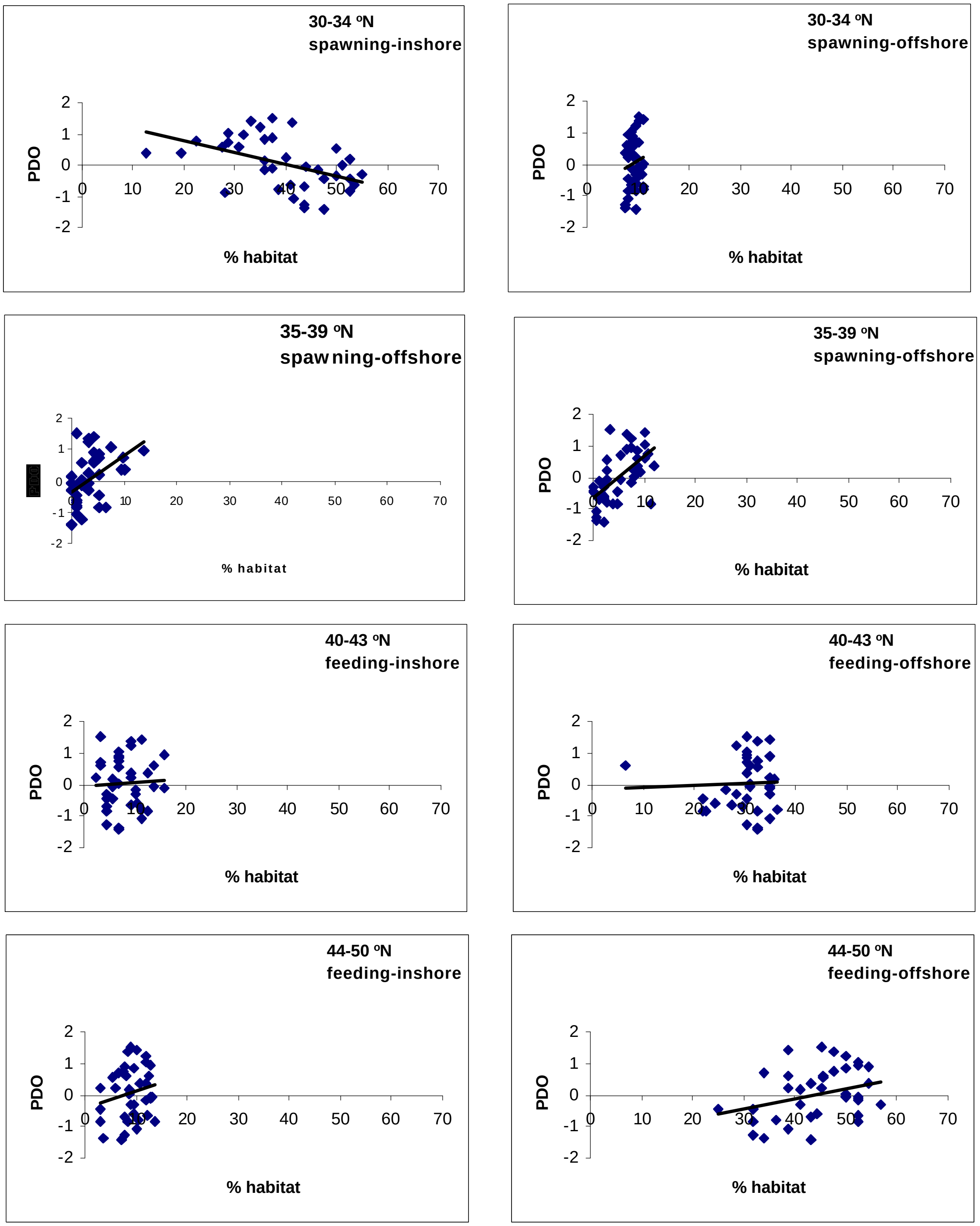


Figure 4.14: Best fit for response variables (% habitat at different sub-areas) with PDO as a predictor variable.

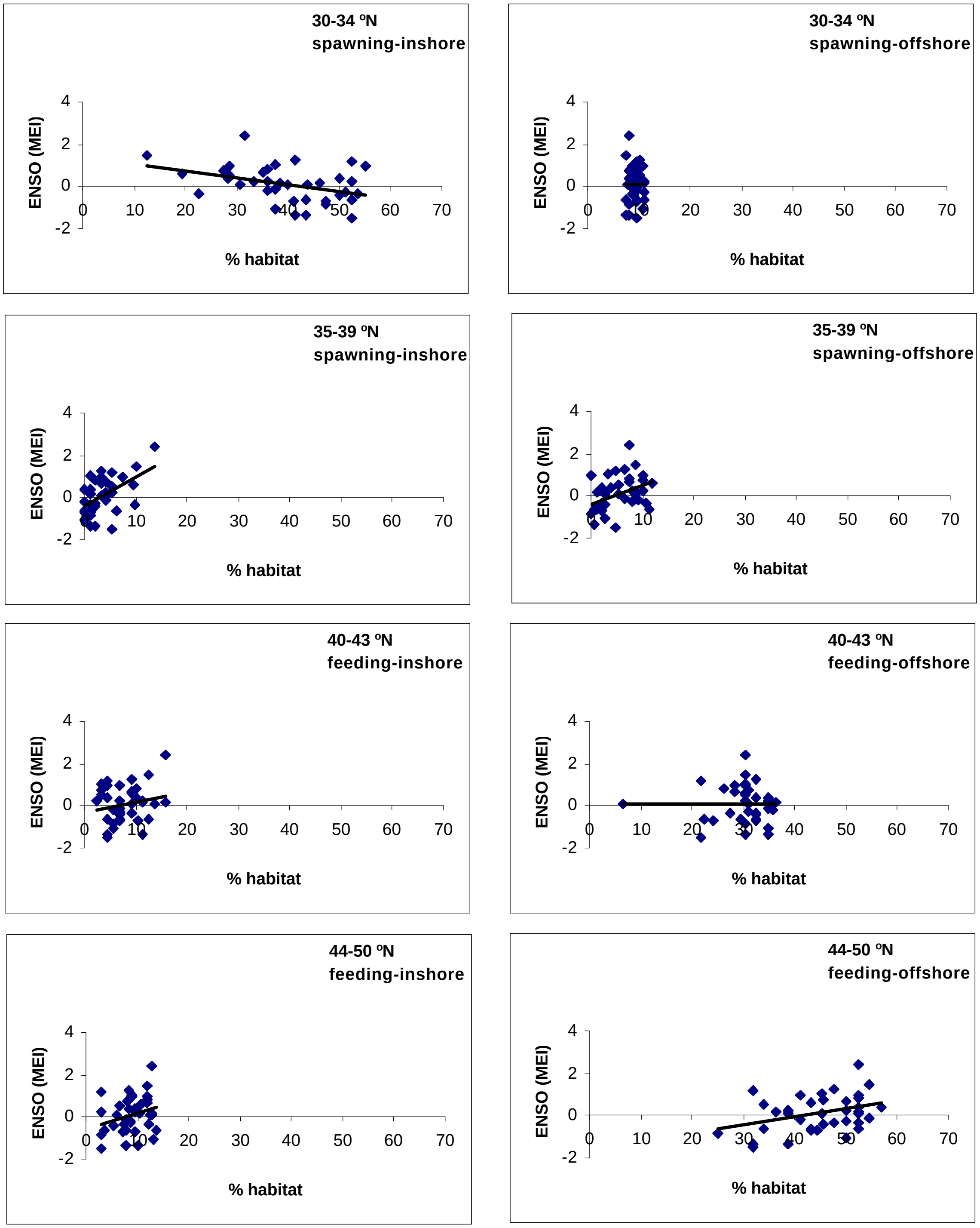


Figure 4.15: Best fit for response variables (% habitat at different sub-areas) with ENSO as a predictor variable.

