

OCEANOGRAPHIC INFLUENCES ON PACIFIC HAKE (*Merluccius productus*)
DISTRIBUTION AND BIOLOGY

by

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ABSTRACT

There are persistent decadal scale states in atmosphere-ocean conditions that are called *regimes*, and a shift from one set of stable conditions to another is called a *regime shift*. Regime shifts have been identified in 1925, 1947, 1977, 1989, and possibly 1998. In recent years, a substantial amount of effort has been directed at understanding the effects of regime shifts on fish populations. A synthesis of the available information for the eastern North Pacific and Bering Sea is presented in Chapter 1. What is most evident from the review is that pelagic fish exhibit the most dramatic responses to changes in climate-ocean conditions. Pacific hake (*Merluccius productus*) is the most abundant pelagic fish species in the California Current ecosystem, and is important both commercially and in terms of its large predatory biomass.

A review of the life history and ecology of hake is presented in Chapter 2. Hake is a widely distributed species that migrates seasonally between winter spawning grounds off California and summer feeding grounds off the coast of British Columbia. The feeding and spawning distribution of hake shifted northwards following the 1989 regime shift and the biomass of hake present in Canadian waters increased by a factor of two. These changes resulted in disputes on catch allocation between Canadian and United States fisheries management agencies. A method of forecasting would aid in negotiations. Early studies established a link between hake distribution and physical oceanographic conditions, but the exact mechanisms remained to be identified. The objectives of this study are to develop a predictive index of the proportion of the stock that migrates into Canadian waters, and to examine the possibility that the change in distribution coincided with a change in hake growth.

The key findings of this study are that the best predictor of hake distribution is the Bakun upwelling index off the coast of California, and that juveniles produced in northern waters off Canada during the 1990s grew faster than those produced in the south. These changes in

distribution and juvenile growth are probably related to biomass and/or availability of euphausiids, which are the key prey item of hake.

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OVERVIEW

The objectives of this study are to develop a predictive index of the proportion of the offshore stock of Pacific hake (*Merluccius productus*) that migrates into Canadian waters on both an interannual and decadal scale, and to explore the possibility that changes in ocean conditions in the North Pacific Ocean coincided with changes in hake growth. The objectives and the study are not addressed until Chapter 3, and are preceded by two separate literature reviews. A review of regime shifts and their effects on production in the Northeast Pacific Ocean is presented in Chapter 1. This review illustrates the complexity of regime shift effects on oceanic ecosystems, and the importance of the effects of regime shifts on pelagic fish species, including hake. Hake has been the focus of a considerable amount of research, the majority of which is summarized in Chapter 2. Relationships between oceanographic factors and hake biology are emphasized in this chapter and provide the necessary background information for the study in Chapter 3.

CHAPTER I

Ecological Effects of Regime Shifts in the Eastern North Pacific Ocean

1.1 THE REGIME CONCEPT

The idea of 'locked in' states of climatic, oceanic and biological systems was introduced to fishery science by Isaacs (1975), who called these persistent trends *regimes*. Regimes have been defined as multiyear periods of linked recruitment patterns in fish populations or as stable conditions in physical data series (Beamish et al., 1999). Concurrent (and sometimes abrupt) changes in these biological and physical variables indicate a *regime shift*. These natural patterns of variability raise questions about the biological basis of sustainability of fisheries (Beamish, 1995), and are leading ecologists away from a single, steady state view of ecosystems to one that recognizes that ecosystems fluctuate because of internal and external sources of variability (e.g., Steele, 1996; Trites et al., 1999).

1.2 CLIMATE/OCEAN VARIABILITY

The basic state of the atmosphere-ocean climate system over the North Pacific Ocean changed abruptly in the late 1970's (Ebbesmeyer et al., 1991; Graham, 1994). Atmospheric circulation changed throughout the troposphere (Trenberth, 1990), and the Aleutian Low pressure system, which is the dominant low pressure system in the North Pacific, deepened (Miller et al., 1994), shifted eastward (Trenberth, 1990), and brought warm, moist air over Alaska and colder air over the North Pacific. Concurrently, sea surface temperatures cooled in the central Pacific and warmed along the west coast of North America (Miller et al., 1994). Sea ice decreased in the Bering Sea (Manak and Mysak, 1987) and changes were observed in the surface wind stress (Trenberth, 1991) that probably affected ocean currents in the North Pacific.

Indices of climate-ocean conditions indicate that a synchronous change occurred in the North Pacific in 1977. Since then, there has been a tendency for more frequent El Niño and fewer La Nina events (Trenberth and Hoar, 1996). The similar timing of the large-scale changes suggest that an as yet unidentified common, global teleconnection may be responsible for the shift (Beamish et al., 2000).

The climatic shift observed in the late 1970's was not the first time such a change had occurred in the North Pacific. In fact, it appears to have occurred at least three other times in the 20th century. Mantua et al. (1997) and Minobe (1997) identified shifts in the atmosphere-ocean climate record in 1925, 1947 and 1977. A shift in 1989 was reported by Overland et al. (1999) and Beamish et al. (1999); and there are indications that a fifth shift occurred around 1998 (e.g. McFarlane et al. (2000)).

The climatic and oceanographic events observed in the North Pacific in the mid 1970s and at other times the past century have been quantified by a number of different indices. Commonly cited indices for the Pacific Ocean include the Southern Oscillation Index (SOI), which describes the oscillation of air masses between the eastern and western tropical regions of the Pacific Ocean (Walker, 1924; Trenberth and Hoar, 1996), the Pacific Decadal Oscillation (PDO) which is defined as the first empirical orthogonal function of sea surface temperature in the North Pacific (Mantua et al., 1997), and the Aleutian Low Pressure Index (ALPI) (Beamish and Bouillon, 1993) and the North Pacific Index (NPI) (Trenberth and Hurrell, 1995), both of which are measures of the intensity of the Aleutian Low atmospheric pressure system. Because the ALPI measures the area of low pressure and the NPI is the area weighted mean sea level pressure over the region 30°N to 65°N, 160°E to 140°W (Trenberth and Hurrell, 1995) the two are inversely related. Although the 1977 shift is evident in all indices, it should be noted that not every regime shift is apparent in all indices. For example, the 1989 regime shift is not evident in

the PDO (Beamish et al., 2000), but it is in the Atmospheric Forcing Index (AFI) (McFarlane et al., 2000).

The AFI is a composite climate index based on the ALPI, PDO, and the Pacific Circulation Index (PCI) (McFarlane et al., 2000). The three indices are combined using principle components analysis. The AFI is the first principle component of the combined indices, and expresses 70% of the total variation. Changes in the intensity of the Aleutian Low are reflected in all three indices, and because of this, McFarlane et al. (2000) suggest that the ALPI may be the most appropriate measure of climate-ocean dynamics in the North Pacific. Due to this fact, and because most of the regime research has focused on the North Pacific, the ALPI (Figure 1.1) is the focus of the present review. However, it should be noted that other indices have also been developed for the Atlantic Ocean. These include the North Atlantic Oscillation Index (NAOI) (Walker and Bliss, 1932) and the Atmospheric Circulation Index (ACI) (Beamish et al. 1999). A detailed discussion of these and other indices is presented in Beamish et al. (2000).

The Aleutian Low is the dominant winter (September to January) atmospheric pressure system in the northeast Pacific. It develops in the fall of each year, producing strong, cyclonic (counterclockwise) winter winds, and breaks down in the spring of the following year (Beamish and Bouillon, 1995). In early spring, the North Pacific High intensifies and dominates most of the North Pacific, resulting in weaker, anticyclonic summer winds. As mentioned previously, the ALPI is a measure of the area of low surface pressure (<100.5 kPa) in the North Pacific Ocean (Beamish et al., 2000). A positive ALPI value indicates that the Aleutian Low is intense (large in size) and the converse is true for negative values. From 1947-1976, the ALPI was generally negative (i.e., the Aleutian Lows were smaller), while from 1977-1988, the ALPI was positive (reflecting a period of more intense Aleutian Lows) (Figure 1.1). The intense period ended after 1989.

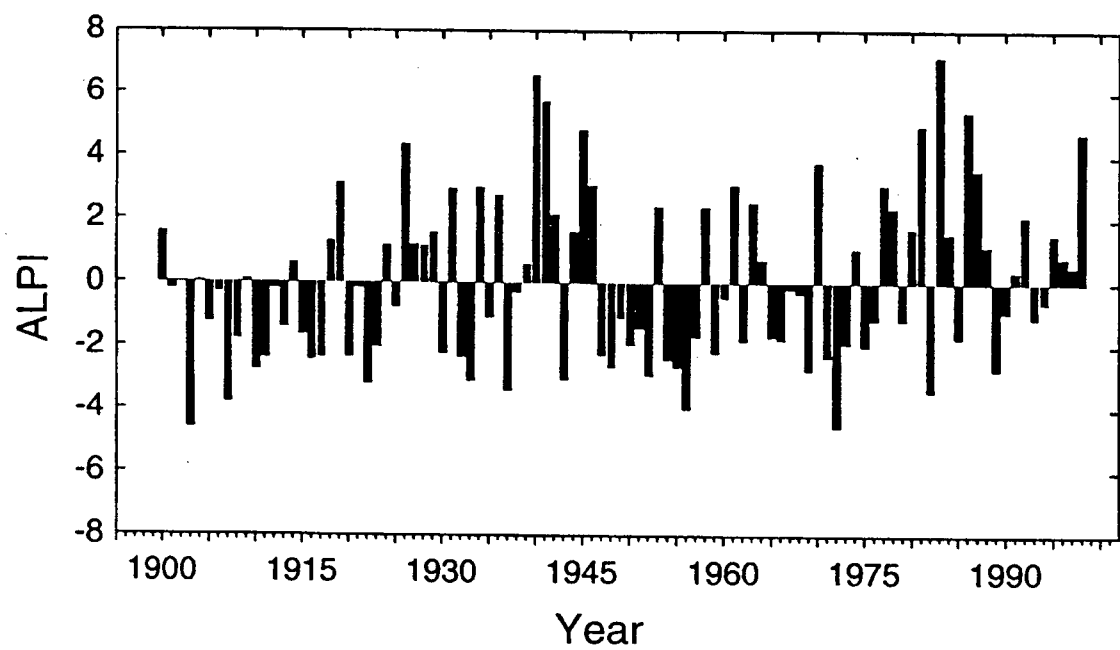


Figure 1.1 The Aleutian Low Pressure Index from Beamish et al. (2000).

In the present review, the current knowledge of the ecological effects of regime shifts in the northeast Pacific Ocean is updated from Hayward (1997) and Francis et al. (1998), and evidence that the 1989 regime shift was not a simple reversal of the 1977 regime shift is summarized. The oceanographic effects of atmospheric variability over the northeast Pacific are first presented as a basis for understanding the connection between changes in the atmosphere and the subsequent effects on marine organisms. Throughout, connections are made to the Aleutian Low, and the ALPI is considered a proxy for a variety of climatic and oceanic processes.

1.3 GLOBAL CLIMATE AND REGIME SHIFTS

The timing of changes between regimes is similar, if not exact, in many of the climate indices developed to date (Beamish et al., 1999), which is to be expected if climate and climate variability are global phenomena. It has been shown in several studies (reviewed in Mann and Lazier, 1996) that ENSO events are connected to weather changes outside the Pacific Ocean. These events are linked in the atmosphere by remote associations, or atmospheric teleconnections (Mann and Lazier, 1996). What this means is that a change in the position and intensity of atmospheric convection in one area will result in adjustments in pressure cells in adjacent areas and lead to altered wind and ocean current patterns. These changes can occur on a global scale.

Beamish et al. (1999) suggested that the close correspondence in worldwide climate indices points to a common event (or energy source) as the cause of regime shifts. The common cause is as yet undetermined, but there are indications that it is related to the Earth's rotation dynamics and global energy transfers. Yndestad (1999) proposed a General system theory of the influence of the Earth's nutation (wobbling motion of the Earth's axis around the poles on an

18.6 year cycle) on the temperature in the Barents Sea whereby the dynamics of the Earth's axis act as a forced oscillator that transfers energy to the sea system via a set of energy cycles that modulate the amplitude of ocean currents. Nutation involves the varying attraction of the Moon on the Earth's equatorial bulge, and according to this theory, the Moon is the ultimate cause of low frequency temperature cycles in the Barents Sea. Yndestad points out that if this theory is to be confirmed, worldwide oceanographic data sets must be examined for matches to the Earth's nutation.

There is extensive research on the relationship between the Earth's rotational speed and climate; an index of the rotation speed, the length of day (LOD) has been developed (see Beamish et al. (2000) for an overview). In brief, there are four shells of the Earth: the core, mantle and crust, hydrosphere and atmosphere - they all rotate at different speeds. The connection between changes in the rotation speed of the solid earth and changes in the atmosphere lies in the exchange of energy (Beamish et al., 1999). The principle of conservation of angular momentum means that when the atmosphere loses or gains momentum, the solid earth must gain or lose a similar amount (Beamish et al., 1999). The redistribution of angular momentum (energy) among the four shells results in changes in the LOD, while changes in atmospheric circulation are reflected in atmospheric indices such as the ALPI. Beamish et al., (2000) documented recent changes in the LOD. Around 1974, the rotation speed of the solid earth increased, and resulted in a decreased LOD. The trend reversed in the late 1980s.

Although the majority of the regime research has been conducted in the Pacific Ocean, regime shifts are not specific to this region. A good example of global scale climate shifts can be found by examining the long term trends and the close correspondence in the timing of changes between the North Atlantic Oscillation (NAO), first described by Walker (1924) around the time that ENSO was first detected, and the SOI. Like ENSO, the NAO is an alternation of atmospheric

pressure, but it occurs between the subtropical high pressure cells over the Azores and low pressure cells over Iceland (Planque and Taylor, 1998). The state of NAO determines the location, speed and direction of the westerlies, and relative humidity and winter temperatures on both sides of the Atlantic basin. The NAO index is the winter pressure difference between the Azores and Iceland (Hurrell, 1995). Positive anomalies of the index occur when the Icelandic low is strong (Beamish et al., 2000). In the positive phase, winters in Greenland and Labrador are cold. In the negative phase, the Icelandic low is relatively weak, this results in cold winter air over western Europe and warmer conditions in Greenland and Labrador. The trends in the NAO are similar to those of the SOI. In the mid-1970s, both the NAO and the SOI showed a change in pattern, and there were extreme values of both the NAO and the SOI in the late 1990s (Beamish et al., 2000). In 1996, there was an extreme negative NAO that persisted through 1997 and 1998, while in the Pacific, there was a strong La Nina in 1996, followed by the strongest El Niño of this century in 1997-1998.

Anomalous climate-ocean conditions have also been studied elsewhere. In the Benguela upwelling ecosystem, summer-autumn conditions in 1976-77 varied from the average, but what interested scientists more was the warm 1982-83 anomaly, which was associated with the large 1982-83 ENSO in the Pacific. Shannon et al. (1992) reviewed the oceanographic changes that took place in the Benguela ecosystem from 1950 through to the end of the 1980s and reported a warming phase throughout the 1980s that was associated with a reduction in equatorward (upwelling) wind stress. The anomalous conditions ended in 1988/89. This was accompanied by other dramatic changes that occurred in much of the South Atlantic and South Indian oceans.

Many of the climate-ocean indices, including the global LOD, exhibit similar timing of changes from one state to another, but the intensity and direction of the change in the indices are not necessarily the same. Additionally, as the following sections illustrate, the physical and

biological effects of regime shifts differ dramatically on both a large-scale (basin wide) and small scale (regional).

1.4 OCEANOGRAPHIC IMPACTS OF ATMOSPHERIC VARIABILITY

Five large production domains (Figure 1.2) exist in the eastern North Pacific Ocean. Ware and McFarlane (1989) identified the 1) Coastal Downwelling Domain, the 2) Transition Zone, the 3) Coastal Upwelling Domain, and the 4) Central Sub-Arctic Domain. The location of these domains is delineated by the persistent surface currents in the Northeast Pacific. The Bering Sea can be considered a fifth domain, and is delineated by the Aleutian Islands and Alaskan Peninsula. All five domains are unique in terms of the dominant fish species and their response to regime shifts.

A zero in the wind stress curl near the coast of North America causes a bifurcation of the eastward flowing Subarctic Current, which creates the Northward flowing Alaska Current and the southward flowing California Current (Thomson, 1981). The location of the separation of the Subarctic Current is variable (Thomson, 1981), and this is most evident on a seasonal basis, because the Aleutian Low and North Pacific High atmospheric pressure systems vary in location and intensity between summer and winter.

The dominant feature in the Central Subarctic Domain (Central Gulf of Alaska) is the Alaska Gyre, which rotates in a counter-clockwise (cyclonic) direction (Ware and McFarlane, 1989). Divergence (upwelling) at the core of the gyre is believed to be the reason this domain is relatively productive (Reid, 1962). Intensification of winds might improve productivity and result in increased divergence and upwelling of nutrient rich water at the core of the gyre (Reid, 1962; Brodeur and Ware, 1992). Miller (1996) found that flow in the Alaska gyre was stronger than usual after the 1977 regime shift, while in the California Current (Coastal Upwelling Domain)

there was no change. This result appears to support the hypothesis of Chelton and Davis (1982) that oceanographic changes in the Alaska and California Currents are not in phase.

Establishment of the wintertime Aleutian Low in the subarctic North Pacific results in increased precipitation. This freshwater input has a strong, stabilizing effect on oceanographic conditions. Intensification of the Aleutian Low leads to winds that are unfavorable for upwelling further south along the coast of North America, which also leads to increased water column stability. Although the water column stability might vary in phase between the two regions, the effects on production would differ (Gargett, 1997). In the Gulf of Alaska, increased stability means that the phytoplankton can be maintained in the euphotic zone for longer periods of time, thereby increasing primary production, while, off California, increased stability and less upwelling results in a decreased nutrient supply. Since the phytoplankton in this area are primarily limited by nutrients and not light, increased stability will decrease primary production (and by inference, secondary production).

The Bering Sea is characterized by the presence of winter sea ice and a subsurface pool of cold ($<2.0^{\circ}\text{C}$) water in summer (Wyllie-Echeverria and Wooster, 1998). The extent of the sea ice coverage is dependent on air temperature and the winter storm tracks generated by the Aleutian Low (Overland and Pease, 1982). When the Aleutian Low is strong relative to the high pressure systems that move in from the north, warm air is pumped northward and the sea ice does not penetrate far south, and the cold pool of water is not well developed. The cold pool of water is significant because of its size (on the order of 100s of km wide and up to 70m thick), and its effects on temperature-sensitive species assemblages (Wyllie-Echeverria and Wooster, 1998).

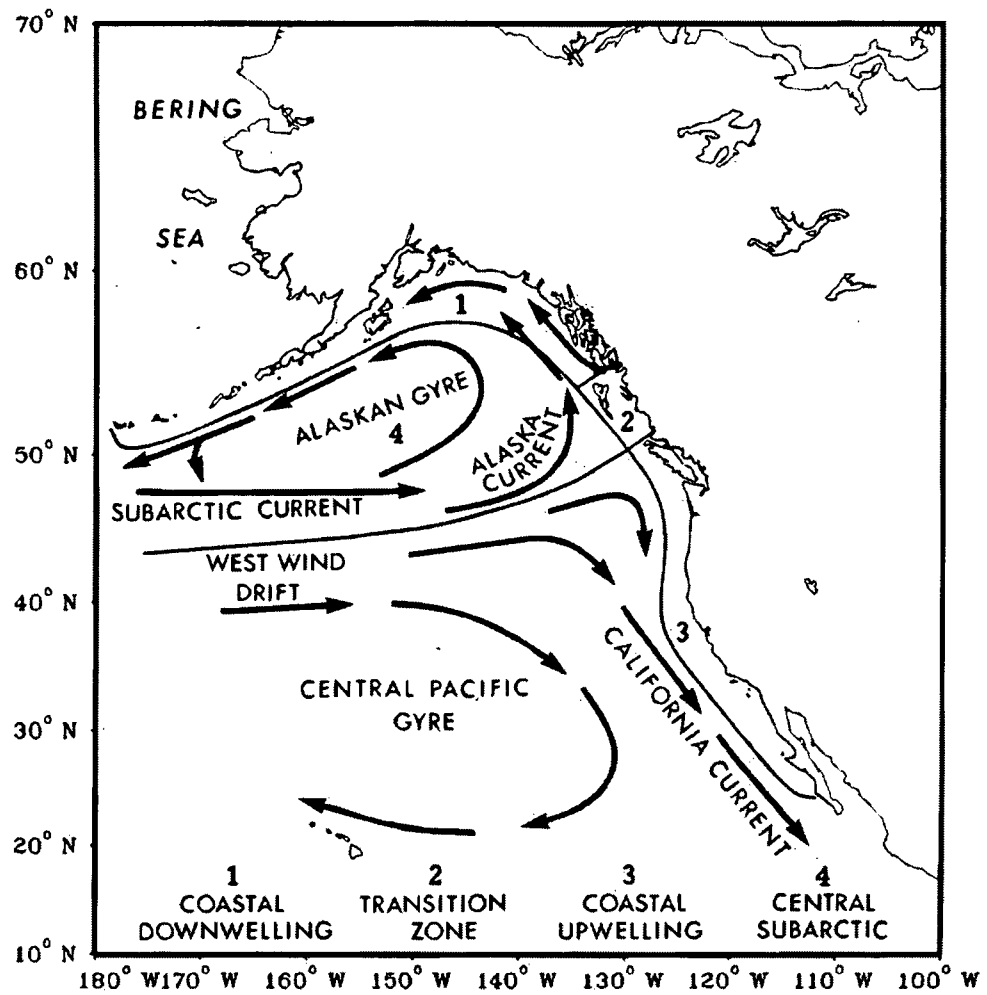


Figure 1.2 Prevailing ocean currents and the four major domains defined by Ware and McFarlane (1989).

The Bering Sea reflects large-scale ocean variations, but the timing of the events is not necessarily synchronous with those further south (Wooster and Hollowed, 1995). There was a cool era from about 1965 to 1978, and a warm period beginning in 1978 (Wooster and Hollowed, 1995), that was related to a significant decrease in the winter ice cover after 1977 (Niebauer, 1977). Variability in the climate-ocean conditions in the Bering Sea appears to be related to conditions elsewhere. The mechanism of connection may be the Aleutian Low.

1.5 ECOLOGICAL IMPACTS OF ATMOSPHERIC VARIABILITY

1.5.1 Phytoplankton and Zooplankton

Venrick et al. (1987) showed that in the central North Pacific (just north of Hawaii) the total chlorophyll *a* (a proxy for phytoplankton biomass) nearly doubled around the time of the 1977 regime shift. Venrick (1994) subsequently showed that this was due to a deepening of the mixed layer, which resulted in increased phytoplankton production in deep water. Polovina et al. (1995) provided supporting evidence by demonstrating that concurrent with the persistent intensification of the Aleutian Low after 1977, there was a deepening of the mixed layer in the subtropical domain near the Hawaiian Islands, while the mixed layer became 20-30% shallower in the Gulf of Alaska. Polovina et al. predicted that primary and secondary production would increase in the two areas by increasing the exposure of phytoplankton to light in the Gulf of Alaska and by mixing deeper, nutrient rich, water into the euphotic zone in the subtropical North Pacific.

Ware and Thomson (1991) examined the relationship between the strength of the upwelling-favorable northerly winds and primary production in the Southern California Bight and found that they are positively related. This result was verified by Ware (1992), who used data from upwelling systems around the world to show that primary production is roughly

proportional to upwelling. Ware and Thomson (1991) noted that there was a decline in primary production in the Southern California Bight between 1916 and 1942, concurrent with a reduction of wind-induced upwelling. They proposed that there is a long period oscillation (on the order of 40 years) in primary and secondary production in the area that is driven by a similar cycle in wind-induced upwelling.

The biomass of copepods in the Alaska Gyre increased in 1976-77, concurrent with cooling of the central North Pacific and intensification of the Aleutian Low (McFarlane and Beamish, 1992). Large-scale sampling of oceanic areas in the North Pacific also showed a significant increase in zooplankton biomass from 1956-62 to 1980-89 (Brodeur and Ware, 1992; Brodeur et al. 1999a). After 1988, the biomass remained above the long-term mean but with considerable variability from year to year.

Decadal-scale changes in mixed layer depth have reported throughout the North Pacific, and may affect the spatial production and biomass of zooplankton (Polovina et al., 1995). In 1956-62 the highest zooplankton biomass in the North Pacific occurred in the central part of the Alaska Gyre, while in the 1980s the elevated biomass was contained in a steady band from the transition zone to the northern coast of Canada and Alaska (Brodeur et al. 1999a). One explanation for the spatial difference in zooplankton biomass is that in the 1980s, intensified winds increased the speed of the gyre and advected zooplankton to the outer margins of the gyre (Brodeur and Ware, 1992).

Temperatures in the surface layer of the Coastal Upwelling Domain (California Current) have warmed by at least 0.8°C since 1952 (Roemmich and McGowan, 1995). Over the same period, macrozooplankton biomass (measured as displacement volume) decreased by approximately 80%. Roemmich and McGowan related the decline of zooplankton biomass to coastal warming associated with the 1977 regime shift that increased stratification and reduced

upwelling of nutrients into the surface waters of the California Current. They further proposed that the stratification was the result of a climate-induced change in ocean circulation that brought warmer water into the area and limited the supply of nutrients. Ongoing retrospective analyses of the California data suggest that much of the decline in biomass can be attributed to a decline in salps and dolioidids, which are composed mainly of water and have relatively low 'meat' content, and that rather than a simultaneous decline in all zooplankton species, some taxa increased while others decreased in abundance (Rebstock, 2001).

Mackas et al. (2001) examined zooplankton biomass and community structure anomalies in a 15-year (1985-1999) time series collected off southern Vancouver Island, which is located at the northern tip of the California Current ecosystem. They found that species-specific anomalies (the 'type' of zooplankton present in a given year) were much larger than the anomalies of the total annual biomass, meaning that there was more variability in the structure of the zooplankton community than in the total biomass. A dramatic shift in the dominant species occurred from 1990-1998: there were order of magnitude declines in the anomalies of 'boreal' zooplankton species, traditionally found from 40°N to the Bering Sea, while southerly species of copepods and chaetognaths, more common in collections off California, exhibited order of magnitude increases. The shift occurred on a large spatial scale (>100km), both on and seaward of the continental shelf. The trend reversed abruptly in 1999. Mackas et al. (2001) found that many of the zooplankton anomalies were correlated with both local (temperature, salinity, currents) and large scale (e.g. SOI, NOI, PDO) physical environmental indices. They concluded that the relative strength of the poleward versus equatorward longshore flow strongly affects the community structure in this area.

Zooplankton biomass and chlorophyll concentration in the eastern Bering Sea and eastern subarctic Pacific increased in the mid-1960s and remained high until the end of the 1980s.

Sugimoto and Tadokoro (1997) demonstrated a significant positive correlation between summer plankton biomass and winter wind speed in the eastern Bering Sea. They also found that the zooplankton biomass and chlorophyll concentration during the mid 1960s to early 1970s were higher than those in the preceding and following decades in the central and western subarctic Pacific. The values declined in the late 1980s.

1.5.2 Fish

1.5.2.1 Small Pelagics

Long-term variability has persisted in fish populations for centuries. Soutar and Isaacs (1974) analyzed fish scale deposition (a proxy for fish abundance) in the anaerobic sediments of the Santa Barbara Basin and found evidence of large, natural, long-term fluctuations in the abundance of pelagic fishes, including Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*). Baumgartner et al. (1992) examined these scale depositions over a much longer time period, spanning the last 1700 years, and found persistent variability in both sardine and anchovy deposition that showed peaks approximately every 60 years. Ware (1995) identified a peak in the range of 50-75 years. MacCall (1996) examined coastal pelagic fish abundances throughout the 1900s in the California Current ecosystem and found low frequency fluctuations in the dominant species that are cyclic and related to cold and warm periods that occur every 50 to 70 years. Interestingly, the sequence appears to alternate between piscivores (Pacific bonito (*Sarda chiliensis*) and Pacific mackerel (*Scomber japonicus*)), and planktivores (sardine and anchovy).

Kawasaki (1991) examined catches from three sardine populations in the Pacific Ocean, and the European pilchard in the Atlantic Ocean from 1910 to the late 1980s, and found simultaneous changes in their abundance. Kawasaki also examined herring in the Atlantic and

Pacific and showed that their abundance also fluctuated synchronously, although with a different phase than the sardines. Sardines were the focus of the largest fishery in British Columbia from the 1920s to the mid-1940s, after which they disappeared (McFarlane and Beamish, 1999). This collapse occurred simultaneously off the coast of Canada and the United States and has traditionally been touted as a prime example of overfishing (e.g. Hilborn and Walters, 1992).

The trends in abundance of sardine populations off Japan, California and Chile are synchronous - the collapse of the sardine stocks off the United States and Canada was concurrent with the collapse of the Japanese stocks (Kawasaki and Omori, 1988). This synchrony is strong evidence that the reason for the collapse had more to do with changes in ocean habitat than with fishing (McFarlane and Beamish, 1999). In the early 1980s, the sardine population off the coast of California began to recover and has been steadily increasing (Barnes et al., 1992). A recovery in British Columbia began in 1992 when sardines were reported in catches of Pacific hake (*Merluccius productus*) (McFarlane and Beamish, 1999). Furthermore, the behaviour of sardines changed. Their distribution shifted north, they moved into the Strait of Georgia, and began spawning off the west coast of Vancouver Island (McFarlane and Beamish, 1999). McFarlane and Beamish (2001) found that sardines did not respond to every identified regime shift, but the disappearance of sardines from British Columbia waters corresponded with the 1947 regime shift, and their reappearance corresponded with the 1989 regime shift. This response indicates that the links between sardine dynamics and climate are complex, and that indicators of ecosystem change, such as temperature, should be used as proxies for change, rather than direct regulators of fish distribution and abundance (McFarlane and Beamish, 2001). Favorable conditions for sardines are created by changes in the aggregate of factors that characterize the ecosystem, the specifics of which remain a mystery (McFarlane and Beamish, 2001).

Zebdi and Collie (1995) found a relationship between Pacific herring (*Clupea pallasii*) recruitment in Sitka Sound from 1972-1990 and sea surface temperature. Based on the mismatch hypothesis of Cushing (1975), they concluded that warmer temperatures lead to earlier spawning, and that herring survival improved because early hatched larvae found conditions (plankton blooms) favorable to their survival. It is also possible that the increase that occurred in zooplankton biomass in the Gulf of Alaska during the same period (Brodeur and Ware, 1992) improved overall feeding conditions for herring larvae. Zebdi and Collie (1995) also found that herring recruitment was synchronous within, but not between, production domains, and that the northern and southern stocks were out of phase by one year. In addition, the recruitment response to sea surface temperature differed between production domains. Sitka Sound herring responded positively to warmer temperatures while the southern stocks responded negatively.

1.5.2.2 Groundfish

McFarlane et al. (2001) studied the effects of the 1989 regime shift on the SOG and WCVI ecosystems and found that the two systems exhibited opposite responses to the change. After 1989, the feeding distribution of the offshore stock of Pacific hake (*Merluccius productus*) shifted north (McFarlane and Beamish, 1999), and resulted in a greater total abundance of hake off the WCVI (McFarlane et al., 2000). The spawning distribution also shifted north. Hake traditionally spawned offshore along the Californian coast. However, they have spawned off the WCVI since 1994 (McFarlane et al., 2000). The herring stock off the WCVI declined throughout the 1990s, presumably due to the increased predation pressure by migratory hake. In the SOG, the herring stock increased to high levels of abundance because of the elimination of herring in the hake diet, as a consequence of a decline in mean body size of the SOG hake (McFarlane et al., 2001), (hake smaller than 40cm feed primarily on euphausiids (Tanasichuk et al., 1991)).

McFarlane et al (2001) suggest that herring in the two ecosystem responded oppositely to the 1989 regime shift because of differences in ecosystem reorganization.

The study by McFarlane et al. (2001) is unusual in that it compares the response of fish in two adjacent ecosystems within the same production domain. Much of the regime research has focused on comparing the response of stocks across production domains. For example, Hollowed and Wooster (1995) examined recruitment time series between 1950 and 1989 for six Pacific herring stocks, one northern anchovy stock and 16 groundfish stocks. They found parallel recruitment patterns in several groundfish species that were related to switching between two alternating (warm and cool) ocean states. They also found that strong year classes were infrequent in the northernmost regions (transitional and downwelling domains), while strong year classes were more common in the coastal upwelling domain. Most of the stocks that exhibited strong year classes did so prior to 1977, but not after. Conversely, herring and widow rockfish in the Gulf of Alaska and off Prince Rupert had strong year classes only after 1977. This suggests that there was a shift in production that differentially affected northern and southern stocks, although McFarlane et al. (2000) and Hare and Mantua (2000) suggest that, for the most part, the response of groundfish was North Pacific-wide.

King et al. (2000) generated an index of year-class strength for sablefish (*Anoplopoma fimbria*) within British Columbia waters from 1960 through 1997. They found that year classes from 1960-1976 were weaker than average, and from 1977-1989 the year classes were stronger than average. The 1977 year class was the largest on record, and sablefish year classes have been below average since 1990 (King et al., 2000). The relative strength or weakness of the year class appears to be related to climate-ocean conditions, as above-average year class strengths occurred during periods of intense Aleutian Lows, more frequent south-westerly winds and warmer coastal sea surface temperatures off the WCVI (King et al., 2000).

In a unique step towards incorporating regime shift effects in stock assessment and management, King et al. (2001) produced a 'report card' that grades the ecosystem of sablefish on decadal-scales. The report card rates climate and ocean indices, and regional biological and environmental indices, as good or bad depending on their effects on the critical life stage of the species of interest (in this case, the larval phase of sablefish). The authors note that the indices do not always match each other, and that it is the integrated picture of climate-ocean effects on the species that is important for management. In agreement with the findings of King et al. (2000), the report card indicates that the conditions for sablefish year class were good between 1977 and 1988. The climate-ocean conditions during this productive period were characterized by persistent, strong Aleutian Lows, more frequent southwesterly winds, cooling in the central sub-arctic Pacific and warming along the coast (as indicated by positive values of the PDO), above-average abundance of subarctic and boreal copepods, relatively weak winter downwelling and strong summer upwelling along the coast of British Columbia.. The conditions did not persist into the 1990s (King et al. 2001). Armed with the report card, fisheries managers have more information on which to base their exploitation strategies, and fishing plans for the near future can therefore be adapted to protect adult spawning biomass for more productive conditions in the future.

1.5.2.3 Pacific Salmon

Pacific salmon (*Oncorhynchus spp.*) inhabit or pass through at least two large production domains in their lifecycle. For example, Alaska pink (*O. gorbuscha*) and sockeye (*O. nerka*) spend most of their life in the Central Subarctic Domain (Ware and McFarlane, 1989), but on their seaward and return migrations they pass through the Coastal Downwelling Domain (Figure 1.6). Oceanographic conditions in both areas must therefore be included in studies on the effects

of climate on these species (Hare and Francis, 1995). Fluctuations in Pacific salmon production trends as they relate to large-scale climate variability, have been studied extensively (e.g. Beamish and Bouillon, 1993; Francis and Hare, 1994; Beamish and Bouillon, 1995; Hare and Francis, 1995; Mantua et al., 1997).

Evidence that large-scale salmon production is related to climate processes in the North Pacific is presented in the form of synchronous shifts in production among several species or stocks in response to a physical regime shift (Beamish and Bouillon, 1995; Hare and Francis, 1995; Hollowed and Wooster, 1995). There are indications that salmon abundance has varied with climate for centuries (Beamish et al., 1999) and that large-scale climate impacts occur in the oceanic, not the freshwater phase of the salmon lifecycle, at least for coho (*O. kisutch*) (Bradford, 1999). Production has generally been estimated by catches or by abundance of recruits because salmon exploitation rates are high and are therefore considered to track abundance well (Beamish et al., 1999). However, use of these simple indices of production have been criticized because they can be confounded by changes in spawner abundance (Peterman et al., 1998).

Salmon production trends in Alaska are generally the out of phase from those in the Pacific Northwest (Hare and Francis, 1995). Landings for the northern North Pacific and Alaskan salmon stocks were high in the 1930s and 1940s, low from the late 1940s through to the mid-1970s, and began to increase in the mid-1970s (Beamish and Bouillon, 1993; Hare and Francis, 1995). As the Alaskan landings increased in the 1970s, several North American west coast stocks, especially the Oregon coho salmon stock, began to decline (Pearcy, 1992). Additionally, the 1989 regime shift was associated with some of the lowest catches in the history of the Canadian fishery and this decline was most evident for the southern British Columbia stocks (Beamish et al., 2000).

Two mechanisms have been proposed to explain the increased production in the northern stocks in the late 1970s. The first mechanism involves improved feeding conditions as a result of the 1977 regime shift. Beamish and Bouillon (1993) proposed that increased salmon productivity is linked with increased copepod production which occurs during periods of intense Aleutian Lows (McFarlane and Beamish, 1992). The other proposed mechanism relates to improved marine survival of migrating salmon in their last year at sea (Rogers, 1984). The improved survival is hypothesized to be a result of reduced vulnerability to predation by marine mammals because of an altered timing and route of migration that results from warming of the surface waters in the Gulf of Alaska (Hare and Francis, 1995). Supporting evidence for both hypotheses is given by Brodeur and Ware (1995).

1.5.2.4 Pollock and Other Northern Species

The Gulf of Alaska and the Bering Sea have both exhibited changes in their environment and biota in recent decades (Livingston et al., 1999; Trites et al., 1999). Brodeur et al. (1999b) surveyed catches of large medusae from the eastern Bering Sea from 1979 to 1997 and found a tenfold increase in biomass that was gradual from 1979-1989, and increased dramatically after 1990. It is unknown whether this increase was due to human intervention or environmental changes. However, the authors point out that there were concurrent changes in atmospheric and oceanographic variables in 1990, and that these changes are strong indications of a regime shift. Even though the biomass of medusae increased dramatically, no negative effects on recruitment of any fish species have been detected. However, walleye pollock (*Theragra chalcogramma*) has had only one strong year class since 1989 and summer zooplankton biomass on the south-east Bering Sea shelf declined slightly during the 1990s (Brodeur et al., 1999b). According to Wepestad et al. (2000), walleye pollock remains the single most abundant and commercially

important fish species in the eastern Bering Sea, and due to its large biomass, variations in the abundance of pollock are felt throughout the food web (Livingston, 1991).

The distribution of Bering Sea fish is affected by variations in ice cover. As mentioned previously, the extent of ice cover in the Bering Sea was smaller beginning in 1976 (Niebauer, 1988). During periods of intense Aleutian Lows and warm temperatures, northward blowing winds push the ice northward and reduce the ice cover (Wyllie-Echeverria, 1995). Pollock were not reported north of Bering Strait before 1976 (Wyllie-Echeverria, 1995), but since then, in years of light ice cover, pollock are present north of the Strait. Additionally, larval pollock were found in the Chukchi Sea, north of Bering Strait in 1988, which suggests a change in the spawning distribution, at least for a portion of the population.

Wyllie-Echeverria and Wooster (1998) proposed that the distribution of fish stocks that are sensitive to temperatures around 2°C reflect ocean conditions. They found that Arctic cod (*Boreogadus saida*) are present only within the persistent winter pool of cold (<2°C) subsurface water, while the distribution of pollock, a subarctic species, is more variable. In cold years, pollock are rarely found in the cold pool of water and are found in greater abundance along the outer continental shelf, but in warm years they are dispersed across the entire shelf. Therefore, during warm regimes, the distribution of pollock expands while the distribution of Arctic cod contracts.

Quinn and Niebauer (1995) found consistent relationships between pollock recruitment at age 2 and environmental variables on a one year lag, and suggested that age 2 pollock recruitment is related to above normal air and sea temperatures and reduced sea ice extent 6-18 months earlier. They also found that environmental effects are "felt" more strongly at the juvenile stage than at the larval or egg stage. Another factor that affects recruitment is density dependent (i.e. biological) regulation (Livingston, 1993).

The roles of environment and density dependence should not be considered separately. For example, Wepestad et al. (2000) proposed that water mass transport (advection) due to wind forcing was the important regulating factor in pollock recruitment because advection separates the juveniles and adults. During warm years, juvenile pollock are transported inshore and away from the highly cannibalistic adults, and this results in strong year classes. In cold years, transport is reduced and the distributions of juvenile and adult pollock overlap, which can result in weak year classes as a result of adult on juvenile cannibalism.

The Gulf of Alaska nekton community structure changed after the 1977 regime shift from one that was dominated by forage species such as shrimps and capelin (*Mallotus villosus*) to one dominated by piscivorous gadids and flatfish (Anderson et al., 1997; Anderson and Piatt, 1999; Trites et al., 1999; Mueter and Norcross, 2000). The observed decline in shrimp species can be attributed more to increased predation by the large piscivorous fish rather than to fishing, because the decline followed, rather than preceded, the increase in large piscivores (Mueter and Norcross, 2000). It is also possible that the shrimp populations were initially depressed by fishing and were therefore more vulnerable to predation by the increasing population of piscivores (Orensanz et al., 1998). It is interesting to note that most of the declining species were pelagic while the species on the rise tended to be benthic or demersal (cod and flatfish) (Anderson and Piatt, 1999).

1.5.3 Marine Mammals and Sea Birds

The responses of top predators to climate change are difficult to interpret due to the confounding effects of natural responses and human influences (e.g., the 1989 Exxon Valdez oil spill, commercial pinniped harvest) (Francis et al., 1998). In addition, climatic impacts may indirectly or directly affect birds and mammals, which will affect the time scale of response (York, 1995).

The piscivorous marine bird population in the Gulf of Alaska declined between the 1970s and the 1990s concurrent with a shift in diet, from one dominated by capelin to one in which capelin was essentially absent (Piatt and Anderson, 1996). Decker et al. (1995) found a change in the diets of marine birds nesting on the Pribilof Islands beginning in 1978. They also found that reproductive performance declined.

Declines in the Bering Sea and Gulf of Alaska populations of Steller sea lions, fur and harbor seals have been observed since the mid-1970s (Springer, 1992; Francis et al., 1998; Trites, 1992; Trites and Larkin, 1996; Rosen and Trites, 2000). The timing of the pinniped declines corresponds with the regime shift of 1977. Conversely, the portion of the Steller sea lion (*Eumetopias jubatus*) population breeding between southeast Alaska and Oregon has been increasing (Calkins et al., 1999).

Several hypotheses have been offered to explain the decline of the Steller sea lion in the northeast Pacific such as: a temporary population decline, delayed consequences of the pre-1972 pup harvest, short term variability in environmental conditions, and deterministic changes in the environment (Pascual and Adkinson, 1994). The latter might result from either long-term global environmental changes or from human intervention. Pascual and Adkinson (1994) tested the likelihood of each of these hypotheses and concluded that either long-term change in the environment or a catastrophic change in conditions is responsible for the sea lion decline.

Diet diversity and sea lion population size are strongly related in the Gulf of Alaska (Merrick et al., 1997). It is therefore likely that the population size declined in parallel with a decline in diet diversity after 1977. Merrick et al. examined sea lion diets from six areas in the Aleutian Islands and the Gulf of Alaska between 1990-1993 and found that in every area, the diet was dominated by either walleye pollock or Atka mackerel (*Pleurogrammus monopterygius*). The diet composition of Steller sea lions was different prior to the declining trends that began in

the early 1970s in the eastern Aleutian Islands and the early 1980s in the Gulf of Alaska (Merrick et al., 1987). In the mid-1970s, capelin were found in well over half the sea lion stomachs sampled near Kodiak Island in the Gulf of Alaska. Since then, capelin have rarely been found (Merrick et al., 1997). Between 1985 and 1986 the diet of sea lions in the Gulf of Alaska became more concentrated on walleye pollock (Merrick and Calkins, 1996), and during 1990-1993 the diet became even more focused (Merrick et al., 1997). In addition the abundance of alternate prey (sandlance and capelin) decreased concurrent with the decreasing diversity in the diet of sea lions (Merrick and Calkins, 1996).

It is troublesome that no sea lion population has shown an increasing trend when the diet consists mainly of walleye pollock or Atka mackerel (Merrick et al., 1997). It appears that at a minimum, two commonly available prey items are required. This suggests that a diverse diet is advantageous because it improves foraging efficiency, as diverse prey are easier to find, capture and handle. Merrick et al. (1997) point to work done by Fadley et al. (1994) to disregard the possibility that the need for multiple prey is due to differential energetic density (calories per gram) of the prey.

Fadley et al. (1994) found that captive California sea lions (*Zalophus californianus*) could maintain mass equally well on diets that consist entirely of herring or pollock. However, Rosen and Trites (2000) found evidence to the contrary for young Steller sea lions by testing the 'junk-food hypothesis' which states that Steller sea lion populations are declining because they are eating more pollock, which contains fewer calories than fattier fishes like herring (Alverson, 1992). Rosen and Trites found that sea lions on a pollock-only diet showed metabolic depression and lost weight, and that Steller sea lions would have to eat 35-80% more pollock than herring to maintain similar energy intakes, which is consistent with the junk food hypothesis. Rosen and

Trites did not observe an increase in food intake in response to the lower calorie diet. It appears that once physically sated, sea lions will not continue to feed.

1.6. THE 1977 AND 1989 SHIFTS SUMMARIZED

A summary of changes in large-scale atmosphere-ocean conditions in the North Pacific after the 1977 and 1989 regime shifts is presented in Table 1.1., and summary of the impacts on biological production in the Bering Sea/Gulf of Alaska and California Current regions is provided in Table 1.2. Hare and Mantua (2000) updated and assembled time series of zooplankton and fish production from the North Pacific and Bering Sea for 1965-1997. They divided the data into three periods: 1965-76, 1977-88, and 1989-1997, and compared the means between the periods. Much of the data presented by Hare and Mantua (2000) was first presented in the studies reviewed in the previous sections of this chapter, but because they updated the time series and calculated the difference between regimes, Hare and Mantua are chiefly credited Table 1.2. Where available, studies that cover the periods of interest are cited.

In comparing the environmental changes and the production indices of zooplankton, fish, and marine birds and mammals, it is evident that the 1989 regime shift was not a simple reversal of the 1977 regime shift (Tables 1.1, 1.2). Additionally, the 1977 regime shift affected the biology of northern and southern areas of the North Pacific differently. After 1977, production of most zooplankton and fish increased in the Bering Sea and Gulf of Alaska. The increase in production is most evident for the pelagic fish species and is less pronounced for demersal and benthic species. The higher organisms (marine mammals, birds) showed the opposite response. After 1977 in the California Current, the majority of pelagic, demersal, and benthic fish species exhibited declines in production, while the productivity of Steller sea lions increased.

Table 1.1 Changes in North Pacific atmosphere-ocean conditions after the 1977 and 1989 regime shifts as indicated by changes in the listed climate ocean indices.

Physical System	1977	1989	INDEX
Aleutian Low Pressure System	Intensification of low pressure system	Intense period ended	NPI (Trenberth & Hurrell 1995) ALPI (Beamish & Bouillon 1993) AFI (McFarlane et al. 2000)
North Pacific westerlies	above average meridional circulation	return to average circulation	PCI (King et al. 1998) AFI (McFarlane et al. 2000)
equatorial Pacific atmosphere-ocean state	frequent El Nino events	more intense, persistent El Nino events	SOI (Trenberth & Hurrell 1995) NOIx (Schwing et al. 2000)
eastern Pacific coastal SST	warming	warming	SOI (Trenberth & Hurrell 1995) PDO (Mantua et al. 1997) BC lighthouse data
central Pacific SST	cooling	-	PDO (Mantua et al. 1997)
eastern Pacific coastal wind stress	equatorward (upwelling)	poleward (downwelling)	Bakun upwelling index

Table 1.2. Production indices in the Bering Sea (BS), Gulf of Alaska (GOA) and California Current domains (British Columbia (BC), and areas off the west coast of North America (WCN/Am)). Arrows indicate direction of change in production from the previous regime. ⇔ indicates no change.