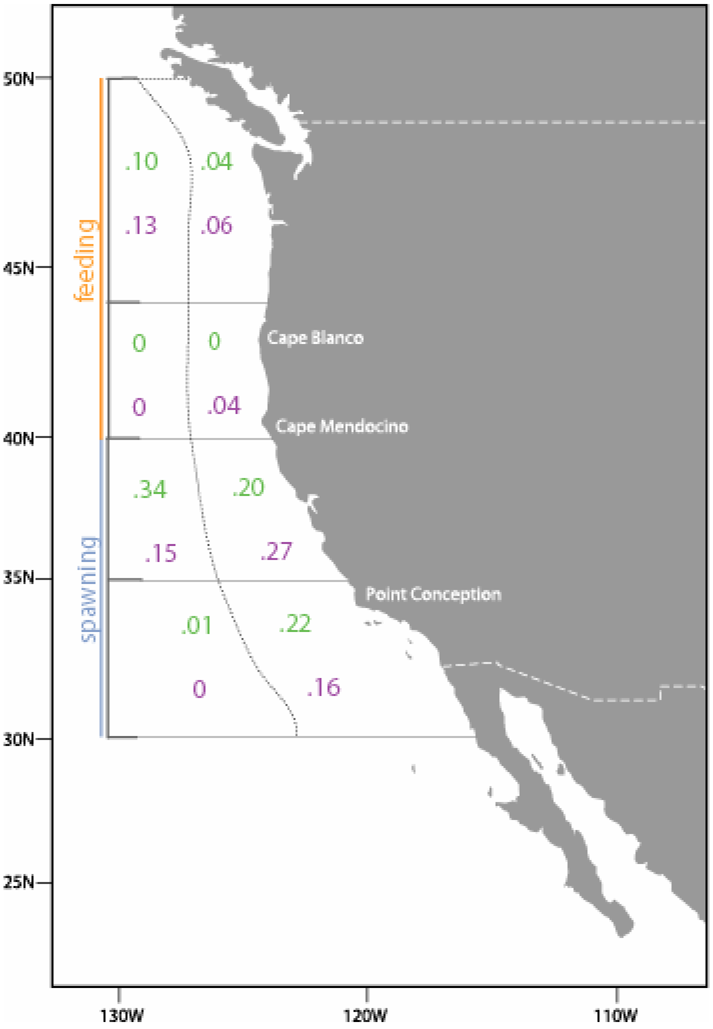


Figure 4.16: r^2 values for habitat-PDO (in green) and habitat-ENSO (in purple) linear regression models for inshore and offshore waters at each sub-area. Figure is not drawn to scale.

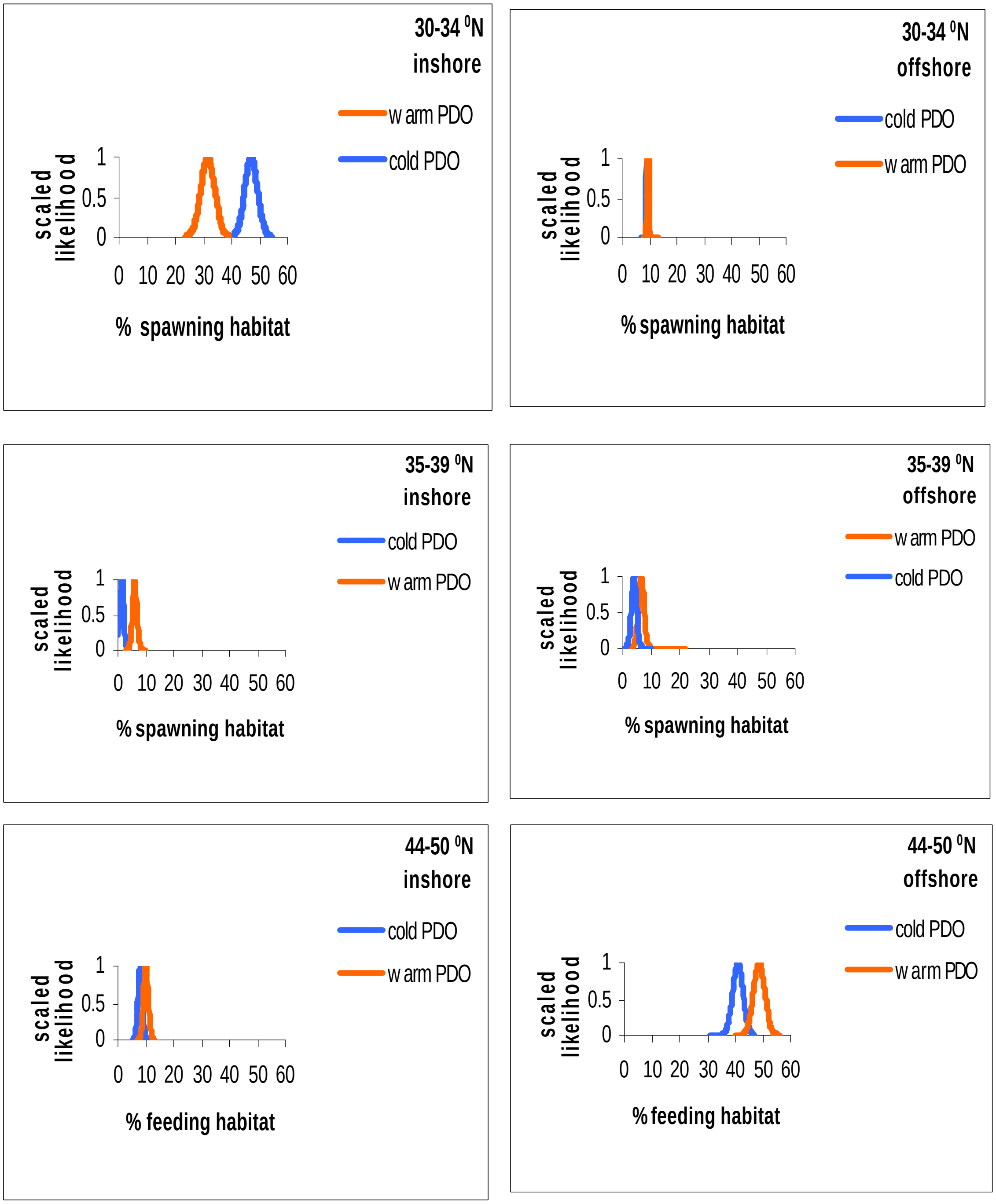


Figure 4.17: Likelihood profiles of quantitative changes in habitat area as a result of conditions during an extreme warm PDO year and an extreme cold PDO year (for definition see methods section) (the x-axis shows the expected habitat area given specific PDO conditions).

CHAPTER 5. Sardine and hake pelagic habitat: implications for management.

5.1 Introduction

Thus far, the focus of this dissertation has been on the relationship between climate, oceanography and ecology of sardine and hake. I have examined various aspects of sardine and hake pelagic habitat and placed them within the context of the life history of these two species. Chapter Five outlines how this information may contribute to the management process. Implications for both single species and ecosystem management will be examined.

Recently a great deal of discussion in the scientific and governance community has revolved around developing a more holistic view of marine systems (Botsford et al,1997; EPAP 1999; NRC 1999; Pauly et al., 2002; Pikitch et al., 2004). Although much debate exists regarding how best to do this, the awareness of its importance for the achievement of sustainable fisheries is widespread (Botsford et al., 1997; Pikitch et al. 2004; FAO, 2003; Babckock et al., in press). Two elements have been proposed as the essential core of this view: knowledge of how species interact, and of the physical environment they occupy (Botsford et al., 1997). While considerable research has been conducted independently in each of these areas, placing this knowledge within an ecosystem context has been challenging. Considerable attention has been devoted to examining trophic interactions, but our knowledge of bio-physical interactions is lagging behind. My work on pelagic habitats is an attempt to begin to fill this gap.