PRODUCTION DOMAIN	GROUP	REGION	INDEX	SPECIES	1977	1989	REFERENCE
Bering Sea/ Gulf of Alaska	PLANKTON	BS	biomass	jellyfish	↑	↑	Brodeur et al. (1999b)
		GOA	biomass	zooplankton	↑	↓	Hare & Mantua (2000)
	PELAGIC FISH	BS	biomass	zooplankton	↓	↓	Hare & Mantua (2000)
		W. Alaska	catch	coho salmon	↑	↑	Hare & Mantua (2000)
		W. Alaska	catch	sockeye salmon	↑	↑	Hare & Mantua (2000)
		C. Alaska	catch	chinook	↑	↑	Hare & Mantua (2000)
		C. Alaska	catch	coho	↑	↑	Hare & Mantua (2000)
		C. Alaska	catch	pink	↑	↑	Hare & Mantua (2000)
		C. Alaska	catch	sockeye	↑	↑	Hare & Mantua (2000)
		SE Alaska	catch	chum	↑	↑	Hare & Mantua (2000)
		SE Alaska	catch	coho	↑	↑	Hare & Mantua (2000)
		SE Alaska	catch	pink	↑	↑	Hare & Mantua (2000)
		SE Alaska	catch	sockeye	↑	↑	Hare & Mantua (2000)
		W. Alaska	catch	chinook salmon	↑	↓	Hare & Mantua (2000)
		W. Alaska	catch	chum salmon	↑	↓	Hare & Mantua (2000)
		W. Alaska	catch	pink salmon	↑	↓	Hare & Mantua (2000)
		C. Alaska	catch	chum	↑	↓	Hare & Mantua (2000)
		BS	recruitment	walleye pollock	↑	↓	Hare & Mantua (2000)
		GOA	recruitment	walleye pollock	↑	↓	Hare & Mantua (2000)
		BS	recruitment	herring	↑	↓	Hare & Mantua (2000)
		SE Alaska	catch	chinook	↓	↓	Hare & Mantua (2000)
	DEMERSAL FISH	GOA	recruitment	shortspine thornyhead	↑	↓	Hare & Mantua (2000)
		GOA	recruitment	Pacific Ocean Perch	↑	↓	Hare & Mantua (2000)
		BS	recruitment	Pacific Ocean Perch	↓	↑	Hare & Mantua (2000)
		BS	recruitment	Pacific cod	--	↓	Hare & Mantua (2000)
		GOA	recruitment	Pacific cod	--	↓	Hare & Mantua (2000)
		GOA	recruitment	sablefish	--	↓	Hare & Mantua (2000)

Table 1.2 (cont)

PRODUCTION DOMAIN	GROUP	REGION	INDEX	SPECIES	1977	1989	REFERENCE
Bering Sea/ Gulf of Alaska	BENTHIC FISH	GOA	recruitment	arrowtooth flounder	↑	↑	Hare & Mantua (2000)
		BS	recruitment	arrowtooth flounder	↑	⇔	Hare & Mantua (2000)
		GOA	recruitment	halibut	↑	--	Hare & Mantua (2000)
		BS	recruitment	yellowfin sole	↓	↑	Hare & Mantua (2000)
		BS	recruitment	Greenland turbot	↓	↓	Hare & Mantua (2000)
		BS	recruitment	Alaska plaice	↓	↓	Hare & Mantua (2000)
		BS	recruitment	rock sole	--	↓	Hare & Mantua (2000)
		BS	recruitment	flathead sole	--	↓	Hare & Mantua (2000)
		GOA	abundance	marine birds	↓	--	Piatt & Anderson (1995)
		GOA/BS	abundance	Steller sea lion	↓	--	Trites & Larkin (1996)
California Current	HIGHER ORGS.	GOA/BS	abundance	fur seal	↓	--	Trites (1992)
		GOA/BS	abundance	harbor seal	↓	--	Springer (1992)
		BC	biomass	southerly copepods	--	↑	Mackas et al. (2001)
		BC	biomass	euphausiids	--	↑	Mackas et al. (2001)
		E. Pacific	biomass	zooplankton	--	↓	Hare & Mantua (2000)
		BC	biomass	boreal copepods	--	↓	Mackas et al. (2001)
		California	biomass	zooplankton	↓	↓	Hare & Mantua (2000)
		California	abundance	Pacific sardine	↑	↑	Barnes et al. (1992)
		WCNAM.	recruitment	mackerel	↑	↓	Hare & Mantua (2000)
		WCNAM.	recruitment	Pacific hake	↑	↓	Hare & Mantua (2000)
California Current	PELAGIC FISH	BC	catch	chum salmon	↑	↓	Beamish et al. (2000)
		Wash.	catch	chum salmon	↑	↓	Hare & Mantua (2000)
		BC	catch	pink salmon	↑	↓	Beamish et al. (2000)
		BC	catch	sockeye salmon	↑	↓	Beamish et al. (2000)
		BC	recruitment	Pacific hake (SOG ¹)	⇔	↑	McFarlane et al. (2000)
		BC	catch	Pacific sardine	⇔	↑	McFarlane & Beamish (1999)
		BC	abundance	Pacific herring (SOG)	↓	↑	McFarlane et al. (2001)
		BC	abundance	Pacific herring (WCVI ²)	↓	↓	McFarlane et al. (2001)
		WCNAM.	recruitment	anchovy	↓	↓	Hare & Mantua (2000)

Table 1.2 (cont)

PRODUCTION DOMAIN	GROUP	REGION	INDEX	SPECIES	1977	1989	REFERENCE
California Current	PELAGIC FISH	BC	catch	chinook salmon	→	→	Beamish et al. (2000)
		BC	catch	coho salmon	→	→	Beamish et al. (2000)
		Wash.	catch	chinook salmon	→	→	Hare & Mantua (2000)
		Wash.	catch	coho salmon	→	→	Hare & Mantua (2000)
		Wash.	catch	pink salmon	→	→	Hare & Mantua (2000)
		Wash.	catch	sockeye salmon	→	→	Hare & Mantua (2000)
		Oregon	catch	chinook salmon	→	→	Hare & Mantua (2000)
		Oregon	catch	coho salmon	→	→	Hare & Mantua (2000)
		California	catch	chinook salmon	→	→	Hare & Mantua (2000)
		California	catch	coho salmon	→	→	Hare & Mantua (2000)
		WCNAM.	recruitment	Pacific Ocean Perch	↑	↑	Hare & Mantua (2000)
		BC	recruitment	sablefish	↑	→	King et al. (2000)
		WCNAM.	recruitment	widow rockfish	↑	→	Hare & Mantua (2000)
		WCNAM.	recruitment	sablefish	↔	→	Hare & Mantua (2000)
		WCNAM.	recruitment	chilipepper	→	→	Hare & Mantua (2000)
	DEMERSAL FISH	WCNAM.	recruitment	bocaccio	→	→	Hare & Mantua (2000)
		WCNAM.	recruitment	canary rockfish	→	→	Hare & Mantua (2000)
		WCNAM.	recruitment	yellowtail rockfish	→	→	Hare & Mantua (2000)
		WCNAM.	recruitment	Pacific cod	↔	→	McFarlane et al. (2000)
		BC	recruitment	Dover sole	↑	→	McFarlane et al. (2000)
		BC	recruitment	English sole	↑	→	McFarlane et al. (2000)
		BC	recruitment	rock sole	↑	→	McFarlane et al. (2000)
		WCNAM.	recruitment	dover sole	↑	→	Hare & Mantua (2000)
		WCNAM.	abundance	Steller sea lion	↑	→	Calkins et al. (1999)
		WCNAM.	abundance		↑	→	
		WCNAM.	abundance		↑	→	
		WCNAM.	abundance		↑	→	
		WCNAM.	abundance		↑	→	
		WCNAM.	abundance		↑	→	
		WCNAM.	abundance		↑	→	
	BENTHIC FISH	BC	recruitment	Dover sole	↑	→	McFarlane et al. (2000)
		BC	recruitment	English sole	↑	→	McFarlane et al. (2000)
		BC	recruitment	rock sole	↑	→	McFarlane et al. (2000)
	HIGHER ORGS	WCNAM.	recruitment	dover sole	↑	→	Hare & Mantua (2000)
		WCNAM.	abundance	Steller sea lion	↑	→	Calkins et al. (1999)
		WCNAM.	abundance		↑	→	

1 = Strait of Georgia

2 = west coast of Vancouver Island

When fish production is examined by regime, several interesting patterns emerge. The 1977 regime shift was characterized by near balance in the number of stocks in which production increased and decreased, while the 1989 shift was characterized by widespread decline (Hare and Mantua, 2000). In the Bering Sea/Northeast Pacific, 58% of fish stocks exhibited increases in production after 1977, and only 36% increased after 1989. The nearly balanced response of fish production to the 1977 regime shift is also evident when the stocks are grouped and examined by habitat. After 1977, the production of 60% of pelagic species and 55% of demersal and benthic species increased. However, after 1989, production increased for 36% of the pelagic species and for only 17% of the demersal and benthic species. The overall decline in production can be chiefly attributed to the deep water fishes.

In addition to different responses between regimes, there are indications that the regime shifts differentially affected fish production in the northern and southern ecosystems. Increases in production were observed for 69% of the fish stocks in the Gulf of Alaska/Bering Sea and 45% of the California Current stocks after the 1977 shift. After 1989, production increased in 40% of the Gulf of Alaska/Bering Sea stocks and 15% of the California Current stocks.

The different responses of the north and south production domains occurred mainly in the pelagic species. The production of essentially all (94%) pelagic species in the Gulf of Alaska/Bering Sea increased after 1977, while increases in production were observed for only 32% in the California Current. The response of demersal and benthic species was similar across domains – productivity improved by 56% and 54% in the Gulf of Alaska/Bering Sea and California Current, respectively. The response of pelagic species to the 1989 shift was generally positive in the northern area, although to a lesser extent than the previous shift (59%), and production improved for only 18% of pelagic species in the California Current. The latter

proportion is small, but the species involved (hake, herring, sardine) are key species in the region.

1.7 SYNTHESIS

Environmental variability occurs across many spatial and temporal scales (Francis et al., 1998). The research reviewed focused on decadal or longer-term variability in both physical and biological time series. The intent of this review was to provide a synthesis of the current knowledge on the timing of the regime shifts that occurred in the North Pacific in the 20th century, and to characterize the nature of the biological responses from primary producers through to the top predators in the food chain.

The regime shift literature provides evidence that large-scale changes in atmosphere-ocean conditions should not be considered random variations. Instead, they should be thought of as long term, stable conditions that can abruptly change state, such as occurred over the North Pacific in 1925, 1947, 1977, 1989, and possibly 1998 (Mantua et al., 1997; Minobe, 1997; Beamish et al., 1999; Overland et al., 1999; McFarlane et al., 2000). Changes in atmosphere-ocean conditions occur on a global scale, and evidence of this is found in the close correspondence observed in the trends in many climate-ocean indices (Beamish et al., 1999).

Changes in atmospheric pressure result in altered wind patterns that affect oceanic circulation and physical properties such as salinity and depth of the halo- and thermoclines. Phytoplankton productivity is directly affected by these oceanographic conditions, as shown by the near doubling of the chlorophyll *a* biomass in the central North Pacific around the time of the 1977 regime shift (Venrick et al., 1987; Venrick, 1994). This doubling was due to a deepening of the mixed layer that resulted from the intensification of the Aleutian Low in 1977 (Polovina et al., 1995).

There are two interdecadal climatic oscillations operating at periods of 50-70 years and 15-25 years (Minobe, 1997; Hare and Mantua, 2000). Hare and Mantua found that the 1977 shift was evident in all biological and physical time series while the 1989 shift was most evident in the biological time series. As a result, they classified the 1977 shift as a major shift and the 1989 as a minor shift. By way of explanation, Hare and Mantua (2000) proposed that the 1977 shift was stronger than 1989 because in 1977 both the 50-70 year oscillation and the 15-25 year oscillation changed, while only the 15-25 year oscillation changed in 1989.

Regime shifts can have opposite effects on species living in different domains, or can affect different species living within a single domain in opposite ways. For example, the macrozooplankton biomass in the central North Pacific more than doubled between the 1950s and the 1980s (Brodeur and Ware, 1992), while off the coast of California the macrozooplankton biomass declined by more than 80% (Roemmich and McGowan, 1995). Another example is how the trends of salmon populations in the California Current and Gulf of Alaska regions have gone in opposite directions (Francis et al., 1998). Even within the same production domain, groups of species, such as hake and herring in the SOG and off the WCVI, can respond differently (McFarlane et al., 2001). The opposite response of populations in different regions is also observed for the top predators in the system. For example, Steller sea lion populations have been declining since the mid-1970s in the Bering Sea and Gulf of Alaska (Springer, 1992; Francis et al., 1998; Trites and Larkin, 1996), while populations off south-eastern Alaska to Oregon have been increasing (Calkins et al., 1999).

The effects of climatic forcing on fish are not necessarily easy to predict. Climate can indirectly affect fish populations through changes in predator distribution and abundance. Examples of indirect effects on fishes include the hake-herring interaction in B.C. (McFarlane et al., 2001), and the overlap of adult and juvenile walleye pollock distributions in the Bering Sea

(Bailey, 2000). Climate is also more likely to affect sea birds and mammals in the North Pacific and Bering Sea through indirect means. There are indications that the Steller sea lion decline since the mid-1970s in the Gulf of Alaska and the Aleutian Islands is the result of a change in the relative abundance of different types of prey that are available. This change, from a diet dominated by herring and other fatty fishes to one dominated by gadids, may have adversely affected the health of Steller sea lions (Rosen and Trites, 2000).

The summary presented in Table 1.1 is limited in that it masks important changes in distribution and subsequent predator-prey interactions. For example, the distribution of certain key species in the California Current (hake, sardine) changed in response to the 1989 shift, and the change impacted commercially important herring stocks. This effect is lost when expressed in simple table form. The large scale response to climate change is important, but fisheries are not managed on a large scale. Localized responses are perhaps most important because they must be incorporated in stock assessment.

Fisheries stock assessment has traditionally focused on imposing controls and limits on the effects of fishing in order to maintain fish populations at fixed, viable levels. In addition, the yields from these populations are considered to be indefinitely sustainable. The key inputs required for traditional stock assessment models are the stock-recruitment relationship and the virgin unfished biomass, both of which are assumed to be constant. However, a considerable body of scientific literature indicates that the productivity of fish stocks varies naturally in association with climate, and that the effects of fishing are superimposed on this natural regulation. A new approach to managing the world's fisheries, one that incorporates climatic as well as fishing effects, is required.

CHAPTER II

Pacific hake (*Merluccius productus*) Ecology

2.1 INTRODUCTION

Hake are present in all of the major coastal upwelling regions of the world, and appear to be upwelling zone specialists. This is reflected in their diet: juveniles prefer large copepods and euphausiids while the adults are ambush predators, preying on the fast moving pelagic fishes that inhabit upwelling zones (Pitcher and Alheit, 1995). There are twelve recognized 'true hake' species within the genus *Merluccius* (translated as 'sea pike'), and the genus is presently one of the most heavily exploited fish groups worldwide. However, in spite of consistently high exploitation rates, all hakes are extremely resistant to fishing pressure (Pitcher and Alheit, 1995). This chapter focuses on *Merluccius productus*, the Pacific hake, which is the most abundant commercial fish species off the west coast of North America. The biology and life history of Pacific hake have been studied in great detail, and the available literature is summarized below.

2.2 PACIFIC HAKE POPULATION STRUCTURE AND HABITAT

2.2.1 The Habitat of Pacific hake: The Coastal Upwelling Domain

The Coastal Upwelling Domain (CUD), also referred to as the California Current ecosystem, is an upwelling system that extends from Baja, California to the northern tip of Vancouver Island. The large-scale oceanic circulation in this region is dominated year round by the equatorward California Current and the poleward California Undercurrent. The California Current is a slow, shallow flow that is subarctic (low salinity and temperature) in nature, while

the Undercurrent is a more intense northward flow of high salinity, high temperature water that is located below the pycnocline, seaward of the continental shelf (Bailey et al., 1982).

There is considerable seasonal variability in current speed and direction in the CUD. In the winter, there is a prevailing poleward flow along the continental shelf and wind-induced onshore transport (downwelling) (Hickey, 1998). During this period, north of 35°N, the equatorward California Current is displaced offshore by the poleward Davidson Current, which has been proposed to be the surfacing of the California Undercurrent (McLain and Thomas, 1983), however, the Davidson Current is often stronger and broader than the poleward flow in other seasons (Hickey, 1998). The appearance of the Davidson Current coincides with a gradual reversal of the prevailing coastal winds from the northeast to the southwest, which occurs during the fall transition (Thomson, 1981). In late March - early April, the flow abruptly reverses and the currents and water properties change over a period of several days (Hickey, 1998). This rapid change is known as the spring transition (Thomson, 1981). The reversal of the flow begins off California and propagates north to Vancouver Island. The prevailing northwesterly winds blow the surface water equatorward and cause upwelling of intermediate-depth water onto the continental shelf along the entire west coast to approximately 50.5°N (McLain and Thomas, 1983). The flow in both the California Current and California Undercurrent is strongest in late summer-early fall (Hickey, 1998).

2.2.2 Distribution

Several stocks of Pacific hake exist in the eastern north Pacific Ocean. There are resident stocks located in the coastal inlets of B.C., Puget Sound, the Strait of Georgia, and offshore near Baja California. There is also a migratory stock that moves along the west coast of North America (Bailey et al., 1982). On the west coast of Vancouver Island (WCVI), there are two

stocks of hake – residents and migrants (Beamish and McFarlane, 1985). The migrant, offshore stock moves north to the WCVI from California in the summer, while the resident stocks stay year round. The biomass of the resident stocks is smaller than the biomass of the migratory stock. All of the hake stocks in the eastern North Pacific appear to be discrete populations. McFarlane and Beamish (1985) found that hake in the Strait of Georgia constitute a population distinct from the migratory offshore stock in that they are smaller, their otoliths are distinctive in shape and size, and they are free of a parasite found only in the offshore stock. Previous evidence was found by Utter (1971), who determined that the Strait of Georgia and the Puget Sound stocks are genetically distinct from each other and the offshore, migrant population. Unless otherwise indicated, all references to hake from this point on will apply to the offshore, migrant hake stock.

Pacific hake is a highly migratory species whose range extends north from California to Alaska (Hart, 1973). The majority of its biomass is found within the coastal California Current region (Bailey et al., 1982). Hake migratory behavior appears to be closely linked to the oceanic seasons in the CUD, as its latitudinal distribution varies seasonally (Figure 2.1).

The traditional spawning grounds are not well defined because spawning schools have not been observed (Bailey et al., 1982; Smith, 1995). However, the location has been loosely described as being within 300km of the coast of California or northern Mexico, at depths between 100 and 500m (Bailey et al., 1982). Ninety-five percent of spawning takes place between mid-December and early March of each year (Smith, 1995). Young hake (<2 yr old) are found shoreward of where they were spawned (Bailey and Francis, 1985; Beamish and McFarlane, 1985). In the spring of each year (March and April), as their size increases, hake begin a northward feeding migration. The extent of this migration is related to age in that the oldest fish are found the farthest north, (Beamish and McFarlane, 1985), but the northern limit is actually determined by length (Francis, 1983), because swimming speed, and therefore distance

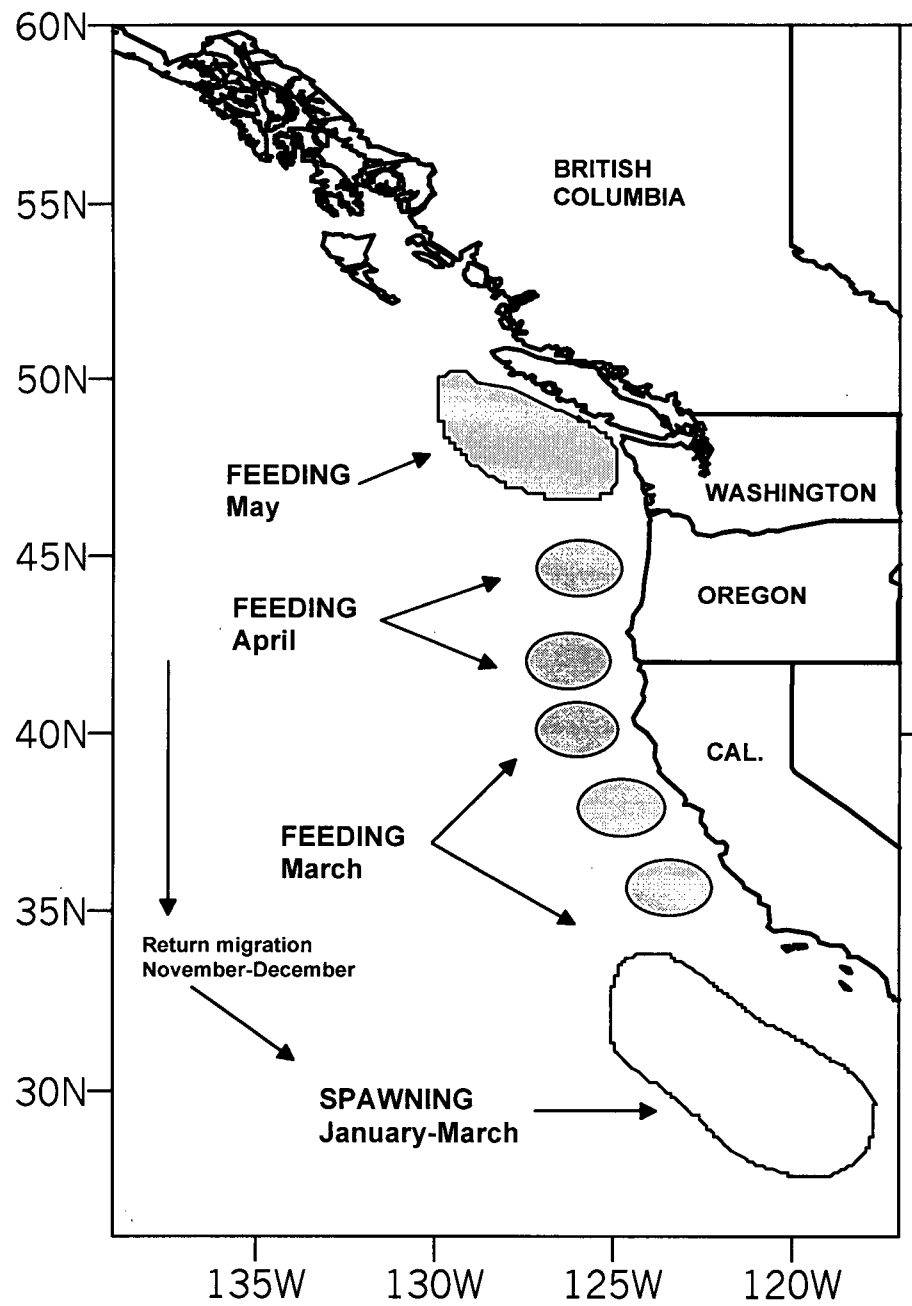


Figure 2.1. Migration patterns of Pacific hake modified from Bailey et al. (1982)

traveled, is related to body size. The northern limit of this migration is not well defined, but it has traditionally been near the northern tip of Vancouver Island (McFarlane et al., 2000). In late autumn (November and December), following the fall transition to winter ocean conditions, hake begin a return spawning migration south to California (Smith et al., 1990). The relative north-south differences in the biological and physical influences on survival and growth can explain the migratory behavior (Horne and Smith, 1997). The adaptive value of the northward migration by adults to the richer feeding grounds north of California would appear to be rapid growth, while the oceanographic conditions in the southern area foster fast growth of eggs and larvae.