I will begin by reviewing the current assessment and management of sardine and hake and outlining how a greater understanding of pelagic habitat could inform this process. I will then summarize discussions to date regarding Ecosystem Based Fisheries Management (EBFM) focusing on areas relevant to the research I have conducted. By drawing from examples of my work with sardine and hake, I will outline how knowledge of pelagic habitat is essential for a more holistic approach to the management of marine systems.

5.2 Status, assessment and management of Pacific sardine and hake

5.2.1 Pacific Hake

Stock status:

Figure 5.1 shows the estimated trajectory of hake biomass and recruitment over the last 30 years. Stock biomass increased to a historical high of 6.4 million mt in 1987 due to exceptionally large 1980 and 1984 year classes; it then declined as these year classes passed through the population and were replaced by more moderate ones. There was a brief period of stabilization between 1995 and 1997, but then the stock declined continuously to its lowest point of 1.09 million mt in 2001. Since 2001, stock biomass has increased substantially as the strong 1999 year class entered the population.

Stock assessment:

The hake assessment implements an age-structured analysis model that uses both fishery dependent and independent data. The U.S. and Canadian fisheries are treated as distinct fisheries in which the fraction of the stock available to exploitation changes over time. The fishery dependent data are: total catch from the US and Canadian fisheries (1966-2003); catch at age from the US (1973-2003) and Canadian fisheries (1977-2003). The fishery independent data are: biomass and age composition from US acoustic/midwater trawl surveys; biomass and age composition from US bottom trawl surveys; biomass and age composition from Canadian acoustic surveys of Pacific hake (1990-96); indices of young-of-the year abundance from the NMFS-Tiburon/Santa Cruz larval rockfish surveys (1986-2003) (these are used as an age-2 tuning index for stock reconstruction and for future projections)

Bayesian analysis is used in parameter estimation and forward projections allowing for treatment of uncertainty. Maximum likelihood theory is applied to fit model estimates to data. Recruitment and fishing mortality are free parameters with no additional error constraints. Process error is used to describe changes in fishery selectivity over time using a random walk.

Harvest guidelines:

Through 1998 Pacific hake was managed under a constant harvest rate policy. Under this policy Allowable Biological Catch (ABC) is calculated by applying the fishing mortality that produces Maximum Sustainable Yield (F_{MSY}) to an estimate of exploitable stock biomass. However it has generally not been possible to directly estimate F_{MSY} reliably for any stock. Consequently, during the 1980s and 1990s, a proxy for F_{MSY} was used ($F_{0.4}$) based on Clark's (1993) analysis of sustainable spawner per recruit estimates for marine fish (SAFE, 2000). The 1999 Stock Assessment Review (STAR) panel concluded that $F_{40\%}$ is a legitimate proxy for F_{MSY} for the hake stock. The Groundfish Management Team could not reach consensus on a single approach and provided a range bounded by $F_{40\%}$ and $F_{45\%}$ (for additional details see SAFE report, 2000).

In 1998 the Pacific Fishery Management Council (PFMC) adopted a harvest control rule (the "40-10" rule) based on biological reference points arrived from spawner recruit analysis. This rule reduces the target fishing mortality rate for stocks whose biomass is below 40% of the estimated unfished biomass (B_0). The current assessment forecasts the female spawning biomass to be at 29% of the unfished stock in 2006 (Helser et al., 2004). If the population reaches 25% of the estimated unfished biomass (B_0), the Magnuson Stevens Sustainable Fisheries Act requires management to declare the stock overfished and develop a rebuilding plan for the population. This could result in an elimination of directed fishing for hake and closer monitoring of incidental catches (bycatch).

5.2.2 Pacific sardine

Stock status:

The sardine fishery has been economically important since the early part of the 20th century. The biomass supporting this fishery began its dramatic decline in the mid- 40s and remained low until the early 80s. At this time the population began to rebuild. In the most recent stock assessment both biomass and recruitment have been estimated to be fairly high (1 million mt and 13 billion recruits respectively) (figure 5.2). However, as is the case with most age-structured assessments, recent recruitment estimates were not estimated precisely (i.e. 95% confidence interval of 5-37 billion recruits) so there is a high degree of uncertainty with respect to stock productivity over the recent years.

Stock assessment (October 2003):

The sardine assessment implements an age-structured analysis model (CANSAR-TAM) that uses both fishery dependent and independent data. Only data for the California fishery are included in the model. The fishery dependent data are: total catch for US (California); catch at age for US fishery; estimates of weight at age. The fishery independent data are: index of sardine egg abundance; index of spawning biomass; index of spawning area; index of pre-adult biomass from aerial spotter plane survey.

The model is based on a forward simulation approach; non linear least squares estimation is used to select parameters. The terms in the objective function to be minimized include the sum of squared difference in log-observed and log-predicted estimates from the catch-at-age and various sources of ancillary data used to tune the model (e.g indices of abundance from research survey data). Bootstrap procedures are used to calculate variance and bias (95% confidence intervals) of biomass and recruitment estimates generated from the assessment model.

Recognizing that part of the available sardine biomass moves outside of the fishery and survey range when the population size increases, a ‘two area’ migration model (CANSAR-TAM) is implemented for the sardine assessment. This model makes the following assumptions: a) Two habitat areas exist; b) sardine in Area 1 are adequately sampled by the fishery and abundance indices; c) sardines in Area 2 are either to the north or off-shore of Area 1; c) individuals in Area 2 are completely unavailable to the fishery or abundance indices; d) unidirectional movement is assumed (sardine move from Area 1 to Area 2 but there is no movement back from Area 2 to Area 1.).

Harvest guidelines:
Currently a quota based (e.g. harvest guidelines) management scheme regulates the US sardine fishery (California, Oregon and Washington landings), whereas the Mexican fishery remains unregulated. Since the mid-1990s, landings from both the California and U.S coastwide fishery have been less than the recommended harvest guidelines.

The harvest guideline for the Pacific sardine fishery (122,747 mt for 2004) was set based on a MSY rule defined in the Coastal Pelagic Species Fishery Management Plan (CPS/FMP). The proxy used for F_{MSY} (i.e. the fishing mortality rate that achieves MSY under "equilibrium" assumptions) has been determined by taking into account sea surface ocean temperatures, as stock productivity has been observed to increase when warm-water ocean conditions persist. For any given year, sea surface temperature is the running average sea surface temperature taken at Scripps Pier (La Jolla, CA) during the three preceding years. The exploitation fraction can range between 5-15% and is an explicit part of the algorithm used to determine the annual harvest guideline (quota) for the coastwide U.S. fishery. Based on the temperature values observed during the last two decades (1983-2003) the appropriate harvest rate has consistently been at 15% (figure 5.3).

A reduction in harvest guideline might be necessary in the next few years for of the following reasons: 1) a decrease in ocean temperatures observed during the recent years; 2) lower recruitment levels than presently estimated (due to uncertainty in present estimations); 3) adherence to a "population guide" HG that will take into account Mexican, Pacific Northwest and Canadian landings.

5.3 Pelagic habitat and single species management

There is considerable evidence that environmental variability plays a major role in controlling abundance and distribution of marine populations (Cury, 2003). However, incorporating this information in the management process remains a challenge. The current sardine and hake management frameworks indirectly achieve this in very different ways. The hake assessment implicitly incorporates effects of ocean conditions on stock distribution in the fishery selectivity[2] parameter, but environmental information is not included in the harvest control rule. By contrast, the sardine management plan attempts to explicitly incorporate environmental effects: a two area model simulating sardine migration is implemented in the assessment framework and an environmental co-variate is included in the harvest control rule. In the sub-sections below I will discuss each one of these approaches and the associated limitations. I will also draw from results presented in Chapters Two, Three and Four, to illustrate how current single species management of sardine and hake could benefit from information on pelagic habitat.