In warm years there is a tendency for more small hake to be present off the southern WCVI (Smith et al., 1990). In an attempt to explain the marked interannual variability in the average lengths-at-age observed in this area, Smith et al. (1990) examined the effects of oceanographic variability on the average size of hake in Canadian research samples. They found that in years of stronger than average northward flow, which is related to higher than average sea level height (much higher during El Niño events), northward migration is facilitated. The end result is that, in El Niño years, there are more, smaller fish of any year class present off WCVI.

The seasonal, north-south distribution pattern of hake remained fairly constant from the 1960s to the late 1980s (Francis, 1983) - only the northern and southern extent of the distribution varied between years. This pattern changed in the early 1990s, when the biomass of hake off the WCVI increased dramatically from an average of 210 000 tons (25 to 30% of the stock) to >400 000 tons, or 40% of the total stock (McFarlane et al., 2000). Hake moved progressively farther north throughout the 1990s, so that by 1998 hake were found in Dixon Entrance (Figure 2a). Additionally, a portion of the stock remained in Canadian waters year round. This dramatic shift in distribution and abundance has obvious consequences for both the U.S. and Canadian hake fisheries, and can also be expected to affect the abundance of their preferred prey species. In fact,

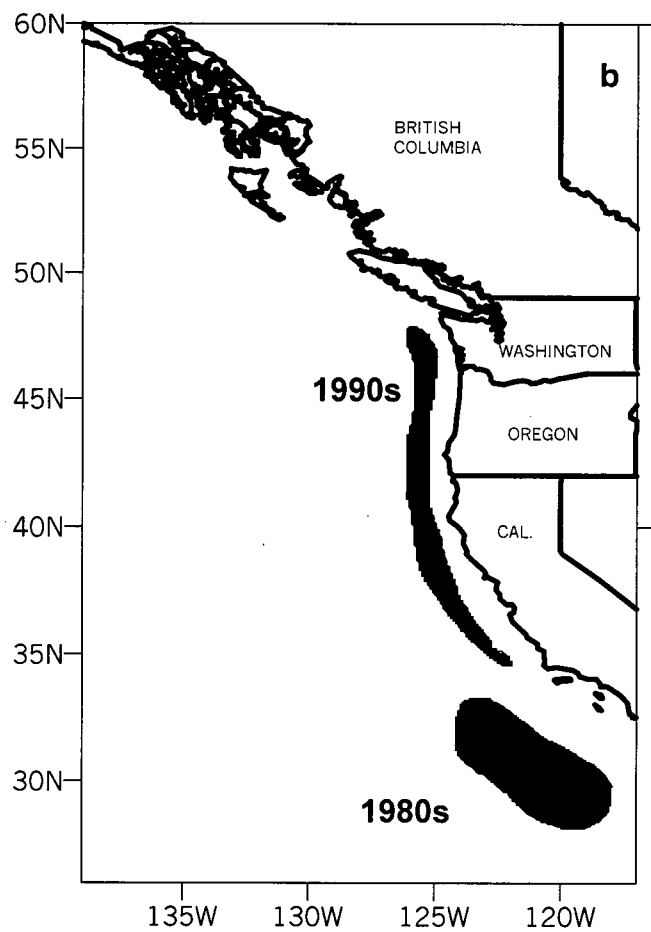
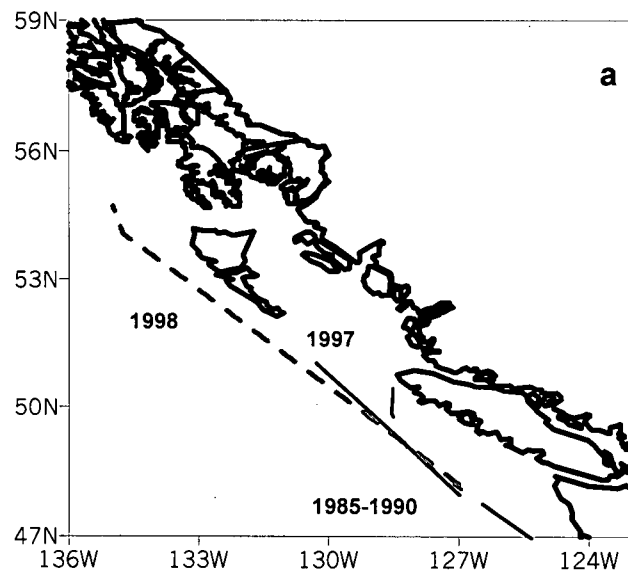


Figure 2.2. Illustration of the change in the distribution and spawning location of Pacific hake in the 1990s, redrawn from McFarlane et al. (2000) a) Northward extension of migration in the 1990s b) Change in spawning location in the 1990s.

McFarlane et al. (2000) pointed to the high abundance of hake off the WCVI as the primary cause of low herring (*Clupea harengus*) abundance in the area throughout the 1990s.

In addition to the changes described above, the spawning location of the migratory hake stock changed in the 1990s. Hake traditionally spawned off the coast of California, however, in the 1990s, they spawned closer to shore and north along the coast (Figure 2.2b). In 1994 hake spawned off the WCVI (Saunders and McFarlane, 1996). One possible result of this change in the location of spawning might be a different recruitment pattern than that observed during the 1980s, because larvae and juveniles produced in northern areas will be exposed to different oceanographic conditions than those produced off California. Perhaps more importantly, during the 1990s, the juvenile hake nursery grounds overlapped with the adult feeding grounds.

2.3 THE DIET OF PACIFIC HAKE

All *Merluccius* species are opportunistic feeders - this is reflected in the daily, seasonal, and regional variability in their diet (Ware, 1992). The dominant prey item in the diet of Pacific hake varies geographically. Early studies (Gotshall, 1969; Outram and Haegele, 1972) of the diet of the coastal stock found that the most common prey items in the waters off California to Washington were euphausiids and Pandalid shrimp (Livingston and Bailey, 1985), while off WCVI, Pacific sandlance (*Ammodytes hexapterus*) and euphausiids were the most common. Euphausiids are the single most important food item for hake throughout their entire range from California to B.C. (Livingston and Bailey, 1985) Not only do hake feed on euphausiids, but they feed on the planktivores that are attracted to aggregations of euphausiids. Buckley and Livingston (1997) examined stomach samples taken from 1989 through 1995 and found that in terms of weight, hake diets were dominated by fishes, but euphausiids were consistently present. Additionally, the importance of euphausiids in the diet decreased north and south of Cape Blanco

(43°N). In the south, anchovy were the most important fish by weight, while to the north herring became increasingly important.

The diet of Pacific hake also varies with size. As mentioned previously, the average size of hake generally increases with latitude because of seasonal and size dependent migrations (Francis, 1983). Therefore, regional differences in the diet may be confounded by the size of hake sampled (Livingston and Bailey, 1985). Off WCVI, only hake larger than 45cm are piscivorous (Outram and Haegele, 1972). Additional evidence was found by Tanasichuk et al. (1991) who showed that the occurrence of herring in hake stomachs increased with the size of the fish. Buckley and Livingston (1997) also found that the relative importance of fishes increased (and euphausiids decreased) with increasing length of hake north and south of Cape Blanco.

The proportion of the euphausiids *Thysanoessa spinifera* and *Euphausia pacifica* in the diet of hake on La Perouse Bank (WCVI) decreases over the summer feeding period while the proportion of herring in the diet increases (Tanasichuk et al., 1991). Hake feeding concentrations are usually located on the continental shelf in early summer and move offshore in the fall. The movement of hake between the shelf and shelf break areas appears to be governed by changes in euphausiid biomass. The feeding conditions on the shelf are superior to those offshore in early summer, while in the late summer, the offshore area becomes more important because the biomass of euphausiids on the shelf is depleted by this time, possibly due to hake predation (Tanasichuk et al., 1991). It should be noted that these results do not agree with those of Mullin and Conversi (1989), who found no change in euphausiid biomass after the initiation of a hake fishery (and a presumed decrease in hake predation). The disparity might be attributed to the difference in scale. Mullin and Conversi (1989) examined euphausiid biomass on a large scale (northern and southern CalCOFI surveys), while the Tanasichuk et al. (1991) study was of a much smaller region on La Perouse Bank.

Evidence of a strong spatiotemporal relationship between euphausiids and hake was presented by Ware and McFarlane (1995), who observed that independently mapped distributions of hake and euphausiids off British Columbia overlapped, and were located in regions of steep bathymetry along the shelf break that coincide with upwelling (Mackas et al., 1997). Euphausiids aggregate in and beneath upwelling water because it allows them to maintain their position relative to the high food densities in the overlying surface layer. It is therefore possible that hake also position themselves near upwelling regions because the food concentration is likely to be high in these areas. There is a relationship between upwelling and the availability of euphausiids to predation: in strong upwelling years off the west coast of Washington and Oregon, euphausiids are the predominant food item in the diets of key predator species, Pacific hake included (Brodeur and Pearcy, 1992). In years of weak upwelling, however, the diets of all predators were more varied. It is possible that dense swarms of euphausiids are located near the surface during years of high productivity (strong upwelling) and are therefore more available to predation (Brodeur and Pearcy, 1992).

The importance of euphausiids in hake diets is a global phenomenon. Euphausiids are also the primary food of Namibian hakes (*M. paradoxus* and *M. capensis*) in the Benguela upwelling system (Gordoa et al., 1995) and of the Cape hakes (*M. paradoxus* and *M. capensis*) off the coast of South Africa (Pillar and Barange, 1997). On the Scotian shelf, for example, the abundance of silver hake (*M. bilinearis*) is correlated with the abundance of the euphausiid *Meganyctiphanes norvegica* (Cochrane et al., 2000). The strong correlation between hake and euphausiid abundances on the Scotian Shelf indicates that euphausiids exert an extensive ecological influence in the surrounding waters (Cochrane et al., 2000). This implies that euphausiids are the key to understanding why hake are located in certain areas.

Hake is an important predator in the La Perouse Bank region because of its large biomass. Ware and McFarlane (1995) studied the impact of hake predation on its secondary prey, Pacific herring, and found that the amount of herring in the diet increased over the summer, and additionally that the fraction of herring in the hake diet is a dome-shaped function of sea surface temperature (SST). The authors explained the relationship in terms of the availability of euphausiids. Over the summer, euphausiid productivity and biomass decreases in the area due to the negative influence of increasing temperature on euphausiid productivity and because of stock depletion due to hake predation (however, it should be noted that other studies suggest that WCVI euphausiid biomass is highest in late summer (S.E. Allen, pers. comm.)). As a result, late-summer predation by hake on herring increases, and well over half of the annual herring mortality occurs in the late summer. In addition to the over-the-summer trend, there are large variations in summer herring mortality from year to year, and these variations are related to interannual variations in SST (Ware and McFarlane, 1989). Modeling studies suggest that in warm years the increased hake biomass quickly depletes the euphausiid biomass on the shelf and results in increased predation on herring (Ware and McFarlane, 1995). A negative relationship between temperature and herring survival is supported by the fact that since the warming of the waters in the region with the 1977 regime shift, herring recruitment has been below average off the west coast of Vancouver Island (McFarlane et al., 2000).

2.4 RECRUITMENT

2.4.1 Factors Affecting Recruitment of Marine Fishes

The central problem in traditional fisheries stock assessment is defining the relationship between the parental stock size and subsequent recruitment (Hilborn and Walters, 1992). The

controls on recruitment are not well understood for many fishes, hake included. In addition to the mechanisms limiting recruitment, there is also uncertainty regarding the developmental stage at which the number of recruits is determined. Some believe that year class strength is determined at the larval stage (Hjort, 1914), while others maintain it is the juvenile life stage that is important (Peterman et al., 1988). The difficulty in defining what factors limit recruitment has led many biologists to assume that recruitment is independent of stock size, and is instead limited by some environmental condition. The assumption of density independence can be flawed, because it is possible for recruitment to decrease as parental stock size increases (and vice versa) (Ricker, 1954), and Hilborn and Walters (1992) note that even if there are no records to indicate that spawning biomass affects recruitment *over the range of observed stock sizes*, there is always a stock size below which recruitment will decline. It is therefore important to understand the relationship, at least well enough to know how much the stock size can decrease (as the result of fishing or of natural changes in abundance, see Chapter 1), before recruitment begins to decline.

Starvation during the early life stages was considered a limiting factor in recruitment for most of the 20th century. This hypothesis is based on the assumption that recruitment is regulated during the larval stage. The “critical period” hypothesis of Hjort (1914) links larval survival to food availability during the transition from yolk-sac to free feeding larvae. If food is abundant during this time, recruitment will be high. Leggett and DeBlois (1994) reviewed the available literature on food abundance and larval starvation during this life history stage, and found little evidence of a causal link between food availability at first feeding, larval survival, and subsequent recruitment. Cushing (1972) broadened the “critical period” hypothesis by removing the critical period constraint and including food availability over the entire larval period as a major regulator of larval survival. This hypothesis is called the “match-mismatch” hypothesis, the evidence for which is only marginally more compelling than that for the “critical period”

hypothesis (Leggett and DeBlois, 1994). Although food availability is of course related to larval survival, there are indications that other factors, such as feeding success (which may be more important to larval survival than prey abundance (Leggett and DeBlois, 1994)), are also important factors in the recruitment of marine fishes.

Similar to starvation, predation on the egg and larval stages of marine fish was considered as a limiting factor of recruitment of marine fishes for most of the 20th century. A review of the literature can be found in Bailey and Houde (1989). Compared to starvation, relatively few studies have attempted to quantify mortality due to predation. This can be attributed to the inherent complexity of inter- and intra-specific interactions, and to the fact that the magnitude of predation varies with species, location, and year (Bailey and Houde, 1989). Two hypotheses have been proposed in relation to predation: the first is the “bigger is better” hypothesis which holds that larvae that are hatched at a larger size or grow faster are less susceptible to predation (Leggett and DeBlois, 1994). The second is the “stage duration” or “single process” hypothesis (Cushing, 1975), which holds that larvae that encounter optimal feeding conditions will grow quickly and reach metamorphosis faster, and will experience lower overall mortality (Leggett and DeBlois, 1994). Hard evidence for both hypotheses is limited. Nevertheless, predation on egg and larval stages is considered to be an important regulating factor in recruitment (Bailey and Houde, 1989; Leggett and DeBlois, 1994).

A third factor believed to limit recruitment in marine fishes is advection. Sinclair (1988) proposed the “member-vagrant” hypothesis, which emphasizes membership in a population and geographic location. Membership in a population is a function of being in the right place at the right time, at any stage in the life cycle. A “vagrant” does not meet these requirements and is lost from the population. In terms of recruitment, fish spawn in areas that maximize the likelihood of survival from egg to juveniles. Recruitment can be expected to be high when the currents

transport the eggs and larvae to favorable nursery areas, and low when the larvae are advected to unsuitable habitats. Supporting evidence for this hypothesis is reviewed in Sinclair (1988).

It is likely that the three key processes considered to limit recruitment act together. For example, currents might transport larvae to an area that has a high abundance of food and is virtually free of predators. In this case, it is obvious that the effects of the three processes would be difficult to tease apart. The following section reviews research on recruitment to the coastal stock of Pacific hake. The hypotheses discussed above are addressed by the research, although often not explicitly. What should become obvious is that there are many factors affecting egg and larval survival, and that the answer to the recruitment problem is not a simple one - this is a truism for all marine fishes.

2.4.2 Factors Affecting Recruitment of Pacific Hake

Similar to most other marine fish species, recruitment to the coastal stock of Pacific hake is extremely variable, exhibiting one hundred-fold variation in year class strength between years (Figure 2.3, Methot and Dorn, 1995). This extreme variability means that the stock is dominated by only a few year classes, and this is translated into large variability in the stock size.

Pacific hake is a long lived (>16 years), highly fecund species, with the stock producing billions of eggs during its annual spawning (Bailey and Francis, 1985). Hake are similar to most other gadids in that there does not appear to be a simple relationship between spawning stock biomass and recruitment (Bailey and Francis, 1985): strong year classes have occasionally been produced by low biomass spawning stocks, while weak year classes have been produced by both high and low spawning stock biomass. The stock-recruitment relationship can not be estimated (Methot and Dorn, 1995) as evidenced by poor stock-recruit model fits to the data (Dorn and Saunders, 1997). The poor fit points to either direct or indirect environmental influences as key

factors limiting recruitment (or density dependent interactions that limit recruitment). A similar result was reported by Sanchez and Gil (2000) for the European hake (*M. merluccius*). The authors found that a high degree of independence was evident in the stock-recruitment relationship, and suggested that this implied the existence of a significant relationship between recruitment and some environmental variable(s).

Bailey and Francis (1985) examined survey data from the late 1960s through to the 1980s and found a relationship between the abundance of postlarval hake (3-6 months old) and the number of recruits 3-5 years later. They concluded that the year class strength of Pacific hake is determined at the post-larval stage, and that the resulting extreme variation in recruitment is an indication that larval survival is either very good or very poor. The ability to forecast good or poor recruitment would be useful for managing the hake fishery, primarily because the fishery is focused on only a few year classes. In an attempt to forecast recruitment, Bailey et al. (1986) developed an index of the frequency of occurrence of age-0 (2 months-1 year old) hake in pelagic trawl surveys off California and compared the index to recruitment 3 years later. They found that the index provides a good qualitative assessment of the relative strength or weakness of the recruited year class. Hollowed (1992) extended this work by examining interannual variability in larval and juvenile hake abundance and found that relative year class strength of hake is determined in the late-larva early-juvenile stages. Strong year classes are indicated by high abundances of late-larvae and young-of-the-year juveniles while weak year classes are characterized by low abundances of both. Life table simulations showed that decreases in recruitment can occur at any stage of development, while increases can only originate from either decreased mortality or a shortened duration of the egg and larval stages (i.e. the stage-duration hypothesis). Basically, a small decrease in mortality for the early stages of a highly fecund species can result in huge payoffs in terms of biomass later on (Houde, 1987). The 1984 year

class was an exception (Hollowed, 1992). There were few late larvae and juvenile hake caught in the survey, but subsequent recruitment was high. Mullin et al. (2000) suggested that the reason for good recruitment in spite of a low index was that in 1984, the year class strength was determined during the juvenile life stage. A more likely explanation is that the spawning locations of hake shifted north in that year and the more northerly areas were not well surveyed for hake larvae and juveniles (Hollowed, 1992).

During spawning, hake release their eggs between 130 and 500m, after which most rise to the depth of neutral buoyancy at around 40-60m, near the base of the mixed layer (Bailey et al., 1982). The water at this depth is cold, and as a consequence, growth, metabolism and energy requirements for hake larvae are low compared to other species, such as anchovy (*Engraulis mordax*) larvae, which live higher in the water column in the same geographic area (Bailey, 1982; Bailey and Francis, 1985). Hake yolk-sac larvae are small and are heavily preyed upon by euphausiids, ctenophores, amphipods and copepods (Bailey et al., 1982). The intensity of predation declines as the larvae grow. Hake larvae have large mouths and are capable of feeding on a wide size range of food items, primarily various copepod life stages (Sumida and Moser, 1980).

Horne and Smith (1997) quantified the relative importance of the biological and physical processes influencing production, survival and growth of hake larvae and concluded that changes in larval hake abundance are primarily a function of mortality and inshore drift with the currents. Due to this fact, the authors maintain that, like virtually all marine fish species (Sinclair, 1988), the location of adult spawning is very important to larval survival.

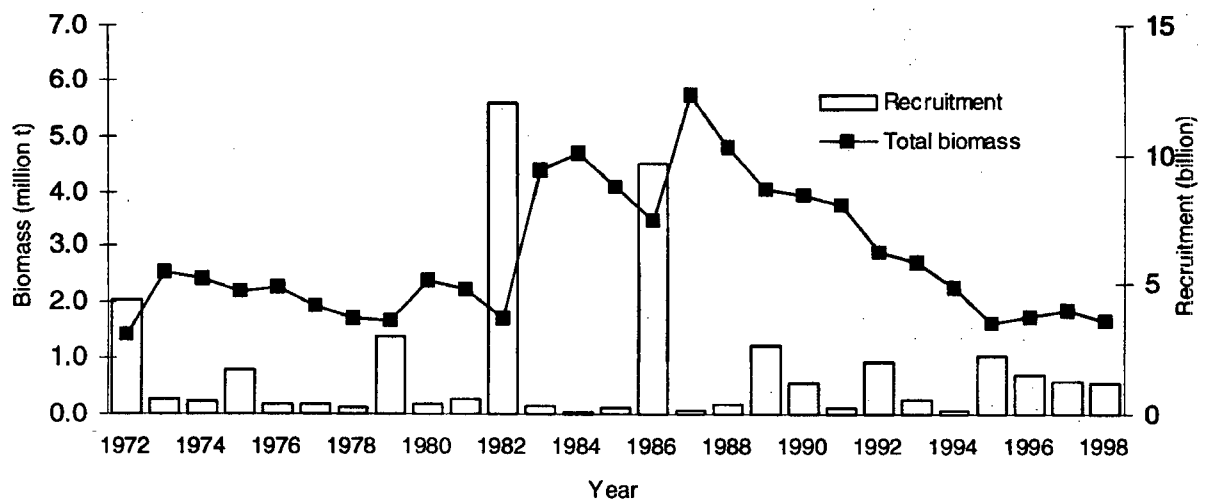


Figure 2.3. Pacific hake biomass and recruitment, 1972-1998. From Dorn et al. (1999).

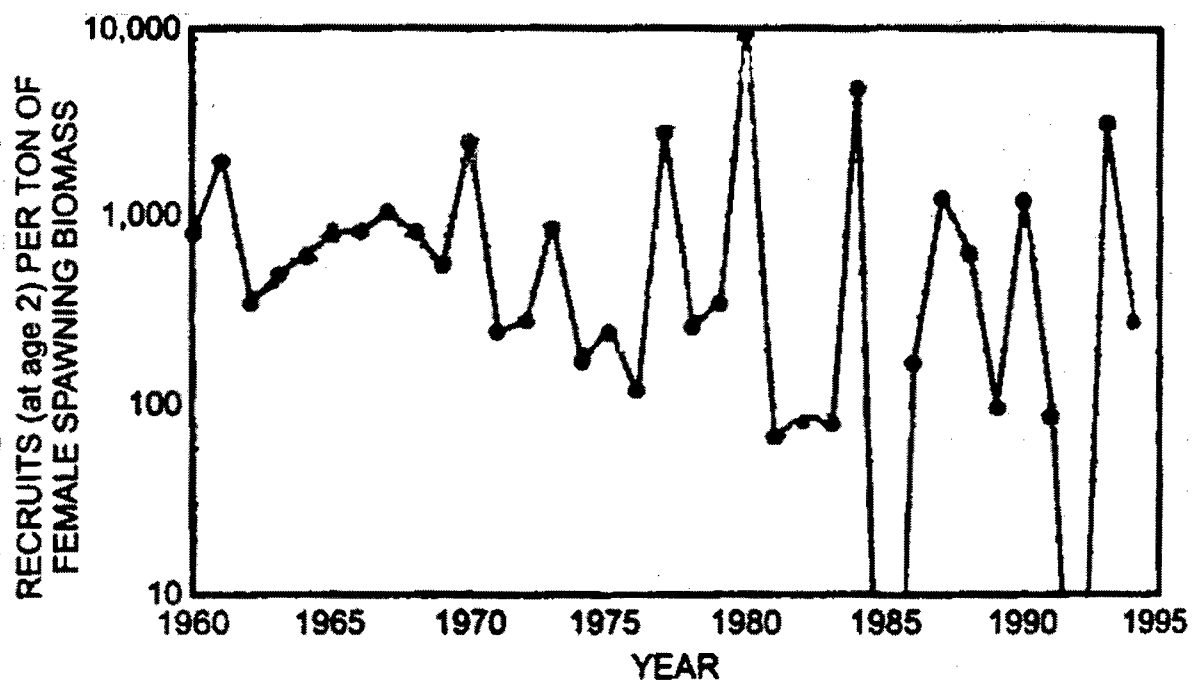


Figure 2.4. Recruitment rate of hake (number of recruits per ton of spawning biomass), from Horne and Smith (1997), showing the erratic recruitment rate of hake since the late 1970s, at the same time as the location of spawning moved north.