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[2] Fishery selectivity is a way of parameterizing the interaction of fish biology and fishing gear. It is usually expressed as a function which represents the proportion of each age (or size) group in a fished population that is likely to be caught by the type of fishing gear used in the area fished. In general, this is different from the age or size composition in the population as a whole, for many reasons. For example, very small and very large fish may not be vulnerable to the gear either because they are not present where the gear fishes or the physical size of the gear is mismatched to the size of the fish. Variable distribution patterns impact fishery selectivity. For example, smaller hake are more vulnerable to the fishery during warm years when the distribution of the population shifts north. During cold years, only larger fish are able to migrate north and the fishery selects for larger sizes. The selectivity parameter often becomes an opportunity to implicitly include in the assessment the effects of changes in distribution linked to changes in ocean conditions.

5.3.2 Pacific hake

The constant rate harvest control policy implemented in the hake management plan essentially aims to maintain F at a level at or below F_{MSY} to achieve a biomass at or above B_{MSY}. The traditional definition of MSY is based on the concept of unfished biomass (B_0) which assumes a single population carrying capacity (B_0). Hake habitat distribution variability suggests that B_0 may be variable and linked to available habitat and ocean conditions. The age structured model currently used in the assessment is fit to data that goes back to 1966, not capturing the variability in B_0 that a historical (longer) time series might reveal.

As documented in Chapter Three, the extent of hake migration varies and is related to oceanic conditions (Dorn, 1995; Saunders and McFarlane, 1997; Benson, 2002). While variable migration of Pacific hake is explicitly acknowledged by stock assessment authors (Dorn et al., 1999; Helser et al., 2004; Helser et al., 2005), agreement on how to include this process in the stock assessment model has not been reached. One of the difficulties lies in identifying the appropriate choice of environmental covariate to represent this variability. Based on previous work linking temperature and hake distribution (Dorn, 1995; Ware and McFarlane, 1995) temperature has been proposed as a possible covariate. However, the results presented in Chapter Three suggest that Pacific hake habitat is defined by poleward sub-surface flow and not temperature, indicating that flow might be a better choice of covariate. While more years of data will be necessary to confirm these results and develop an index, this information could initially be used to guide survey design and fine tune model assumptions and parameter choices.

Survey design

The hake acoustic survey is the primary measure of abundance used in the stock assessment. As a result the extent to which the population is sampled during these surveys is crucial. Accurate sampling is dependent in part on complete geographic coverage of the population. Undersampling northern and/or offshore areas of hake habitat could severely bias our estimate of stock abundance. Increased knowledge of how ocean conditions affect the distribution of hake can help guide survey design. In this study detailed information of sub-surface flow is used to predict hake habitat distribution. While detailed information such as this will not be routinely available, data from moorings along the coast or satellites could be used to derive sub-surface flow patterns and predict the distribution of hake habitat.

Advanced knowledge of potential distribution of hake habitat could also guide juvenile survey design. At the moment indices of young-of-the year abundance from the NMFS Tiburon/Santa Cruz larval rockfish surveys (1986-2003) are used to tune an age 2 index used for stock reconstruction and future projections. Although the index has been demonstrated to correlate well with historical year class strengths (Sakuma and Ralston 1997), one of the major problems is that in the past it has covered a limited range of available juvenile hake habitat. As of 2004, the survey has begun to cover a broader range of potential habitat (from the U.S./Mexican border to just south of Cape Mendocino), and an additional survey by the Pacific Whiting Conservation Cooperative and the Northwest Fisheries Science Center has begun sampling juveniles over an even greater range. The sampling plan for these and other surveys could be informed by predicted hake distribution given the current ocean condtions.

Model assumptions and parameter choice

There are two areas of the assessment models that could be informed by a more detailed analysis of Pacific hake habitat: a) acoustic catchability (q); b) fishery selectivity. The STAR panel (Helser, 2004) suggests improving these areas by developing and informed prior for q, and investigating alternative methods to model annual variability in fishery selectivity.

The dynamic changes in distribution such as the one documented in Chapter Three have an impact on the relative distribution of hake in U.S. and Canadian waters, which in turn affects the vulnerability of each age-class to U.S. and Canadian fisheries (selectivity) and to the acoustic survey (catchability). In order to capture these dynamic changes in selectivity previous assessments have treated selectivity as a time-dependent parameter (Helser et al., 2004). Specifically, a random walk process was used to model time varying selectivity. By using this method the effects of ocean variability on hake distribution are implicitly included. While the selectivity parameter generally offers the opportunity to implicitly incorporate distribution variability of the stock in question, a more explicit treatment of this might be more appropriate. For example, the most recent review of the hake assessment concluded that the current model structure is overparameterized and suggested explicitly treating the variability in hake distribution by incorporating oceanographic indices as covariates for inter-annual changes in selectivity (Martell et al., 2005). By using a set of simulation-estimation experiments and generating hypothetical oceanographic indices, the assessment authors found that including an oceanographic index greatly improved estimation precision for all parameters, including survey catchability (q) and selectivity parameters (Martell et al., 2005).

Acoustic survey catchability (q) will also vary in response to changes in hake distribution. In the past, survey q has been fixed to 1 (Helser et al., 2001). This implies that the acoustic survey estimate of biomass is considered an absolute measure of biomass and not just a relative measure. The selectivity of the acoustic survey is dome shaped, essentially indicating that the younger (small sizes) and older (large sizes) portion of the population are not well sampled. Fixing survey q to 1 ignores this information and assumes the entire population is sampled. This assumption was questioned during the last assessment review and relaxing it was explored (Helser et al., 2005). A few q scenarios were presented to the PFMC, but a value of 1 was eventually adopted. Using this value in the stock assessment effectively generates a biomass estimate that does not take into account a significant and variable fraction of the population, the younger and older fish. Needless to say, the choice of q value is very important as it greatly influences the assessment biomass estimate. Increased understanding of hake habitat variability could lead to a more informed choice and/or strategy for q. Values for q could be adjusted based on current knowledge of hake distribution and its links to variable ocean conditions.

5.3.3 Pacific sardine

In contrast to hake, sardine harvest guidelines are determined in part by an environmental covariate: temperature. These harvest guidelines evolved from work by Jacobson and MacCall (1995) relating recruitment and SST from Scripps Pier. Although the mechanisms explaining this link are not clear, Jacobson and MacCall (1995) suggest that temperature influences the distribution of adult sardine in the California Current, which ultimately has an impact on recruitment. SST at Scripps Pier has been found to correlate well with larger scale climate processes (McGowan et al., 1998), which potentially have an effect on one or multiple life history stages of sardine. Chapter Four concludes that adult sardine habitat distribution is variable and related to climate. Chapter Two suggests that temperature may also influence recruitment by affecting the number of predators of sardine larvae. While more information will be necessary to fully support these findings, the mechanisms presented in these chapters could better explain the temperature, recruitment relationship found by Jacobson and MacCall (1995).

Habitat distribution variability and its effect on adult growth, survival and reproductive output (see discussion in Chapter Four) is potentially one of the mechanisms linking recruitment and temperature. While the current temperature index used to formulate the harvest guideline may represent habitat variability (e.g. more habitat available during warm years), it does not represent spatial patterns of variability. As with hake, these patterns have implications for both survey design and model assumptions and parameter choices.

Survey design

The original sardine assessment modeling framework (Murphy, 1966; McCall, 1979) was conceived at a time when most of the population was in the southern area. As a result, all of the assessment population indices are from the southern portion of the sardine distribution (waters off central and southern California). Since the population has clearly expanded during the last two decades, the PFMC Scientific and Statistical Committee (SSC) and other researchers have recommended exploration of another approach able to represent the associated dynamics of the northern portion of the population. To accomplish this, northern areas of the sardine distribution range will have to be accurately sampled. Knowledge of sardine habitat distribution will be necessary to guide sampling of northern areas and assess location of critical sardine habitat. The approach developed in Chapter Four, although in need of further refinement, is a step in that direction.

Model assumptions and parameter choice

The framework used for sardine assessment (CANSAR-TAM) explicitly allows for migration of the northern component of the population from southern California to the Pacific Northwest. The migration model implemented is simple, and the values for the migration related parameters are poorly defined. The sardine Stock Assessment Team (STAT) has been exploring a different modeling framework able to straightforwardly treat the component of the population in the Pacific Northwest. However, sardine migration to this area is poorly understood and considered one of the greatest sources of uncertainty in the model (SAFE, 2004). Very little fishery independent information from the northern region exists, and the little that does exist does not provide time series of adequate length to use in the most recent assessment. Approaches such as the one presented in Chapter Four could contribute new information on sardine migration dynamics.

The vulnerability of each age-class to U.S. and Canadian fisheries will be affected by dynamic changes in sardine distribution. The fit of the model deteriorates markedly if selectivity for the southern California fishery is assumed to be time-invariant (SAFE, 2004). Clearly sardine habitat expands and contracts in response to changes in climate, so fishery selectivity for the southern California fishery should be adjusted accordingly. The STAT team has experimented by implementing models with two and three periods of selectivity (1983-1991, 1992-1997, 1998-2003) and testing them against models with just one period. The fit greatly improves if two periods of selectivity are used as opposed to one, while three selectivity periods do not seem to affect it much. The choice of periods should be based on knowledge of stock distribution patterns. My analysis could provide such information and possibly guide this choice. For example, I found winter habitat in northern offshore waters to be more variable for the period 1976-1988, compared to the period 1988-1997 (figure 4.10); this suggests that two periods of selectivity might be appropriate, and identifies start and end dates of those periods.

An area that continues to be under scrutiny is the choice of stock recruitment relationship implemented. The STAR review panel suggested environmental covariates when fitting the stock-recruitment relationship. While temperature has proven to be a useful co-variate, experimenting with spatially explicit indices of environmental variability could also be useful.

The sardine habitat index developed in Chapter Four could be an example. Information on mixed layer depth will help refine this metric, as sardine live in the mixed layer thus occupying a three dimensional space and not a two dimensional one as the one quantified in Chapter Four. While the index developed can effectively represent trends, a more accurate representation will be necessary to characterize absolute habitat amount.

5.4 Pelagic habitat and Ecosystem Based Fishery Management

During the last decade we have witnessed a wide spread and growing commitment by fisheries agencies to the Ecosystem Based Fishery Management (EBFM) approach. A growing number of advisory panels have been charged with defining EBFM and developing plans for implementation in specific regions (e.g. Fishery Ecosystem Plan-FEP) (Ecosystem Principles Advisory Panel, 1999; National Oceanic and Atmospheric Administration, 2000; Marine Fisheries Advisory Committee, 2003). Ecosystem management depends on a reasonable understanding of the relationships among and between species complexes, as well as with their environment (Larkin, 1996). Nevertheless our ability to contribute multispecies and ecosystem information useful to fisheries management has remained very limited (Cury, 2003).

The distribution of targeted resources depends on oceanographic habitat and interspecific interactions. Integration of oceanography with fishery science would facilitate EBFM, particularly if oceanographic processes strongly influence population dynamics (Bakun and Broad, 2003). The analysis of pelagic habitat presented in the previous chapters integrates the ecology of sardine and hake and the oceanography of the region. The following sub-sections will discuss how this type of analysis has potential to contribute to the following three key aspects of EBFM:

1) Development of ecosystem indices
2) Definition of relevant ecosystem geographic boundaries
3) Ecosystem context for single species approaches

5.4.1 Ecosystem indices

The desire to represent key ecosystem interactions has lead to the recent focus on ecosystem indices. A number of symposia and working groups have been convened on this topic (e.g.: Ecosystem considerations in fishery management, Anchorage 1998; Responsible Fishing in the Marine Environment, Reykjavik 2001; IOC-SCOR working group 119, Quantitative Indicators for Fisheries Management, Paris 2004; Advancing Scientific Advice for an Ecosystem Approach to Fisheries, Dublin 2004). Most of the indices developed to date represent trophic interactions, while work on indices representing interactions between species and the physical environment is lagging behind. Climate forcing of ecosystems has mostly been described by large scale indices such as PDO and ENSO. Climate impacts are aggregated across large spatial scales and range of species and direct links are made between climate forcing and production variability. However, changes in ecosystem structure are often the result of changes in physical habitat with very distinct spatial structure. In order to fully describe ecosystems, spatially explicit indices representing the physical environment should also be developed.

The focus of my research on pelagic habitat of key trophic species addresses this issue. For example, hake habitat is a dynamic entity whose boundaries are defined by physical characteristic of the system. These boundaries change in response to climate forcing and this has implications for northern CC ecosystem structure (see discussion in Chapter Three). I identify and quantify changes in hake habitat which have potential to impact ecosystem structure. Metrics able to detect these type of changes could be good ecosystem indicators, as they are related to both the physical and biological structure of the ecosystem.

In order to explore potential effects of changes in hake distribution on the northern CC ecosystem structure I used an ecosystem model built by Field (2004). This model is an Ecosim model (Walters et al., 1997; Walters et al., 2000), best described as a multi-species biomass-driven predator/prey surplus production model (Field, 2004). A static versions of this model (Ecopath) was projected forward in time with stock assessment estimates of hake biomass. The model was forced with different levels of hake abundance. The following scenarios were implemented:

Consider B = hake biomass time series from the stock assessment (1966-2003)

a) a baseline model forced by the hake stock assessment biomass time series (B)
b) a model forced by half the amount of hake stock assessment biomass time series (0.5B)
c) a model with 1.5 the amount hake stock assessment biomass time series (1.5B)

Figure 5.4 represent changes in mean biomass from baseline model as a result of scenarios b and c described above. Changes in hake abundance clearly have an effect on the biomass levels of ecosystem components. Increases and decreases in hake abundance do not affect all species groups the same way. Most groups show an inverse relationship with hake biomass, with increases in biomass when hake decline and decreases when hake increase. Seabirds seem to benefit the most, probably due to a reduction in competition for prey they share with hake (forage fish). Similarly, rockfish, salmon and many marine mammals tend to do better when hake biomass is low, again likely a result of competition for forage fish. This result is consistent with other food web studies that have suggested that predators such as marine mammals that feed both on piscivoroius fishes (hake, cod) and the food of piscivorous fishes (herring, anchovy) tend to maintain themselves in the face of piscivore declines as a result of the increased abundance of forage species (Walters et al., in press.). For example, although most marine mammals prey heavily on hake, they also prey heavily on the food of hake, particularly forage fish. Only a few groups that prey heavily on hake, such as arrowtooth flounder, actually decline notably when hake are less abundant. The majority of groups do worse with an increase in hake.