The location of the main hake spawning areas varies from year to year. This can be accounted for in part by demographics, because older, larger, fish spawn farther south than small ones (Mullin et al., 2000). Climate has also been shown to affect spawning location. Bailey et al. (1982) reported that the northern limit of hake spawning is correlated with sea surface temperature, and that in warm years when subtropical water extends farther north, spawning occurs at higher latitudes. Bailey and Francis (1985) compared the north-south and onshore-offshore distribution of hake larvae in a cold year (1954) and a warm year (1959) in the California Current before the commercial fishery was fully established (and therefore, before size selective fishing effects could affect the distribution). In 1959, hake larvae were found closer to shore and northward compared to 1954. The exact location of spawning is unknown, however, because spawning adults have not been sampled successfully (Bailey and Francis, 1985). The distribution of larvae is assumed to reflect the spawning location, but it is more likely that the larval distribution is the result of advection from the theorized spawning location. Nonetheless, this assumption has remained for many, if not all, of the subsequent recruitment studies (e.g. Horne and Smith, 1997). Horne and Smith (1997) examined variation in larval hake distribution (and by inference, the spawning location) by latitude from 1951 through 1984 and found that, in addition to clear interannual variation in the spawning location, there is a northward trend in the time series. The midpoint of hake spawning moved approximately 444km (240nm) poleward over 34 years. The authors examined the time series of age-2 recruitment along with the spawning location time series and found no parallel trend, but they did note that the northward movement coincided with warming in the California Current (Roemmich and McGowan, 1995). Since zooplankton biomass is higher in cold years compared to warm years, the northward shift in warm years may be a result of attempts to match spawning and subsequent larval transport with high food concentration (Horne and Smith, 1997).

In an attempt to determine what factors limit hake recruitment, Bailey (1981) studied the relationship between environmental conditions and the distribution and survival of hake larvae, and found that strong onshore Ekman transport of eggs and larvae is associated with strong year classes. The three strongest year classes of hake between 1960 and 1975 occurred in 1961, 1970, and 1973, which were also the winters with the strongest onshore transport. Bailey proposed that since the juvenile nursery area is located on the continental shelf, eggs and larvae that are advected offshore are likely to exhibit poor survival (i.e. the member-vagrant hypothesis). Bailey found support in the fact that larval growth rates in the offshore area were poor, and therefore, because predation is size-specific (i.e. the stage-duration hypothesis), larvae in the offshore area are susceptible to predation for longer periods of time. Another possibility is that the larvae swept offshore find the food supply inadequate for growth, but although larval growth and survival have been shown to be food limited in some years, it is far from clear that starvation is the dominant determinant of hake recruitment (Mullin et al., 2000). Temperature may also play an important role in determining year class strength, but it is difficult to tease out its effect from upwelling. For example, in cold years, development is slow through the stages most vulnerable to predation (Bailey et al., 1982), but because upwelling and temperature are closely related (Francis et al., 1989), it is unknown whether it is slow growth or the distance offshore that negatively affects recruitment. Bailey and Francis (1985) extended the analysis of Bailey (1981) and showed that the inverse relationship between upwelling and recruitment did not remain strong with the addition of a few years of data. They acknowledged that the previous study was limited by too few data points. This is true of virtually every attempt to link recruitment to single environmental factors (Dower et al. 2000).

In spite of the weak relationship between upwelling and recruitment, Hollowed (1992) maintained that offshore transport can negatively affect the survival of hake larvae. She pointed

to numerous studies on larvae of other species to illustrate the importance of understanding the behavior and processes that reduce offshore transport. For example, Power (1986) showed that spawning location is important in relation to offshore transport. Power simulated drift patterns for anchovy larvae and found that Ekman transport did not negatively affect larvae in the nearshore region. When spawning extended into the offshore regions (as it does in cold years for hake (Bailey and Francis, 1985), there was significant seaward transport of larvae. Hollowed (1992) proposed that diurnal vertical migration might be a mechanism that maintains the larvae in the nearshore region and reduces the influence of offshore transport, as was shown by Myers and Drinkwater (1988/1989) for fish larvae in the northwest Atlantic.

Simple correlations between recruitment and environmental indices, such as sea surface temperature, seldom hold any predictive power in the long term, but this fact does not eliminate the value of examining environmental relationships. For example, it can be said that certain conditions are required for the formation of strong year classes of hake. Cold years (strong upwelling) generally produce weak year classes - from 1960-77 this was shown to be the case 7 out of 7 times - while all strong year classes during the same period were produced in warm years (Bailey and Francis, 1985). However, not all warm years resulted in strong year classes. There is a great deal of variability in hake recruitment that follows spawning in warm years due to the multiplicative effects of the many environmental forces influencing larval survival (Bailey and Francis, 1985).

One potential limiting factor of hake recruitment that remains essentially unexamined is cannibalism. Cannibalism has been observed in all *Merluccius* species (Ware, 1992), and it is hypothesized to be an important population regulating mechanism. The overall incidence of hake cannibalism in the California Current is small relative to that observed in other upwelling systems (Ware 1992), nevertheless, it is considered to be an important source of juvenile

mortality in the southern California Current (Smith, 1995). Evidence of cannibalism in the coastal hake stock was found in the stomach contents of hake collected between California and Vancouver Island in 1989, 1991, 1992 and 1995 (Buckley and Livingston, 1997). In 1989 there were two occurrences of cannibalism in 1989, and both occurred off southern California. In 1995, cannibalism was observed throughout the entire survey area. Adult-on-juvenile cannibalism was found over a wide latitudinal range, but interestingly, cannibalism by age-1 hake on young of the year hake was much more common. The fact that successive years of strong recruitment in the coastal hake stock have never been observed is strong evidence for inter-cohort density dependent regulation (Smith, 1995). The findings of Buckley and Livingston (1997) point to cannibalism, and not competition, as the key mechanism of density dependent regulation of hake recruitment.

Similar to the other limiting factors, the influence of cannibalism on recruitment may also be related to environmental conditions. Since the distribution of the stock and the spawning location shift north in warm years, it is possible that strong year classes are produced in warm years because the spatial overlap of consecutive year classes is reduced. A similar effect has been identified in walleye pollock (*Theragra chalcogramma*) in the Bering Sea, whereby strong year classes occur in warm years when juvenile pollock are transported inshore and away from the highly cannibalistic adults (Wepestad et al., 2000). In cold years, onshore transport is reduced and the spatial distributions of juvenile and adult pollock overlap, resulting in weak year classes.

It is possible that the factors limiting hake recruitment changed with the 1989 regime shift, as the distribution of juveniles changed in the 1990s, and during that period of time, no strong year classes were produced (Figure 2.3). If spatial separation of the juveniles from the rest of the stock is related to year class success, then displacing the juveniles and larvae north can be expected to result in the different recruitment pattern. There are hints that the recruitment pattern

changed as the spawning location shifted north between 1950 and 1985, from low, steady recruitment in the 1950s and 1960s to a more erratic pattern in the late 1970s and 1980s (Figure 2.4). It is possible, therefore, that recruitment is linked to the spatial distribution of the stock, which in turn is related to environmental conditions. More research in this area is required in order to improve the understanding, and possibly the predictive power of the complex environment-recruitment relationship in the offshore stock of Pacific hake.

CHAPTER III

The Response of Pacific hake (*Merluccius productus*) to Recent Ecosystem Change

3.1 INTRODUCTION

3.1.1 Hake Migration and the Environment

The management of Pacific hake is complicated by the fact that it is a migratory stock managed by two countries. Management success has been limited because of disagreement on the division of the acceptable biological catch (ABC) between the Canadian and U.S. fisheries and because the north-south distribution of the stock varies from year to year. There are indications that the extent of the annual northward migration is linked to ocean conditions, but the mechanisms involved remain a mystery. Ware and McFarlane (1995) examined 13 years of survey data collected between 1968 and 1991 on La Perouse Bank and found that the lowest biomass of hake occurred during years of below-average water temperatures. Based on these observations, Ware and McFarlane hypothesized that the number of hake migrating into the La Perouse region increased at higher water temperatures. They found a significant correlation (r^2 n./a, $p = 0.003$) between the average June-July sea surface temperature (SST) at Amphitrite Point, a coastal station on the west coast of Vancouver Island, and the biomass of hake in the area in August. They speculated that the amount of food (euphausiids) the hake encounter when they first arrive (June) determines how many hake remain for the August survey. The average SST in June-July on La Perouse Bank was 12.2°C over the period examined, and at this temperature, 179 000t of hake migrated into the area. On average, a 1°C rise in SST resulted in an 174 000t increase in hake biomass (Ware and McFarlane, 1995).

In an attempt to quantify the transboundary distribution of the stock, Dorn (1995) utilized the stock synthesis model to explore the migratory behavior of hake. Dorn developed annual

coefficients of the parameter that describes the age-specific proportion of the stock that migrates into the Canadian zone. He found that the annual coefficients were most highly correlated with the March-April temperature anomalies at 100m depth between 30° to 42° north latitude. Dorn (1995) suggested that this result indicates that the oceanographic events that are most significant to hake migration occur earlier in the year, in the southern part of the range, at the time the hake begin their migration. The U.S. and Canadian fisheries developed during a predominantly warm oceanic period, and the migration rate into the Canadian zone is likely to change with climate-ocean conditions (Dorn, 1995; Ware and McFarlane, 1995). The Canadian hake fishery is therefore more vulnerable to the effects of climate change, because the proportion of fish in the Canadian fishing zone can be expected to increase or decrease depending on oceanic conditions.

3.1.2 Growth Studies

The average size of hake present in Canadian waters exhibits significant interannual variability, and is a complex function of individual growth rates, length selective fishing mortality, and length dependent migration, which is in turn a function of oceanographic conditions and distance from the spawning grounds (Smith et al., 1990). Additionally, the mean length-at-age of hake aggregations is affected by the sex composition, because male hake are smaller on average than female hake (Smith et al., 1992). Examining the size and sex structure of the stock can therefore provide insight into the dynamics of the population that gross examination of distributional abundance data does not.

The mean length-at-age of hake decreased between the mid to late 1970s and 1988 in both Canadian and U.S. waters (Hollowed et al., 1988; Smith et al., 1990; Dorn, 1992). Smith et al. (1990) examined the length of age 5+ hake in Canadian waters and attributed the overall decline in length-at-age to selective removal of the larger hake by the Canadian fishery. They also observed considerable interannual variability in the mean lengths-at-age, and explained it

using oceanographic factors. Smith et al. (1990) found a negative relationship between sea level anomalies and mean length-at-age and argued that stronger poleward (or weaker equatorward) currents in El Niño years assist the northward migration of small hake. Similarly, Hollowed et al. (1988) hypothesized that the decline observed in hake aged 3-10 in U.S. fishery data was the result of disruption of the normal temperature and current patterns by the 1982/83 El Niño.

Dorn (1992) proposed that the decline in the mean lengths-at-age was a density dependent growth response to increased population abundance, and tested the two hypotheses using a growth-increment regression. Dorn found that temperature had the greatest effect on growth at young ages, and that the effect of population size on growth increased with age. The differential effects of temperature and stock size on hake growth can be explained in terms of their diet (Dorn, 1992). In the California Current, low water temperature is associated with increased production that is the result of either upwelling of nutrient rich water (Bakun and Nelson, 1977), or equatorward transport of nutrient-rich water from the Alaska Gyre (Roesler and Chelton, 1987). A link therefore exists between sea surface temperatures, food and hake growth because the primary prey item is euphausiids (see Chapter 2), and euphausiid abundance is closely linked to upwelling and primary production (Simard and Mackas, 1989). The increased effect of biomass on growth of older fish might be explained by the shift in diet to include fish at the older ages, because predation on fish with multi-year life cycles can reduce their abundance (Dorn, 1992). Dorn (1992) proposed that the inverse relationship between temperature and growth can partially explain the decrease in the mean length of fish age 5+ recruiting to the Canadian fishery in the 1980s. He further suggested that because the magnitude of the decline in mean length-at-age in the U.S. fishery data was the same in all areas from California to Washington, the decline observed in Canadian waters was not entirely the result of size selective removal by the Canadian fishery.

Hake in the Strait of Georgia (SOG) exhibited changes in growth that corresponded with recent climatic events (McFarlane et al., 2001). The mean length of an age 4 hake declined by 7% between 1979 and 1981, and by 13% in the mid 1990s, and the latter decrease was evident in the average size of all age groups. Concurrent with the decline in mean size, the biomass of hake increased.

The dramatic decrease in hake size affected herring (a key prey item in the hake diet) by essentially removing a major predator because only large hake feed on herring. The mean size of age 4 hake in the offshore population was examined and no change was evident (McFarlane et al., 2001). This result is interesting, given the fact that hake in the Strait of Georgia population and the offshore population are the same species, and additionally, because the biomass of hake in the two areas increased over the same period (McFarlane et al., 2001). It is reasonable to assume that the two populations would exhibit similar responses.

3.1.3 Objectives

The objectives of this study are twofold. The first is to explore the relationship between atmosphere-ocean conditions and hake migration, and to develop a predictive index of the proportion of the stock that migrates into Canadian waters on both an interannual and decadal scale. The second objective is to determine if the dramatic shift in latitudinal distribution corresponded to changes in hake growth. Because temperature and stock size have been shown to differentially affect the growth of young and old hake, it is possible that the growth of hake at ages other than 4 was affected. The growth analysis focuses on length rather than weight because weight is closely related to length. For example, the weights used to calculate biomass in hake stock assessments are generated using a length-weight key. Weight-at-age estimates also exhibit seasonal patterns of increase and decrease that are related to spawning, feeding, and migration, while growth in length is a function of *annual* environmental conditions and is always positive

(Dorn, 1992). Perhaps the best reason to focus on the length of hake is because their migration patterns are directly related to length.

3.2 MATERIALS AND METHODS

3.2.1 Hake Data and Study Area

All data used in this study were collected on research surveys conducted by Fisheries and Oceans Canada (DFO) and the U.S. National Oceanic and Atmospheric Administration (NOAA). Surveys are conducted in the summer, when the hake distribution is at its northern limit. Canadian research data were provided by Sandy McFarlane at DFO in Nanaimo B.C., and U.S. data were provided by Martin Dorn, Chris Wilson, and Mike Guttormsen at NOAA in Seattle, WA. Details of the surveys are discussed below.

DFO has conducted annual acoustic surveys in Canadian waters off the west coast of Vancouver Island every August since 1990 (Dorn et al., 1999). Prior to the acoustic surveys, starting in 1985, DFO estimated the annual summer (July-September) biomass of hake in the La Perouse region using midwater trawl surveys from which a swept volume biomass estimate was produced (details presented in Ware and McFarlane, 1995). DFO obtained biological samples using random sampling procedure in which the hake in the catches were sorted and sampled to determine sex, length and weight. Otoliths were collected for age determination. DFO survey data were obtained for the 1985 through 1997 surveys.

To assess the distribution and abundance of hake along the west coast of North America, echo-integration-trawl (EIT) surveys have been conducted every three years since 1977 by the Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service (NMFS), Seattle. In 1992, 1995 and 1998 the coastwide survey was conducted in cooperation with DFO because of a northward shift in the distribution of the stock. Specifics on the acoustic sampling equipment can

be found in the cruise reports (e.g. Wilson and Guttormsen, 1997). The study area extends from Monterey, California (37°N) to the northern limit of the detectable aggregations of hake, usually off the coast of British Columbia. In 1992 and 1995, the northern limit of hake distribution was around 51°N, while in 1998 it was near Cape Spencer, Alaska (58°N) (Wilson et al., 2000). During the surveys, a predetermined series of east-west transects were spaced 18.5km apart along the coast, except in Canadian waters, where the transects were spaced 9.3km apart in order to correspond with the survey design used by DFO. Catches were collected using a midwater trawl set on the hake echo-sign. NOAA employed a two-phase, length-stratified procedure to obtain biological samples (Dorn, 1992). In the first phase, a large sample of fish was obtained for which length and sex of individuals are recorded. In the second phase, a subsample of fixed size was selected for each length category and sex. All these fish were aged using otoliths. Because the sampling procedures are different for the Canadian and U.S. data sets, the data can not be easily combined or analyzed using the same procedures. Acoustic and biological data were obtained for the 1977-1998 triennial surveys for this study.

The survey areas and International North Pacific Fishery Commission (INPFC) geographical areas used in the analysis of the triennial data are shown in Figure 3.1. The survey area for the Canadian research cruises is located off the west coast of Vancouver Island, from the Canadian-U.S. border to the northern limit of hake aggregations, traditionally the northern tip of Vancouver Island.

3.2.2 Environmental Data

A variety of oceanographic data were examined, but two types were used as indices of ocean conditions: sea surface temperature and upwelling. Monthly sea surface temperature (SST) data were obtained for Amphitrite Point (48°33'N), a coastal station at the mouth of Barkley

Sound, which is located adjacent to La Perouse Bank off the south west coast of Vancouver Island. The data are maintained by DFO and are available online at:

<http://www-sci.pac.dfo-mpo.gc.ca/pages/lighthousedata.htm#Amphitrite Point>.

These data were used as an index of ocean state in the northern feeding grounds of hake and are the same data used previously by Ware and McFarlane (1995).

Monthly anomalies (deviations from the long term mean) of the Bakun upwelling index were obtained for a coastal location at 33°N (off the southern California coast) and were taken as an index of ocean conditions in the southern California Current. These data are maintained by NOAA and are available online at:

http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html

The upwelling index is based upon Ekman's theory of mass transport due to wind stress. Under steady state conditions, the transport of the surface water due to wind stress is 90° to the right of the wind in the northern hemisphere. The offshore transport occurs up to 50m depth, in the Ekman layer. Positive values of the upwelling index are the result of equatorward wind stress, and are considered to indicate the amount of water transported offshore. Negative values are the result of poleward wind stress and imply downwelling. Because upwelling is related to the strength and direction of the prevailing winds, the index can be assumed to better reflect large-scale atmosphere-ocean conditions than can measurements of the coastal SST, and also because SST is a function of heating.

3.2.3 Analysis of Distribution

In acoustic fisheries surveys, target strength is a measure of acoustic reflectivity of the fish and is used to scale relative abundance estimates to estimates of absolute abundance. The target strength value used to scale the echo-integration data during the 1977-1992 triennial surveys was -35 dB/kg (model 1), a value based on a literature review of target strength

measurements for other, similar gadoid species (Wilson and Guttormsen, 1997). Analysis of *in situ* measurements suggested that a target strength (TS) to length (L) relationship of $TS = 20\log L - 68$, (model 2) where L represents fish length measured in centimeters, is more appropriate for Pacific hake (Traynor, 1996). A comparison of the two target strength models using 1992 and 1995 survey data showed that lower absolute abundance estimates were produced with the new model (Wilson and Guttormsen, 1997).

Age- and length-specific biomass estimates (in 1000t) were obtained during each survey using the target strength relationship along with length-specific data from the trawl catches. Estimates were summed to provide area-specific and coastwide estimates of total numbers and biomass (Wilson and Guttormsen, 1997). The estimated biomass by INPFC area obtained from both target strength models is available for 1977-1989 in Dorn (1996), and for 1992 and 1995 in Wilson and Guttormsen (1997). The 1998 survey estimates can be found in (Wilson et al., 2000).

The relationship between the proportion of the hake stock in Canadian waters and oceanographic data was explored using linear regression. SST was taken as the average over May and June in the survey years at Amphitrite Point. May and June were chosen because these are the months during which the hake move into the Canadian zone. The upwelling anomalies were taken as the average over April, May and June at 33°N, because these are the months during which hake undertake their northward migration (Bailey and Francis, 1985). Regressions were first run using all available survey data (8 years) and then again with 1989 excluded. The survey covered an insufficient area in the Canadian zone in 1989 (missed La Perouse Bank), therefore the Canadian proportion in this year is probably underestimated.

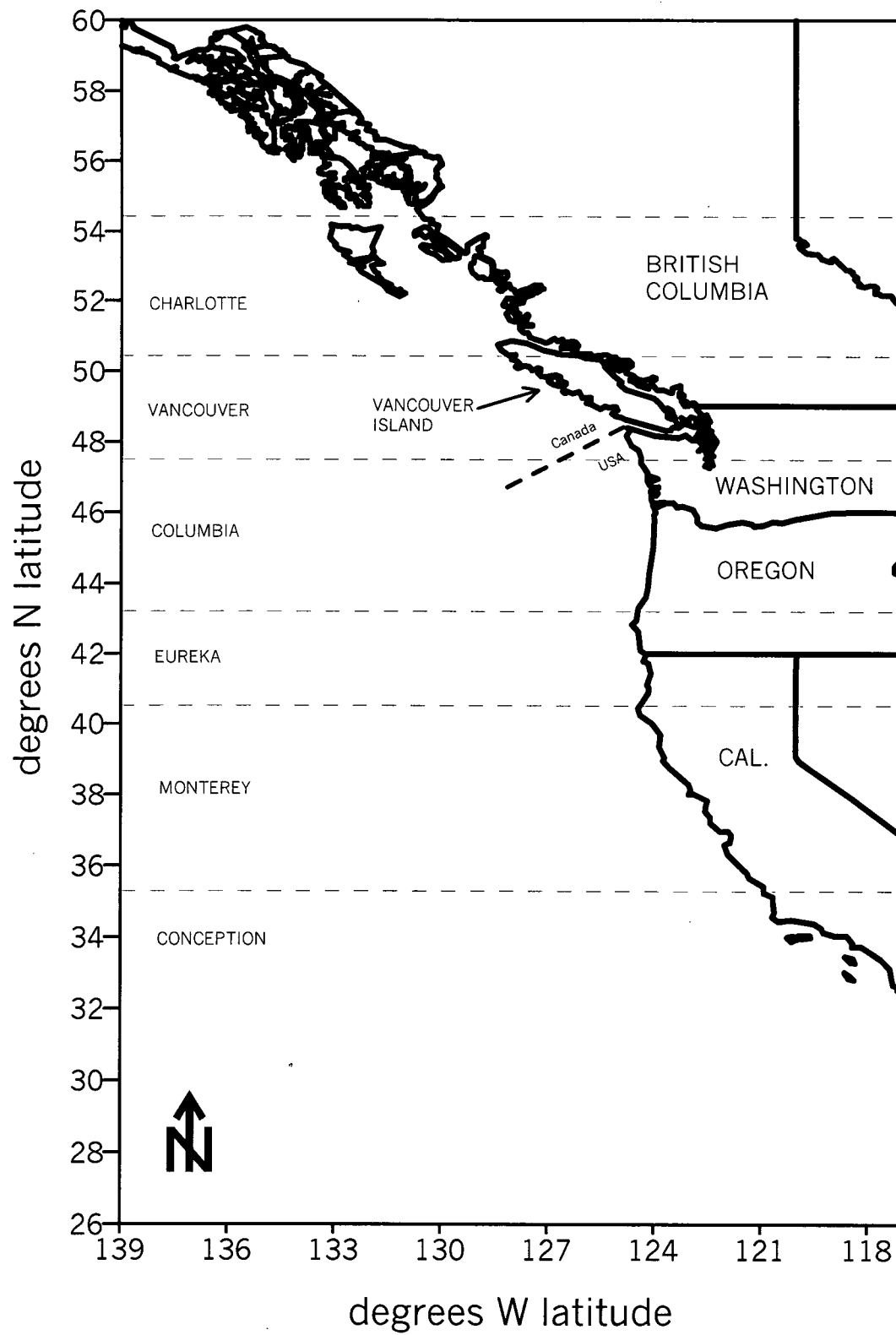


Figure 3.1. Survey area of the U.S. triennial surveys and locations and boundaries of the INPFC geographical areas.