Most of the magnitudes of change outlined for hake decreases also hold for hake increases, the exceptions being toothed whales, coastal sharks, baleen whales, fur and harbor seals. All of these animals are the top of the food web. Hake compete with them for prey, but the system holds enough alternate choices that an increase in hake does not cause a strong effect. There are three groups (sea lions, sable fish and orcas) that benefit from both increases and decreases in hake abundance. This is because hake represents prey (or predation on predators of their prey) and competition for prey to these organisms. For example forage fish are prey to all three of these groups and a major prey item for hake. Decreases in hake, will benefit these three groups by increasing the amount of available forage fish. However, increases in hake represent more competition for forage fish, but also more prey (i.e. hake) for sea lions and sablefish. When hake increases, either more prey is available to these groups (i.e. sablefish and sea lions) or predation (i.e. by orcas) on predators of their prey increases so the groups benefit. When hake decreases, other prey which they normally have to compete for with hake increases, making up for the decrease in prey represented by hake. Figures 5.5 and 5.6 illustrate how changes in hake abundance affect the fisheries. The degree to which removal of species groups changes reflects the trends in biomass changes described above. In summary, changes in hake abundance can have large effects on biomass and yield of many other ecosystem components, as well as performance of fleets, in particular shrimp trawl and salmon.

5.4.2 Definition of geographic boundaries

Delineating the geographic extent of ecosystems is one of the essential components of EBFM (EPAP, 1999; Gislason et al., 2000). The spatial extent of the system dynamics to be studied and/or managed should define the scale of an ecosystem (Sissenwine and Murawski, 2004). Careful analysis of the life history of key species and their habitat dynamics (such as the one conducted here) will greatly inform the choice of ecosystem geographic boundaries. A failure to carefully consider life history and habitat dynamics can lead to inappropriate ecosystem boundaries and lead to ineffective FEPs.

Migratory species such as sardine and hake present a special challenge in this regard. Their residence in a particular ecosystem may vary from year to year as it is linked to ocean variability. Understanding their habitat dynamics is essential to the definition of ecosystem boundaries. The CC ecosystem is a good example of this. As Field (2004) suggests “the proper scale for a CC FEP should be the CC ecosystem as a whole, including recognition of the cross-border nature of many ecosystems processes and commercially important stocks in the northern and southern reaches of the CC". Considering the habitat dynamics of sardine and hake will help define the proper scale for a CC FEP.

5.4.3 Ecosystem context for single species approaches

While detailed single-species assessments still form the core of management advice in most cases, they are increasingly embedded in an ecosystem context, at least qualitatively (Mace, 2001). However, a number of important classes of ecosystem interactions are currently not being routinely evaluated (Sissenwine and Murawski, 2004). Amongst these are relationships between biological and physical components of ecosystems. Stability of biological communities is affected by the interaction between life history, environmental variation and fishing strategies (Sissenwine and Murawski, 2004). Accounting for interactions between biological and physical components of the ecosystem will help determine appropriate spatial scales of data collection, science and management which Hilborn (2004) reports as missing from conventional single species management.

Thus far fishery science has tended to evaluate management performance with indicators based on non-spatial population dynamics models (Pauly et al., 2003), ignoring inherent spatial variability of a stock's distribution (Booth, 2000). For stocks such as Pacific sardine and hake where the biology of the fish has a spatial component, efforts should be made to incorporate spatial structure in indicators. We have become increasingly aware of the distribution patterns of many species, yet what drives these distributions is often poorly understood, making prediction a difficult task (Verity et al., 2002). I have outlined habitat areas for sardine and hake, and examined how climate forcing may affect these areas by identifying critical physical/biological relationships. This addresses both spatial structure and environmental processes of the CC system, facilitating the inclusion of broader ecosystem considerations and objectives in single species assessments and management plans.

Another fundamental aspect of embedding single species management into an ecosystem context is accounting for interactions amongst species. Mangel and Levin (2005) differentiate between viewing fishery problems from the perspective of population ecology and from the perspective of community ecology. The population ecology view focuses on the dynamics of a single species or stock, while the community ecology view explicitly recognizes and takes into account interactions between different stocks and species. Fishery science developed very much with a focus on population ecology (Mangel and Levin, 2005). Beginning in the 1970s this view changed and “most fishery scientist and managers currently recognize that communities are dynamic, often regulated by processes external to the community, may exist in multiple alternative steady states and behave in a more or less stochastic manner” (Mangel and Levin, 2005). This change has led us to the ecosystem approach to fishery management (Mangel and Levin, 2005), although much work still needs to be done to implement it.

Within the context of community ecology and fisheries, understanding the mechanisms underlying the spatial distribution of species acquires new significance. For example, the presence or absence of hake in specific areas has implications for the productivity of both the species as well as the ecosystem it occupies (see discussion in Chapter Three). The northern CC model runs I discussed above clearly show this: biomass levels of a number of species change as more or less hake are present in the ecosystem (figure 5.3). Understanding and predicting spatial distribution patterns of hake will allow us to consider ecosystem implications (e.g. impact on hake predators and prey) and incorporate ecosystem objectives into management plans. Spatially explicit management has been recently discussed as having great potential to improve sustainability of ocean systems (Botsford, 1997; Babcock et al., 2004; Pikitch, 2004).

5.5 Conclusions

I have shown that climate forcing of the CC system results in dynamic distributions of marine populations. The CC ecosystem is spatially heterogeneous, and spatial patterns and processes are important to its structure and function. Efforts to include this information in our current marine resources management frameworks should continue, with particular attention devoted to developing spatially explicit approaches.

The dynamic distribution of sardine and hake has implications for the productivity of species and of the CC ecosystem. Within a single species management context, the distribution variability of sardine and hake presents similar challenges. The assessment and management teams for these two species continue to work independently on the same problem: how to treat the effects of environmental variability on the stock in question. Each team has clearly taken different approaches. A lot could be learned from a comparative and collaborative review of the two assessments.

Within an ecosystem context, considering pelagic habitat of key trophic species is essential. The awareness of habitat has made its way into U.S. management agencies initially because of the requirement of the SFA to evaluate and protect habitat (Essential Fish Habitat-EFH). Habitat also resurfaces within the context of EBFM. Spatial structure and environmental processes are discussed as essential to the development EBFM (Pikitch, 2004). One of the key elements of FEP as envisioned by EPAP (1999) is describing the habitat requirement of different life history stages for key organisms in the food web. However, when it comes to developing approaches to implement EBFM, habitat issues have not received the attention they warrant. While EFH provides a legal context for habitat considerations, most of the work on habitat in both the Pacific and North Pacific Councils is related to benthos. Habitat is often defined as an area delimited by static features (i.e. bottom type), but for pelagic species habitat is often a dynamic entity. Its boundaries are changing according to changes in the physical structure of the system. Increasing our awareness of pelagic habitat will contribute to the development of effective FEPs.

Climate forcing is a key factor in understanding the nature and dynamics of ecosystems. Over the last decade there has been a growing number of ecosystem “status reports” summarizing trends in climate, oceanographic conditions, biological productivity and trends in the abundance of sensitive species. Our next challenge will be to place all of this information into a useful context and effectively communicate it to managers and decision makers. The development of effective EBFM plans depends on this.

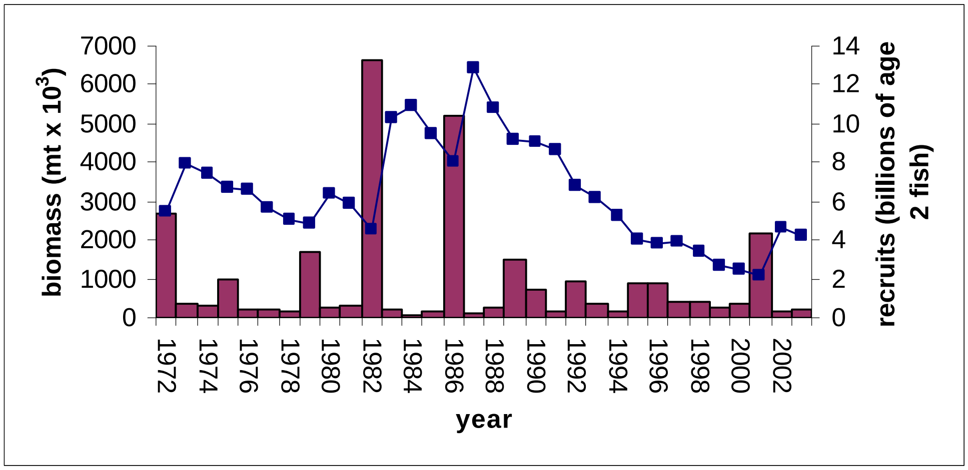


Figure 5.1: Time series of Pacific hake biomass (line) and recruitment (bars) (data from Helser, 2004).

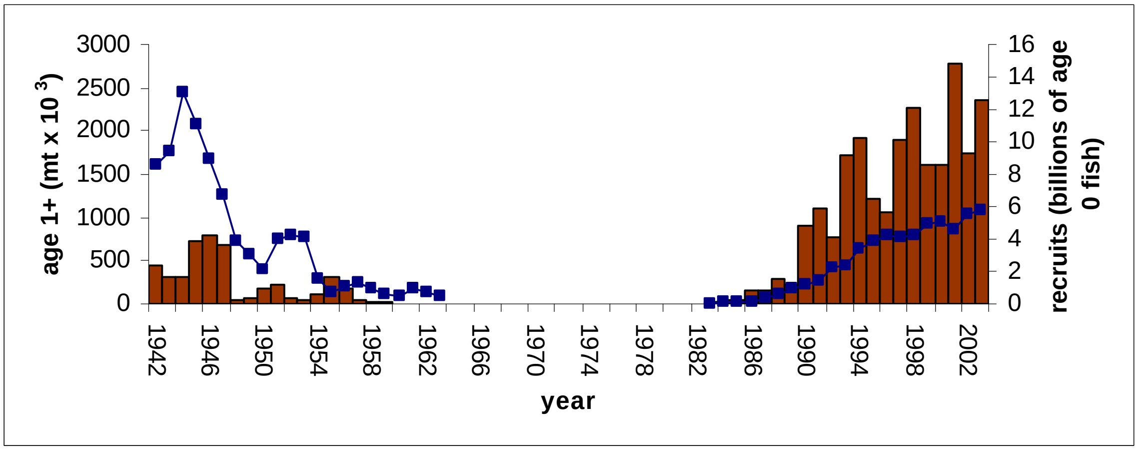


Figure 5.2: Time series of Pacific sardine biomass and recruitment (data from Jacobson and MacCall, 1995 and Conser et al., 2004).

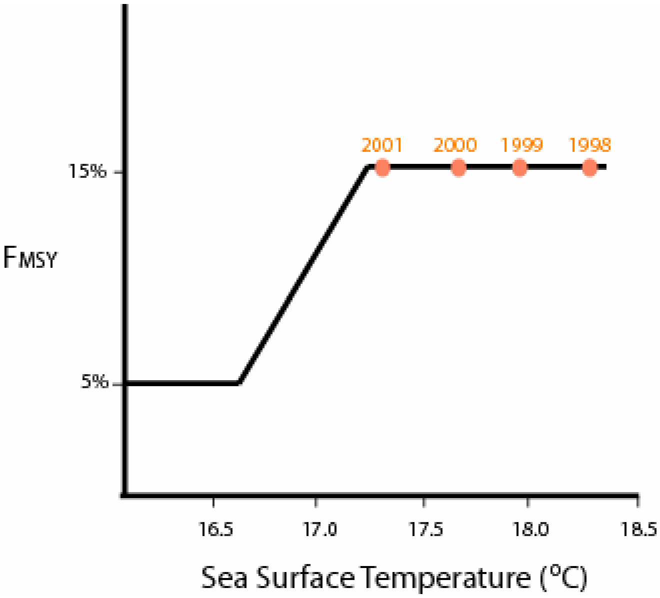
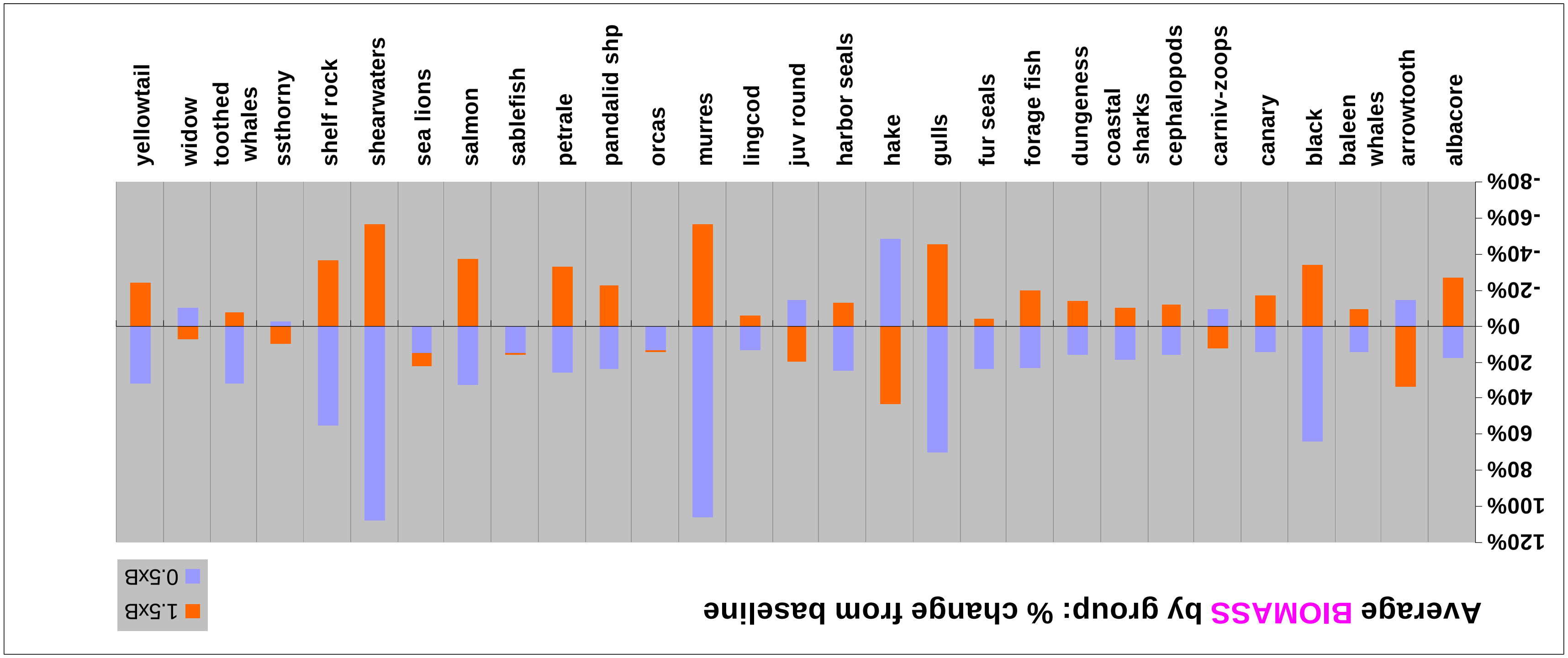
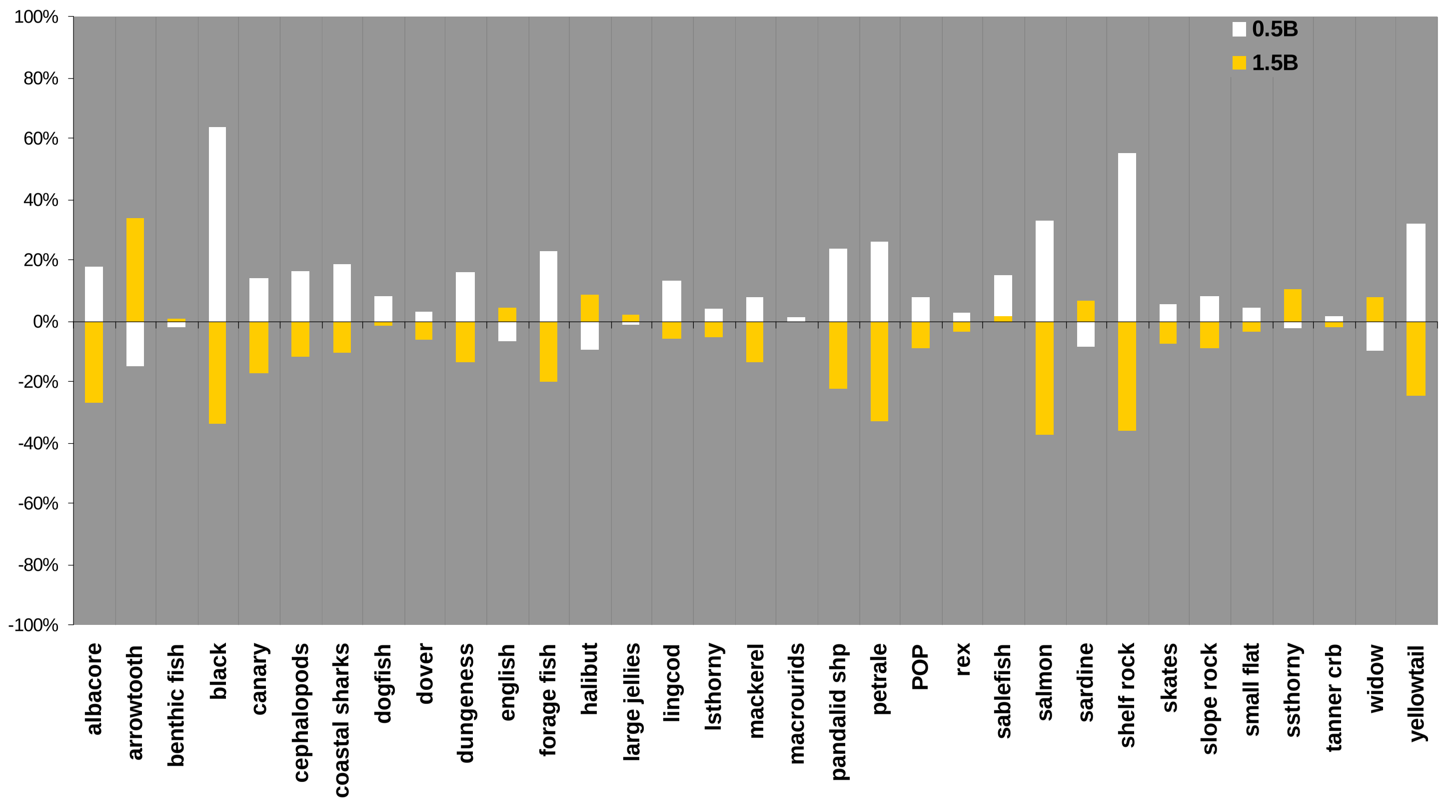