A prior relationship (G.A. McFarlane, pers. comm.) between mature Canadian biomass generated using model 1 for the years 1977-1992, and the average SST in May and June was re-evaluated using additional biomass estimates in 1995 and 1998. In 1992 and 1995, significant aggregations of hake were found in deep water and north of the limits of the earlier surveys (Dorn, 1996). To correct for the limited coverage, the deep water and northern expansion factors [1.5, 1.5, 1.6, 1.7, 1.5] were applied to the mature Canadian biomass estimates in the years [1977, 1980, 1983, 1986, 1989]. The expansion factors represent the northern extent of the distribution that was not covered in the surveys. The expanded Canadian biomass as a proportion of the total was then calculated. Mature Canadian biomass in all years 1977-1998 was estimated by accounting for incomplete recruitment of the youngest age classes by the application of a partial recruitment vector of [0, 0.5, 0.75, 1.0, ... 1.0] to biomass at ages [2, 3, 4, 5, ... 15] for the U.S. and Canada.

The effect of the switch to model 2 on the SST regression was evaluated. Revised total biomass estimates are available for all years, but proportion-at-age data for the model 2 estimates are available for 1992-1998 only. These data are required to determine the mature biomass. In order to obtain the biomass at age in the U.S. and Canada in 1977-1989, the proportion of the total biomass by age from the model 1 estimates was applied to the model 2 estimates.

3.2.4 Analysis of Growth

3.2.4.1 Unbiased Estimates of Length-at-Age

Length frequencies, mean length-at-age, and sex ratio are easily obtained from the DFO data. Annual data are available for 1983-1998, but ages were available up to 1997 at the time of analysis. Due to the latitudinal difference in size and age of hake (Smith et al., 1990), the Canadian data are insufficient for examining the possibility of changes in growth within the population. Samples of hake throughout the distribution are required in order to obtain

population estimates. Such data are available from the U.S. triennial surveys, but they require special consideration.

Estimates of mean length-at-age are biased when they are obtained by averaging data from a two-phase sampling program of the sort used by NOAA (Kimura and Chikuni, 1987). To avoid this bias, estimates of population length-at-age were generated using a method previously described for Pacific hake (Dorn, 1992). The analysis differed from Dorn (1992) in three ways. First, the data used were survey data, therefore, the sample sizes were smaller than those used by Dorn. These data were available every three years from 1983-1998. Dorn (1992) used annual fishery data from 1978-1988. Second, the analyses differ in the definition of the spatial strata. In order to account for latitudinal differences in the average size, separate length-at-age estimates were generated by spatial strata. In order to increase the sample size in each stratum, data in certain INPFC areas were combined. Three spatial strata were defined as follows: i) Conception, Monterey and Eureka were categorized as the "southern" stratum, ii) Columbia and Vancouver were categorized as the "northern" stratum, and iii) all areas north of the Vancouver were categorized as "Charlotte". Samples were collected in Charlotte in 1992, 1995, 1998 only. Dorn (1992) defined his three strata as: i) the northern ($>39^{\circ}\text{N}$) part of Monterey, and all of Eureka, ii) southern Columbia (between 43°N and $45^{\circ}46'$), and iii) the northern part of Columbia and the U.S. portion of Vancouver. A third difference lies in spatial coverage of the stock. Dorn (1992) used samples collected in the U.S. fishery, and therefore missed hake in Canadian waters. Because the triennial surveys sample hake throughout their distribution, growth trends in the whole population (and not simply the fishery) can be examined. The sample sizes by stratum are shown in Table 3.1. Data for 1989 were not used because all fish in the samples were aged, which precludes the use of the methods discussed below, because the methods require unaged length frequency data as well as a smaller subsample of aged fish.

Table 3.1. Sample size (number of fish) of hake length frequency and age samples in U.S. triennial surveys 1983-1998. No hake were sampled in Charlotte prior to 1992.

	North length	North age	South length	South age	Charlotte length	Charlotte age
1983	1760	1222	105	105	-	-
1986	3282	1499	1028	575	-	-
1992	3390	1419	767	589	395	176
1995	3016	1243	1524	793	161	128
1998	4244	1287	1660	817	568	313

In order to obtain length-at-age estimates, mean length-at-age was first estimated for each stratum, these estimates were then combined to give population estimates. Strata-specific estimates of mean length-at-age were obtained by:

$$\bar{l}_j = \sum_i l_i q_{ij} \quad (3.1)$$

where l_i is the midpoint of the i^{th} length category (cm), and q_{ij} is the probability of length i given age j . q_{ij} is obtained by applying Bayes theorem:

$$q_{ij} = \frac{q_i q'_{ij}}{\sum_i q_i q'_{ij}} \quad (3.2)$$

and

$$q_i = \frac{n'_i}{n'}$$

$$q'_{ij} = \frac{n_{ij}}{n_i}$$

where n' is the first phase samples size, n'_i is the number of fish in length category i , n_i is the subsample size, and n_{ij} is the number of subsamples taken from length category i of age j . Dorn (1992) modeled the distribution of n'_i and n_{ij} using a multinomial distribution in order to estimate q_i and q'_{ij} . The observed distribution was used in this analysis. Although the subscript is omitted, the length-at-age estimates were generated for males and females separately.

Unbiased estimates of mean length-at-age from the three strata were combined in order to obtain an unbiased estimate of the mean length-at-age in the population. An estimate for the combined mean length-at-age is obtained using:

$$\bar{l}_i = \sum_h \left(\frac{c_{jh}}{c_j} \right) \bar{l}_{jh} \quad (3.3)$$

where l_{jh} is the length-at-age in the h^{th} stratum, and c_{jh} is the estimated number at age in the h^{th} stratum, and c_j is the estimated total number at age from the U.S. triennial surveys.

3.2.4.2 Growth Parameters L_∞ and K

The relationship between the length and age of a fish is described by the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938) as follows:

$$L_a = L_\infty (1 - e^{(-Ka)}) \quad (3.4)$$

where L_a is the length at age a , L_∞ is the asymptotic length (cm), K (yr^{-1}) is the Brody growth coefficient and represents the growth rate, and a is the age at which the theoretical fish length is zero (Hilborn and Walters, 1992). The von Bertalanffy model predicts that growth increments between adjacent ages are linear, and that the increments approach zero as the fish length approaches L_∞ . Walford (Ricker, 1975) used this to derive a linear model to predict length-at-age based on the previous length-at-age:

$$L_{a+1} = \alpha + \rho \cdot L_a \quad (3.5)$$

where

$$\alpha = L_\infty(1 - e^{-K}) \quad \text{and} \quad \rho = e^{-K}$$

The VBGF parameter estimates are obtained by fitting a Walford line to the observed mean length-at-age. The estimates are:

$$L_{\infty} = \alpha / (1 - \rho) \text{ and } K = -\ln(\rho) \quad (3.6)$$

Because no age-1 hake were sampled in the 1980s, the linear model (3.5) was fit to the unbiased estimates for all years of the mean length-at-ages 1-10 (when available) obtained using (3.3). Age 10 was taken as the maximum age due to increased aging error of older fish. Ages 2-10 only were available in 1986 therefore, the analysis was run using all ages 1-10 for 1992, 1995, 1998 and again using only ages 2-10 for the same years in order to determine whether the loss of 1 year of data affected the estimates. Following Cox (2000), variance estimates of α and ρ were used to obtain variance estimates for L_{∞} and K by applying the Delta method to 3.6 :

$$\text{var}(L_{\infty}) = (1 - \rho)^2 \text{var}(\alpha) + (\alpha / (1 - \rho)^2) \text{var}(\rho)$$

$$\text{var}(K) = (-1/\rho)^2 \text{var}(\rho)$$

3.3 RESULTS

3.3.1 Changes in the Hake Summer Distribution

A dramatic change in the typical summer distribution of migratory hake occurred between the 1980s and 1990s, and the distribution changed again in 1998. The locations of hake catches in the DFO summer research surveys are presented in Figure 3.2. In the 1980s, dense aggregations of hake were located on La Perouse Bank and north along the continental shelf. Between 1990 and 1997, the aggregations extended into Queen Charlotte Sound, as far north as the southern tip of the Queen Charlotte Islands. Following the northern extension of the feeding distribution between 1990 and 1997, in 1998, the distribution extended even farther north along the continental shelf - as far as Alaska (58°N).

The change in distribution did not coincide with a change in overall population size or a range expansion. Rather, the northern extension represents a northward shift in the distribution of the entire stock. A time series of the triennial survey biomass (1000t) estimates for hake by INPFC area is shown in Figure 3.3. The northward shift is most evident in the estimates in the southernmost and northernmost areas of hake distribution. In the Monterey INPFC area (Figure 3.3a), the abundance estimates decreased throughout the 1990s, while in the north, in the Canadian area (Figure 3.3d), the abundance increased over the same time period. The proportion of hake biomass in Canadian waters is also presented in Figure 3.3d. What this figure shows is that the proportions of the stock in Canadian waters throughout the 1990s were higher than those in the 1980s. The proportion in 1998 was higher than any on record.

In examining the distributional abundance on an interannual basis, El Niño signals are evident. A massive El Niño event occurred in 1982/1983 (Trenberth and Hoar, 1996). The hake summer distribution pattern shifted north in this year, as is evident in Figure 3.3 a and d. A dramatic increase in the biomass of hake in Canadian waters concurrent with the 1983 El Niño event was shown by Ware and McFarlane (1995). The biomass in 1983 was higher than any other in the 13 years of survey data they examined between 1968 and 1991. Another, less strong El Niño event occurred in 1992/1993. It is interesting to observe that although the 1992/1993 El Niño was weaker than the 1982/1983 event, more hake were present in the Canadian zone in 1992. This point illustrates the importance of examining environmental relationships on a longer time scale. The 1990s were characterized by persistent El Niño-like conditions (Trenberth and Hoar, 1996) and the 1992/1993 El Niño was superimposed on a warming trend. This may provide an explanation for the more pronounced effect of the 1992/1993 El Niño on hake distribution.

3.3.2 Climate-Ocean Effects on Hake Distribution

The average May-June SST off Amphitrite Point for the period 1977-1998 is shown in Figure 3.4a and summer (April-September) and winter (October-March) SST anomalies, based on the long term monthly averages are shown in Figure 3.4b. Summer and winter SST off the west coast of Vancouver Island were warmer than average for most of the years in the time series.

Although the warmest summer (1997) and winter (1998) temperatures occurred during the 1990s, and there were more consecutive warm years in the 1990s, when the data are tested for an increase with the 1989 regime shift, the result is non-significant (Beamish et al., 2000). The only other year with a summer SST anomaly as strongly positive as 1997 was 1983, the year of the large El Niño. Although the 1990s were a decade of more frequent El Niño-like events (Trenberth and Hoar, 1996), this is not entirely evident in either Amphitrite Point time series.

There is a marked difference between the 1980s and 1990s in the upwelling anomaly data for 33°N (Figure 3.5a and b). When compared to the 1980s, the summers over the period 1990-1998 were characterized by weaker than average upwelling or downwelling. The strongest negative values were recorded in 1992, 1993, and 1998. The strongly negative values of the upwelling anomaly are not evident for any other year (1983 included). Winter downwelling was stronger than average for the majority of years over the period 1977-1998.

Triennial survey estimates of the mature hake biomass and the Canadian proportion of the total, generated using model 1 and model 2 are shown in Tables 3.2 and 3.3, respectively. Mature biomass estimates obtained using model 2 are lower than those obtained using model 1 for all years. However, the Canadian proportions of mature hake biomass are lower for 1977-1989 and higher for 1992-1995. This can be attributed to the lower U.S. biomass estimates in the latter years.

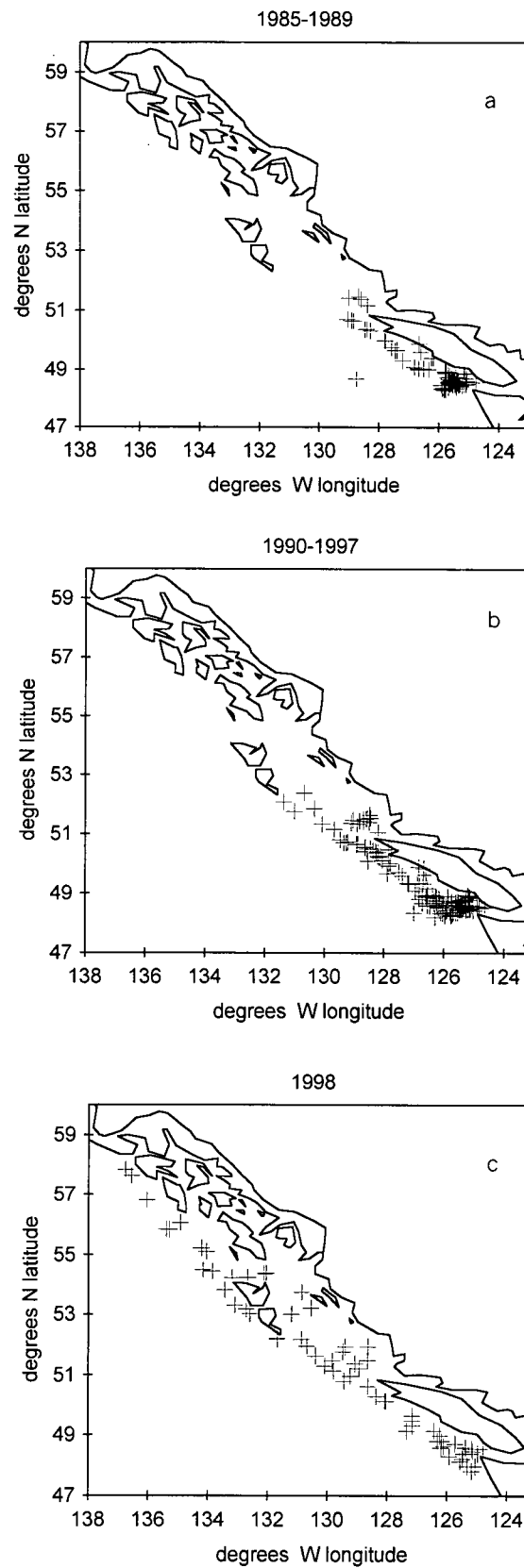


Figure 3.2. Catch locations of Pacific hake in DFO summer research surveys: a) 1985-1989, b) 1990-1997 and c) 1998.

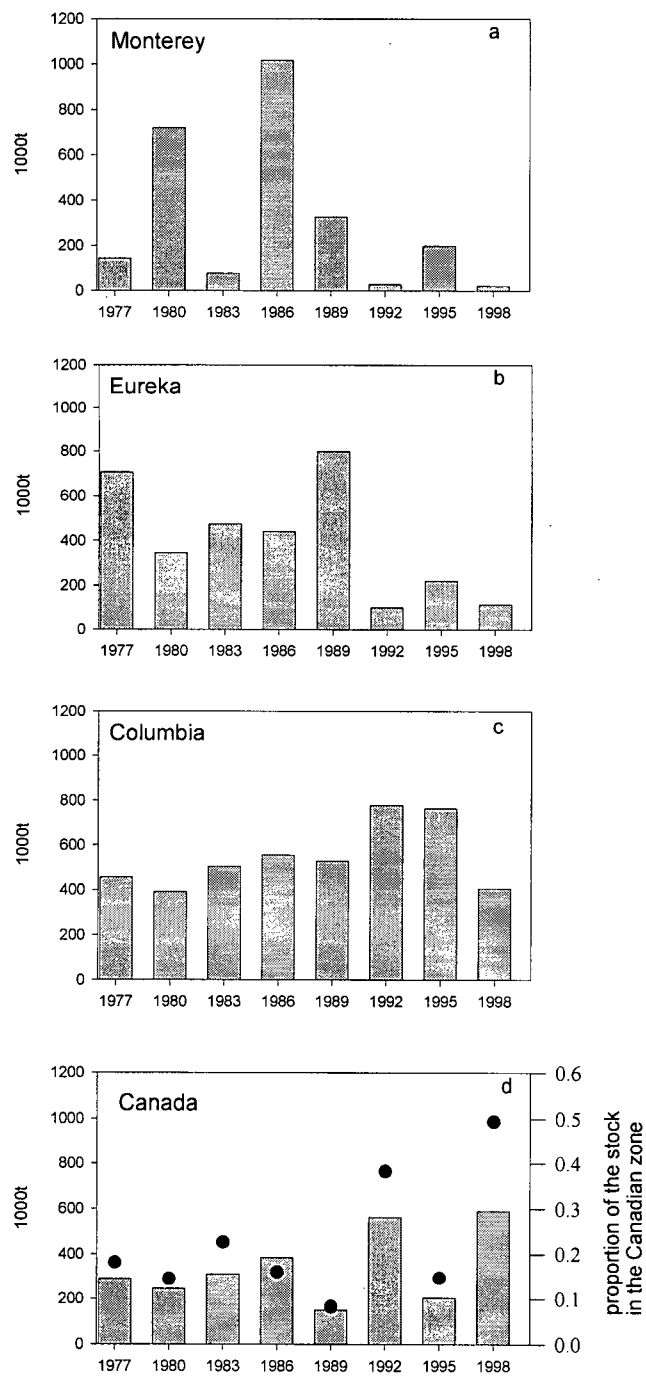


Figure 3.3. Time series of the triennial survey hake biomass estimates for INPFC areas a) Monterey, b) Eureka, c) Columbia in the United States and combined for Canada in d). The proportion of the total biomass by survey year (dots) is included in d) and shows the increased proportion of the stock in Canadian waters in the 1990s.

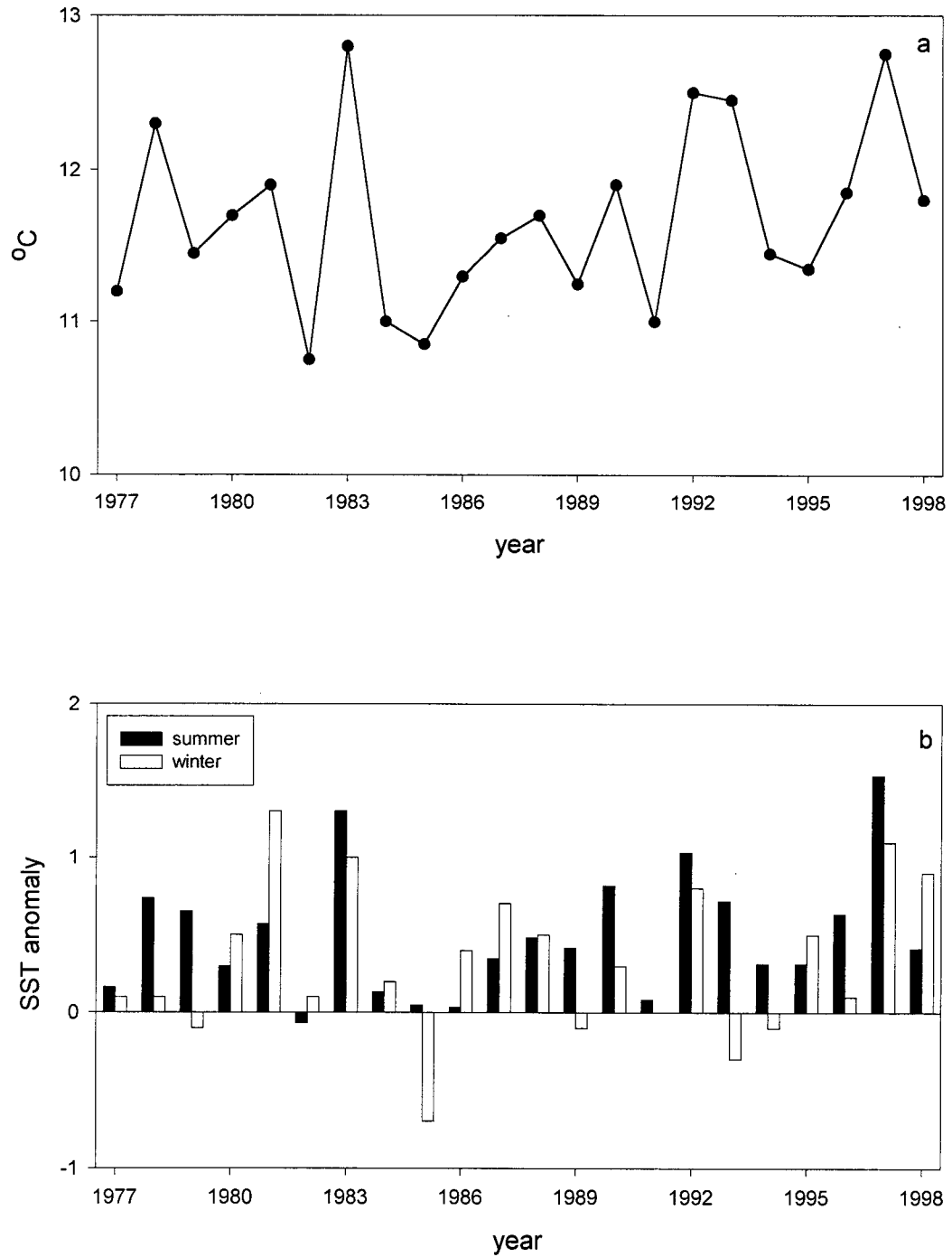


Figure 3.4. Time series of a) average May-June sea surface temperature (SST) and b) average summer (April-September) and winter (October-March) SST anomalies at Amphitrite Point. Figures show above average temperatures for most years during the period 1977-1998.

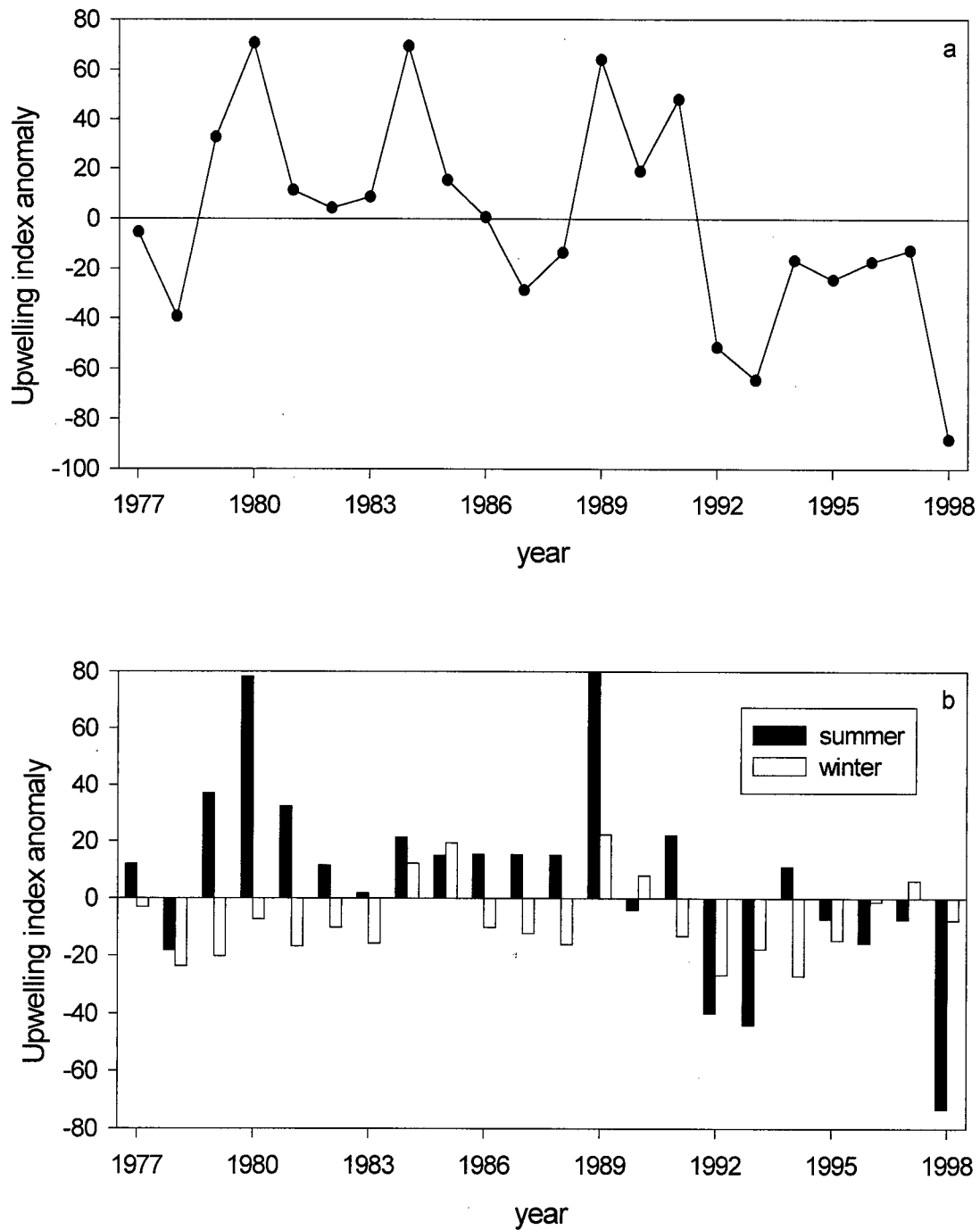


Figure 3.5. Time series of a) the average upwelling anomaly over April, May and June at 33°N, and b) Summer (April-September) and winter (October-March) upwelling anomalies for the period 1977-1998 at 33°N. Positive values indicate equatorward wind stress and offshore transport in the Ekman layer (upwelling), and negative values indicate poleward wind stress and onshore transport (downwelling). Both figures show that there has been either weakened upwelling or downwelling in the summer months since 1989.