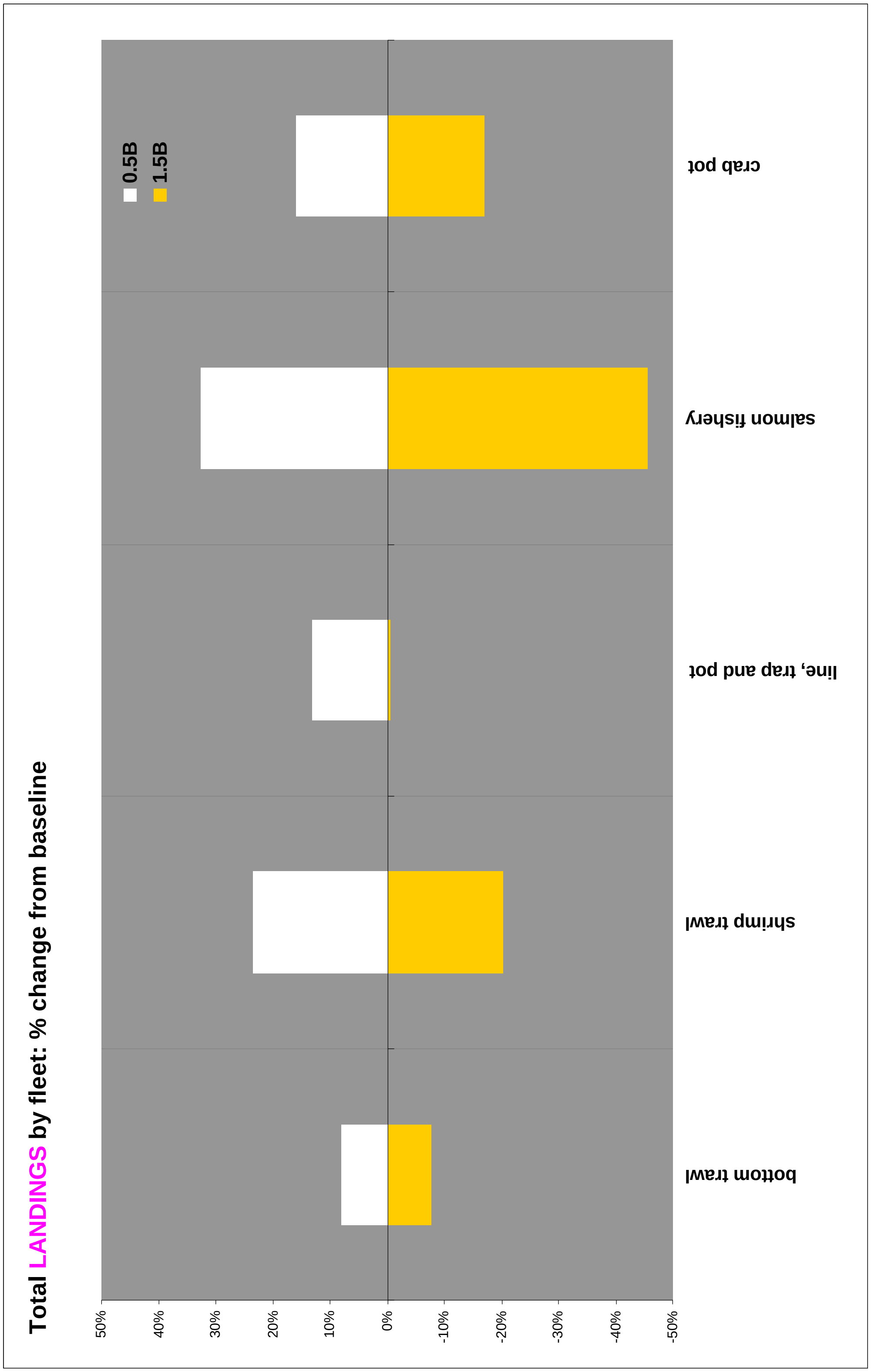
Figure 5.3: Environmentally based harvest rate control rule for Pacific sardine as specified in the Coastal Pelagic Species Fishery Management Plan (PFMC, 1998). Re-drawn from Conser et al., 2001.

Figure 5.4: Percent change of model estimated biomass from baseline run. Groups with changes below 20% in both biomass scenarios are not included in this figure.



Total REMOVALS by species: % change from baseline




Total LANDINGS by fleet: % change from baseline
0.5B
1.5B
crab pot
salmon fishery
line, trap and pot
shrimp trawl
bottom trawl
50%
40%
30%
20%
10%
0%
-10%
-20%
-30%
-40%
-50%

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Vita

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