Table 3.2. Triennial survey estimates of the mature hake biomass (1000t) in the U.S. and Canada, and the Canadian proportion of the total. Estimates generated using model 1.

survey year	total U.S.	total Canadian	expansion factor	expanded Canadian	Canadian proportion
1977	901.03	198.72	1.5	298.07	0.248
1980	1019.96	166.344	1.5	249.52	0.196
1983	616.58	235.92	1.6	377.47	0.379
1986	1072.71	297.47	1.7	505.70	0.320
1989	1341.90	120.82	1.5	181.23	0.119
1992	1414.855	908.56	1.0	908.56	0.391
1995	1600.24	321.32	1.0	321.32	0.167

Table 3.3. Triennial survey estimates of the mature hake biomass (1000t) in the U.S. and Canada, and the Canadian proportion of the total. Estimates generated using model 2.

survey year	total U.S.	total Canadian	Canadian proportion
1977	1193.55	263.23	0.181
1980	1131.32	184.51	0.140
1983	632.08	241.85	0.277
1986	1208.02	334.99	0.217
1989	1532.72	138.00	0.083
1992	785.72	554.15	0.414
1995	909.65	198.48	0.179
1998	447.08	526.20	0.541

Table 3.4. Summary of the data used in and the results of linear regression between oceanographic data and the Canadian proportion of the total mature hake biomass. The relationship was used to predict the Canadian proportion in non-survey years. The average Canadian proportion is calculated using all predicted values for a given time period. Averages were not calculated for non significant relationships.

target strength	years included	oceanographic data used	equation	r ²	p value	average Canadian proportion	standard deviation
-35dB/kg	1977-1992 inclusive	SST May-June	CDN prop = -1.135+(0.119*SSTM,J)	0.58	0.079	24.8%	7.1%
	1977-1995 inclusive	SST May-June	CDN prop = -1.268+(0.130*SSTM,J)	0.61	0.038	24.7%	7.6%
	1977-1992 not 89	SST May-June	CDN prop = -0.748+(0.0881*SSTM,J)	0.56	0.147	-	-
	1977-1995 not 89	SST May-June	CDN prop = -1.015+(0.109*SSTM,J)	0.59	0.074	26.3%	6.5%
20logL-68	1977-1995 inclusive	SST May-June	CDN prop = -1.338+(0.132*SSTM,J)	0.62	0.035	20.0%	7.7%
	1977-1998 inclusive	SST May-June	CDN prop = -1.316+(0.133*SSTM,J)	0.27	0.188	-	-
	1977-1998 not 89	SST May-June	CDN prop = -0.981+(0.106*SSTM,J)	0.19	0.326	-	-
	1977-1998 inclusive	UP April-June	CDN prop = 0.246-(0.0025*UPA,M,J)	0.77	0.004	24.8%	10.4%
	1977-1998 not 89	UP April-June	CDN prop = 0.247-(0.00247*UPA,M,J)	0.71	0.018	24.9%	10.3%

The regression using -35dB/kg estimates of the Canadian proportion of mature hake biomass and the average SST over May and June off Amphitrite Point for 1977-1992 was compared to that for 1977-1995. The results are shown in Figure 3.6a and b. This comparison was performed in order to determine what effect the addition of a single data point had on the relationship. Statistically speaking, the relationship improved. Little explanatory power was gained ($r^2 = 0.58$ versus $r^2 = 0.61$), but the significance of the relationship improved ($p = 0.079$ to $p = 0.038$). Using the two relationships to generate the average Canadian proportion (Table 3.3), the averages (24.8% and 24.7%) and standard deviations (7.1% and 7.6%) are essentially the same over the time periods examined. Excluding 1989 from the analysis rendered the relationship non-significant for 1977-1992 and it degraded slightly for 1977-1995, although the average proportion increased to 26.3% (Table 3.4) for the latter period.

Using estimates generated with model 2 instead of model 1 made little difference to the regression for the years 1977-1995 (compare Figure 3.6b and Figure 3.7a). However, when the new relationship was used to calculate the average Canadian proportion over 1977-1995, it dropped to 20% (standard deviation of 7.7%) (Table 3.3). Removing 1989 from the analyses yielded non-significant results. This is most likely the result of too few data points (Table 3.4). The addition of the 1998 data also rendered the relationship non-significant (Figure 3.7b, Table 3.4). The Canadian proportion of mature hake biomass was unusually high in 1998 (Figure 3.3d), while the SST was not correspondingly high. This result indicates that the relationship between hake biomass in the Canadian zone is not a simple function of sea surface temperature, and it may indicate that the factor(s) controlling hake migration changed with the 1998 regime shift. Exploratory analyses were undertaken for the relationship within a regime (77-89, 92-98) and for other months of SST (e.g. the average over April-May and June-July) but all yielded non-significant results.

The 1977-1998 triennial survey estimates of the Canadian proportion of mature hake biomass generated using model 2 are inversely related to the average upwelling anomaly over the preceding April, May and June at 33°N (Figure 3.8). The average upwelling anomalies account for a large amount of the variance in the Canadian proportions ($r^2 = 0.77$) and the relationship is highly significant ($p = 0.004$). Applying this relationship, the average proportion of mature hake biomass in Canada during 1977-1998 is 24.8% with a standard deviation of 10.4% (Table 3.4). Removing 1989 degrades the relationship slightly, but it nonetheless outperforms the SST relationships (average proportion 24.9%; $r^2 = 0.71$; Table 3.4) and it remains significant ($p = 0.0018$). The observed and predicted proportions of mature hake biomass in the Canadian zone are shown in Figure 3.9. In comparing the predictions based on SST with those based on the spring upwelling anomalies, neither yields a perfect fit. However, the upwelling anomalies are a better predictor of the Canadian proportion from 1989 to 1998.

In order to determine whether upwelling along other parts of the coast affects hake distribution, (and because upwelling at one point along the coast should be correlated with upwelling elsewhere), the relationship between the Canadian proportion and the average April-June upwelling anomalies at 36°N was also examined. The negative relationship remains (Figure 3.10). When the upwelling anomaly is positive, the relationship is not a good predictor of the Canadian proportion, however, it provides more evidence that during El Niño events and El Niño-like conditions, hake migration is negatively related to upwelling. When downwelling or weak summer upwelling occurs along the coast of California, the Canadian proportion increases almost linearly. It may be that when summer upwelling is strong (e.g. 1980), hake movements are governed by some other factor, or it may be that the determination occurs farther south (e.g. 33°N).

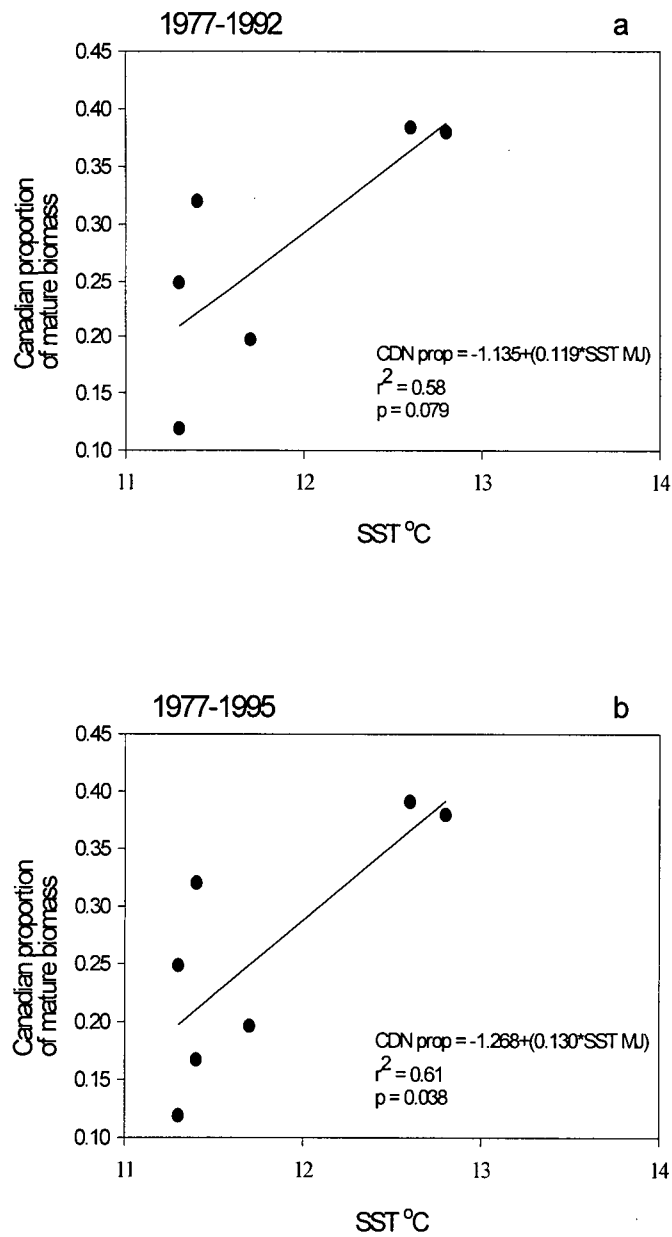


Figure 3.6. Relationship between the proportion of mature hake biomass in the Canadian zone and the average May-June SST at Amphitrite Point for a) 1977-1992 and b) 1977-1995. Mature Canadian proportions are based on biomass estimates generated using the target strength value of -35 dB/kg.

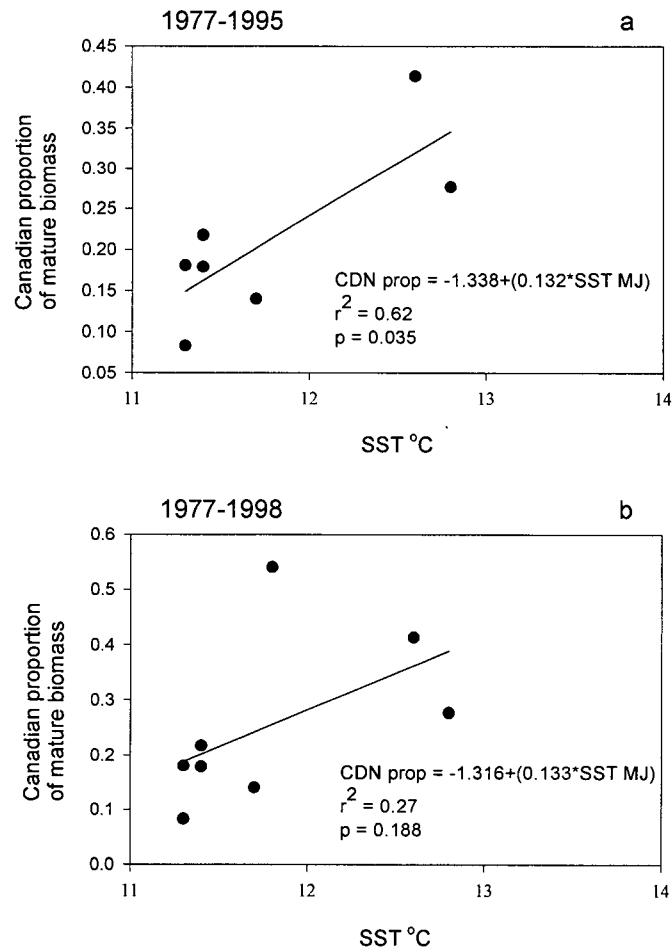


Figure 3.7. Relationship between the proportion of mature hake biomass in the Canadian zone and the average May-June SST at Amphitrite Point: a) 1977-1995 and b) 1977-1998. Proportions are based on biomass estimates generated using the target strength – length relationship of $20 \log L - 68$.

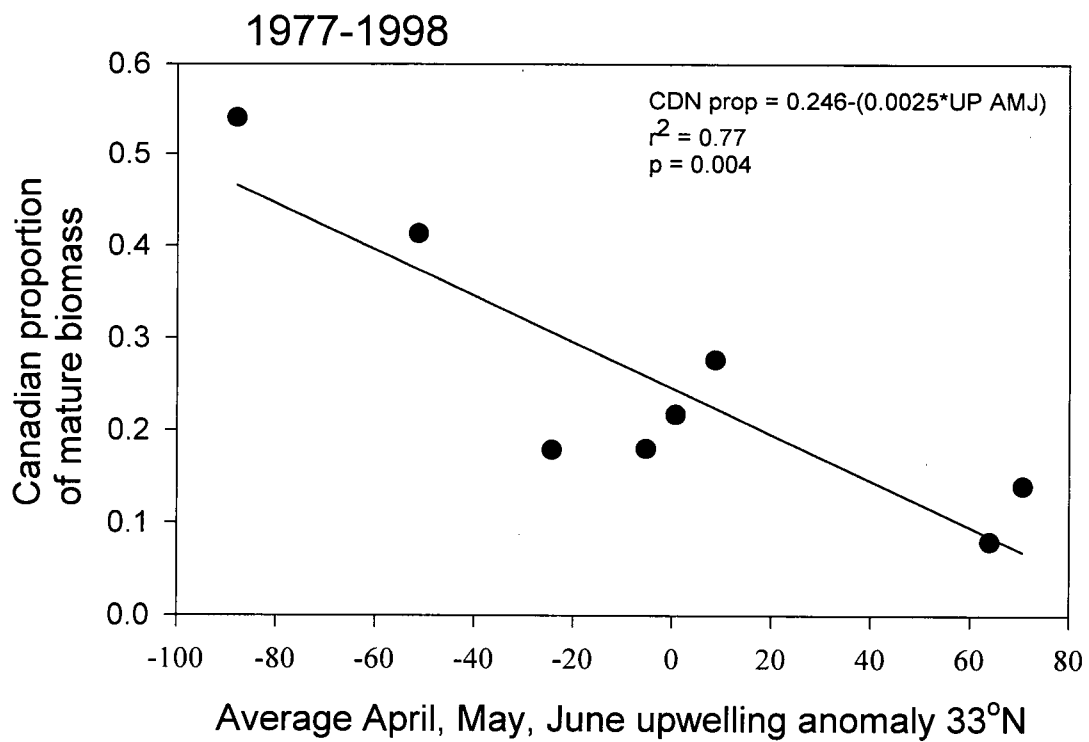


Figure 3.8. Relationship between the proportion of mature hake biomass in the Canadian zone and the average upwelling anomaly over April, May, June at 33°N in the survey years 1977-1998.

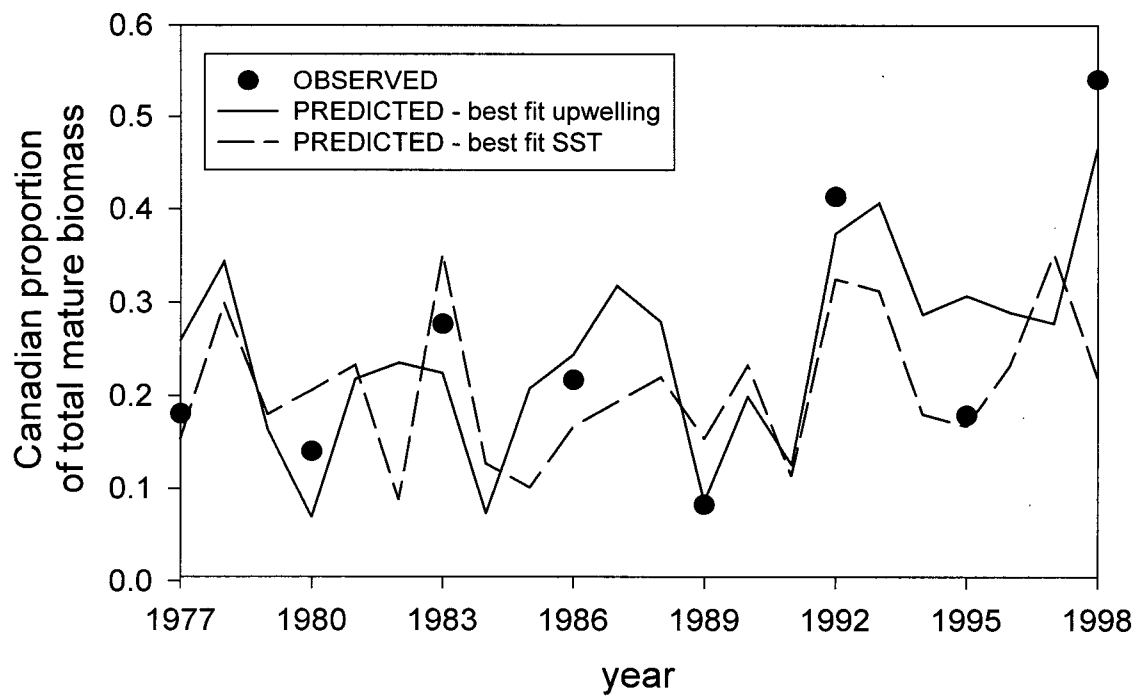


Figure 3.9. Observed and predicted proportions of mature hake biomass in the Canadian zone 1977-1998. The observed proportions were generated using the target strength relationship $TS = 20\log L - 68$. Predictions based on the best fit relationship between the proportions generated using the same target strength relationship, and the average SST over May and June off Amplitrite Point and the average April-June Bakun upwelling anomalies.

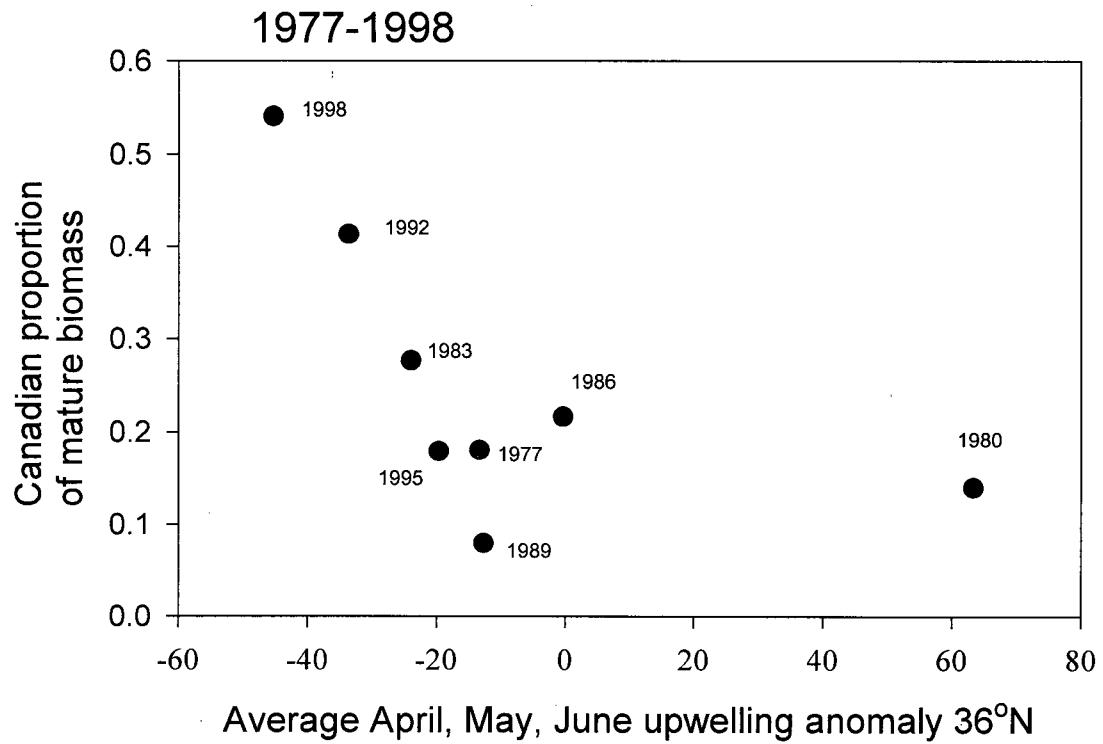


Figure 3.10. Relationship between the proportion of mature hake biomass in the Canadian zone and the average upwelling anomaly over April, May, June at 36°N in the survey years 1977-1998.

3.3.3 Spatial Distribution of Sizes

An examination of the length frequency distributions by INPFC area shows that the proportion of small (<30cm) fish was larger in all areas in the 1990s compared to the 1980s, but this is most evident in the southern areas (Monterey and Eureka) (Figure 3.11 a-d). The migratory distribution (largest fish moving the farthest north) has been shown to be robust in spite of strong environmental variability such as El Niño events (Dorn, 1995), and it persisted in the 1990s (Figure 3.12). A comparison of length frequencies of fish at the northern limit of their migration in 1992, 1995, 1997, and 1998 is shown in Figure 3.13. There was considerable variation in the size of fish at the northern limit throughout the 1990s. The size of fish moving the farthest north declined from 1992 to 1998, concurrent with a northward extension of the distribution. The northern limit was Queen Charlotte Sound in 1992 and 1995, and extended to Cape St. James in 1997 and Dixon Entrance in 1998. The fact that juvenile hake (<25cm) were sampled at the northern limit in 1997 and 1998 is surprising, and may be an indication that spawning occurred farther north than the west coast of Vancouver Island in the late 1990s. Further evidence is presented in Figure 3.14, which compares the length frequencies in the Vancouver and Charlotte INPFC areas with samples collected by DFO between Hecate Strait and Alaska in 1998. The migratory distribution of adults was maintained in that the largest fish moved the farthest north, but additionally, the smallest fish were sampled the farthest north.

3.3.4 Length-at-Age

An increase in the number of small fish present in Canadian and northern waters can result from at least two things: either a change in the composition of the migratory portion of the stock or a decrease in size-at-age (change in growth). The sex ratio of hake in Canadian surveys changed from the 1980s to the 1990s. The fraction of females in Canadian waters and north of 49°N was lower than average from 1992 to 1998 (Figure 3.15a and b). Female hake are larger

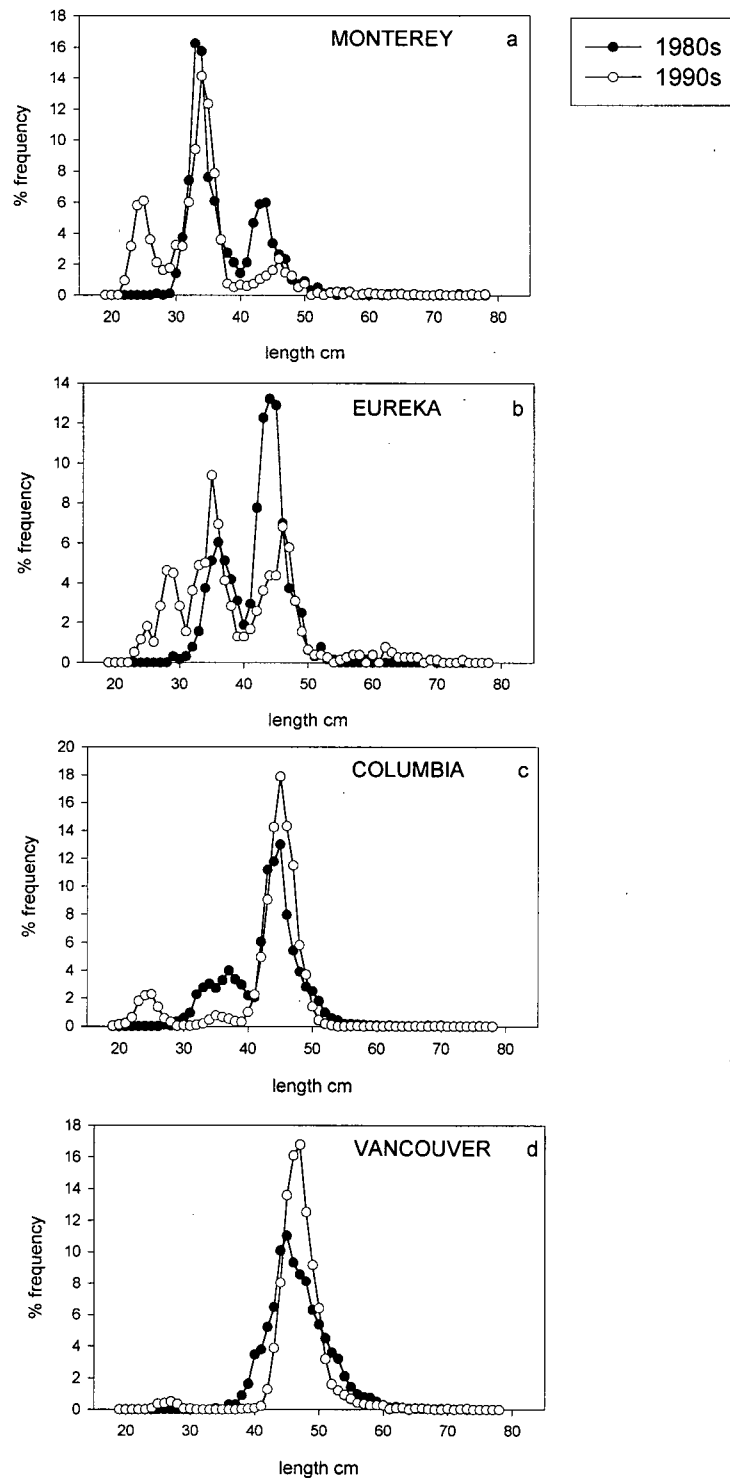


Figure 3.11. Length frequency by INPFC area for the 1980s and the 1990s, showing increased numbers of small fish in all areas in the 1990s, most evident in the southerly areas. U.S. triennial survey data.

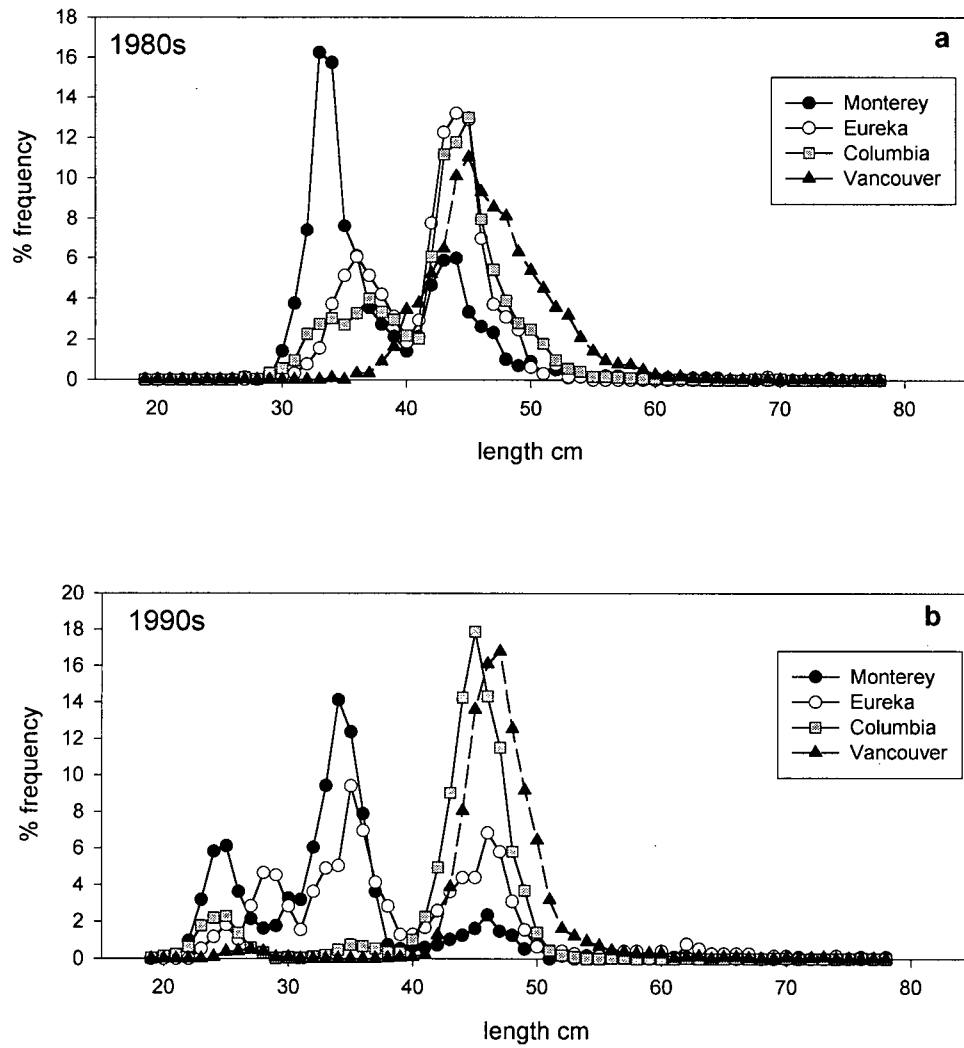


Figure 3.12. Length frequency of hake by INPFC area and decade. Figures show that the migratory distribution of sizes was maintained in the 1990s, with the largest fish present in the most northerly areas. U.S. triennial survey data.

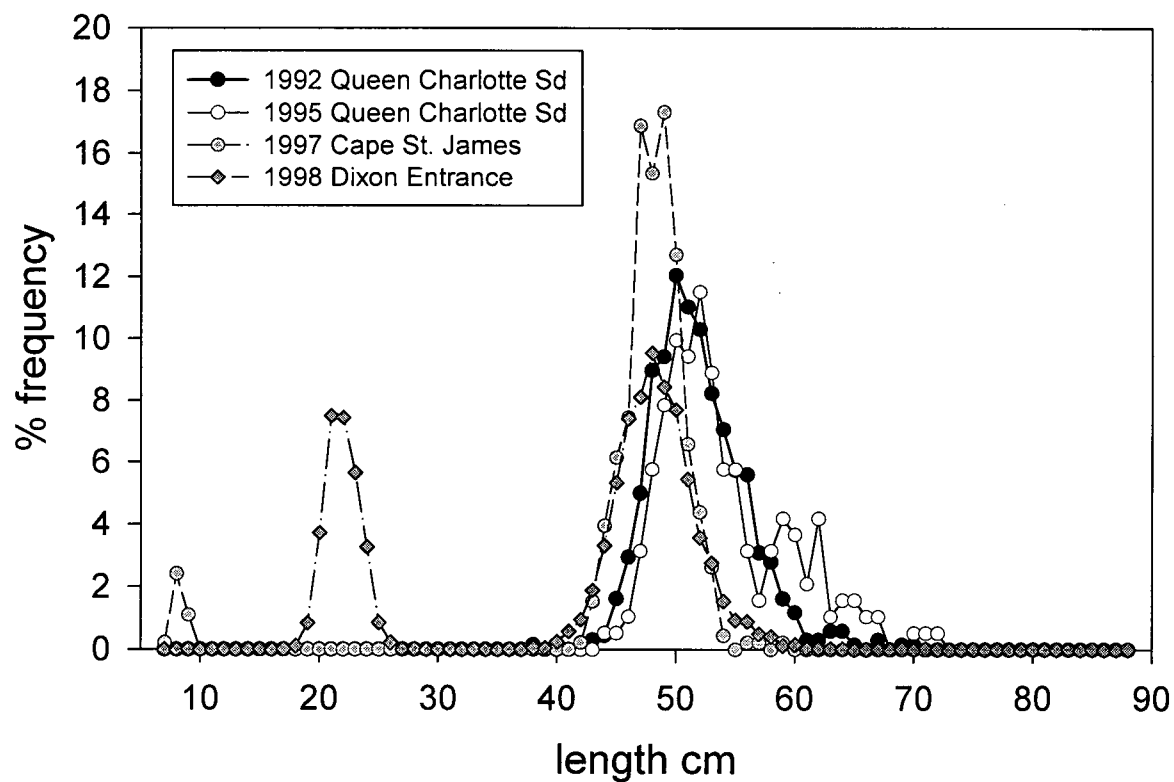


Figure 3.13. Length frequency of hake sampled at the most northerly extent of their distribution in Canadian waters in 1992, 1995, 1997, and 1998. Juvenile hake were sampled at the northern limit in 1997 and 1998. Additionally, there were more smaller fish present farther north in Canadian waters throughout the 1990s. DFO research survey data.

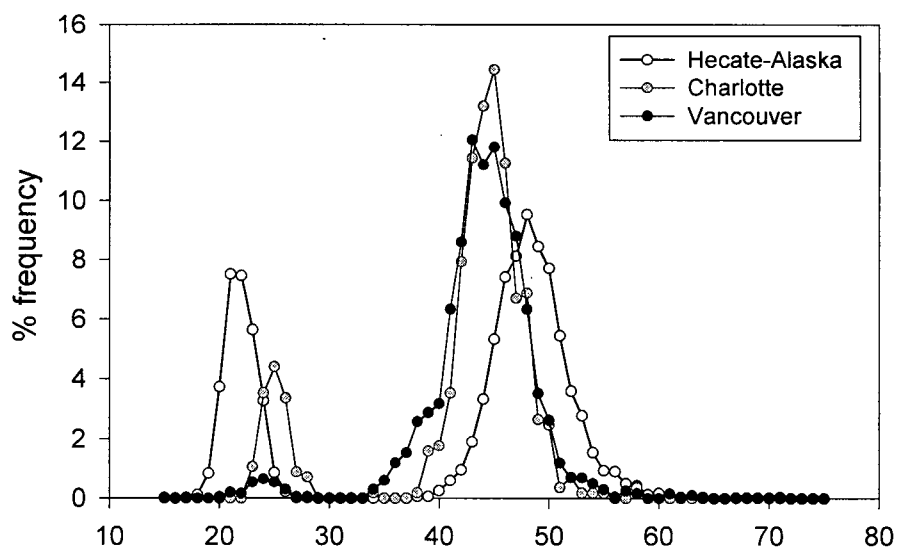


Figure 3.14. Length frequency of hake sampled in the northerly INPFC areas in 1998. Hecate-Alaska samples from DFO survey, Charlotte and Vancouver from U.S. triennial survey. Figure shows that the largest fish were distributed farthest north, and additionally that the smallest fish were the farthest north.

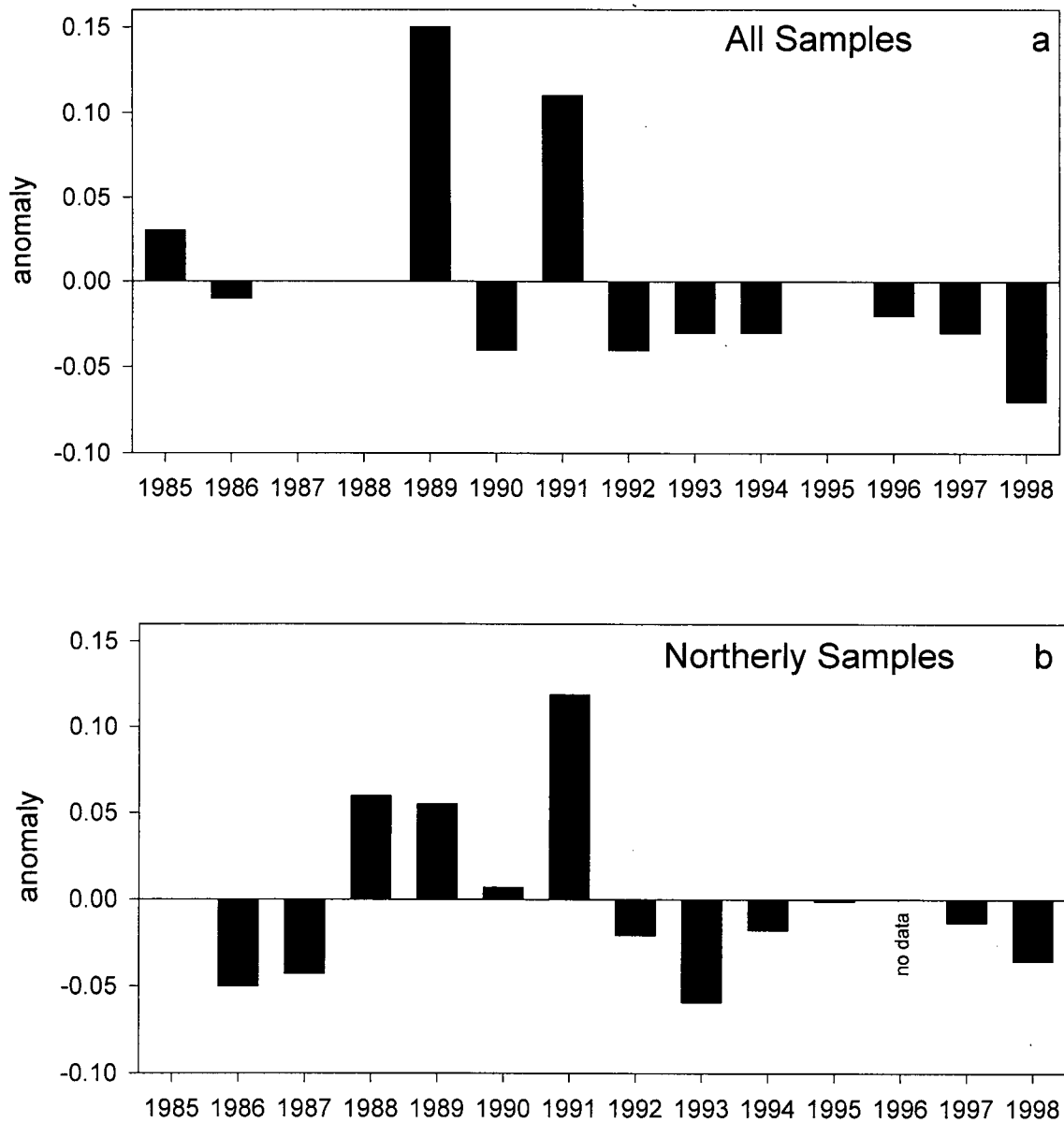


Figure 3.15. Deviations from the mean female proportion over 1985-1998 in a) all Canadian research samples (mean proportion = 0.6, standard deviation = 0.061), and b) Canadian research samples taken north of 49°N (mean proportion = 0.57, standard deviation = 0.053). Figures show that the female proportion was lower than average for most of the 1990s in Canadian waters.

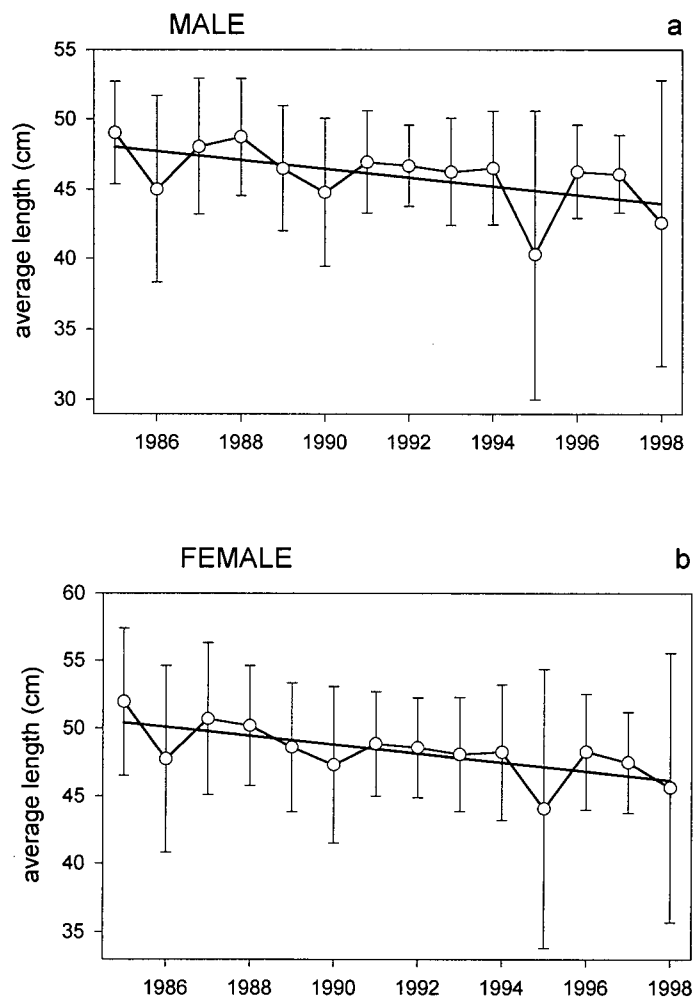


Figure 3.16. Average size of a) male and b) female hake in Canadian waters over 1985-1998. Figures show a general decline in the size of both sexes. Standard error shown.

than males and traditionally the Canadian fraction of the stock has been predominantly female hake. Therefore, it is possible that the change in the length frequency distributions reflects the higher proportion of males in the samples. However, the average size of both male and female hake in the Canadian zone declined by approximately 6cm between 1985 and 1998 (Figure 3.16). The decline does not necessarily indicate a change in growth, it may simply be the result of the inclusion of more small fish in the average. If a change in growth occurred, it would be evident as a change in size-at-age. An examination of the mean size-at-age in Canadian samples shows an increase in the size at the youngest ages (<5yr) and a decline in the size at age 6+ for both sexes in the 1990s compared to the 1980s (Figure 3.17). These differences are not statistically significant, however, and do not necessarily reflect a change in growth in the population. Because smaller, younger fish (and smaller fish of any age) have been shown to be present farther north in El Nino years (Smith et al., 1990), it would be unwise to associate a change in size-at-age in Canadian waters during El Nino-like years with a change in growth. However, because the migratory distribution persisted into the 1990s, a decline in the size-at-age of hake in the northern part of the distribution implies a decline in the size-at-age of the largest fish in the population. It is therefore possible that the previously noted decline (Hollowed, 1988; Smith et al., 1990; Dorn, 1992) persisted.

Unbiased estimates of the population length-at-age could not be obtained for male hake. The samples of males in the 1980s in the southern stratum were all aged 3 or 4, while older fish were caught in the northern stratum. This distribution of sizes is not reflected in the numbers-at-age used to obtain population mean lengths-at-age. The numbers-at-age by strata indicate the presence of fish at all ages 3-10 in the south. Use of these data resulted in gross underestimates of the length-at-age in the population (e.g. 15cm long age-4 hake). The same problem was encountered for females in 1983: all females in the southern stratum were 3 years old. These problems can be attributed to small sample sizes in the southern stratum when compared to the

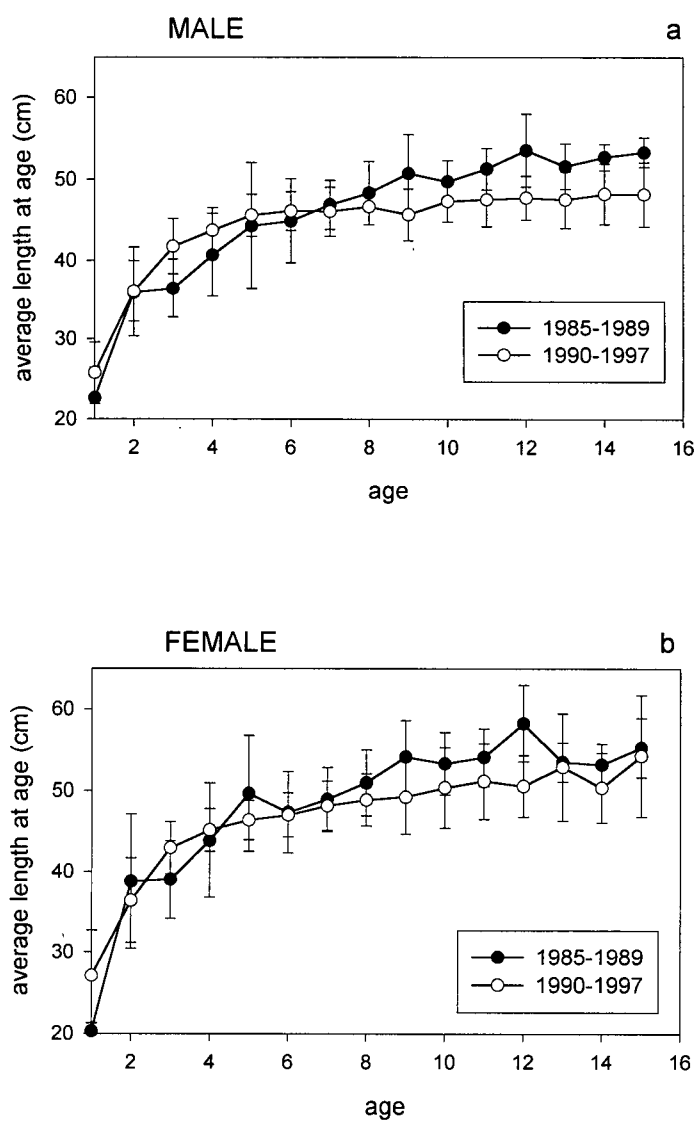


Figure 3.17. Average length-at-age over 1985-1989 and 1990-1997 of a) male and b) female hake sampled in Canadian waters. Standard error shown.

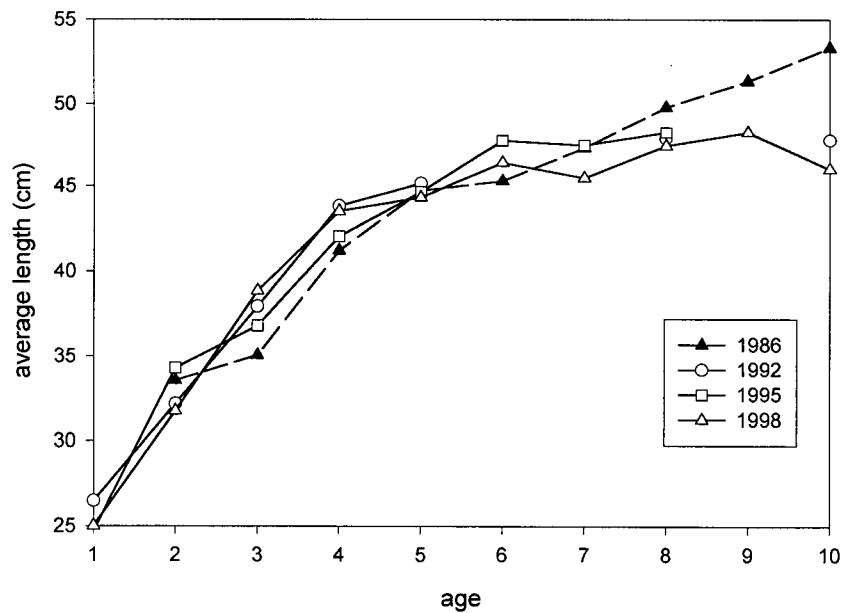


Figure 3.18. Unbiased estimates of average length-at-age of female hake in 1986, 1992, 1995, and 1998. Figure shows a decline in size at ages 8+ over the time period.

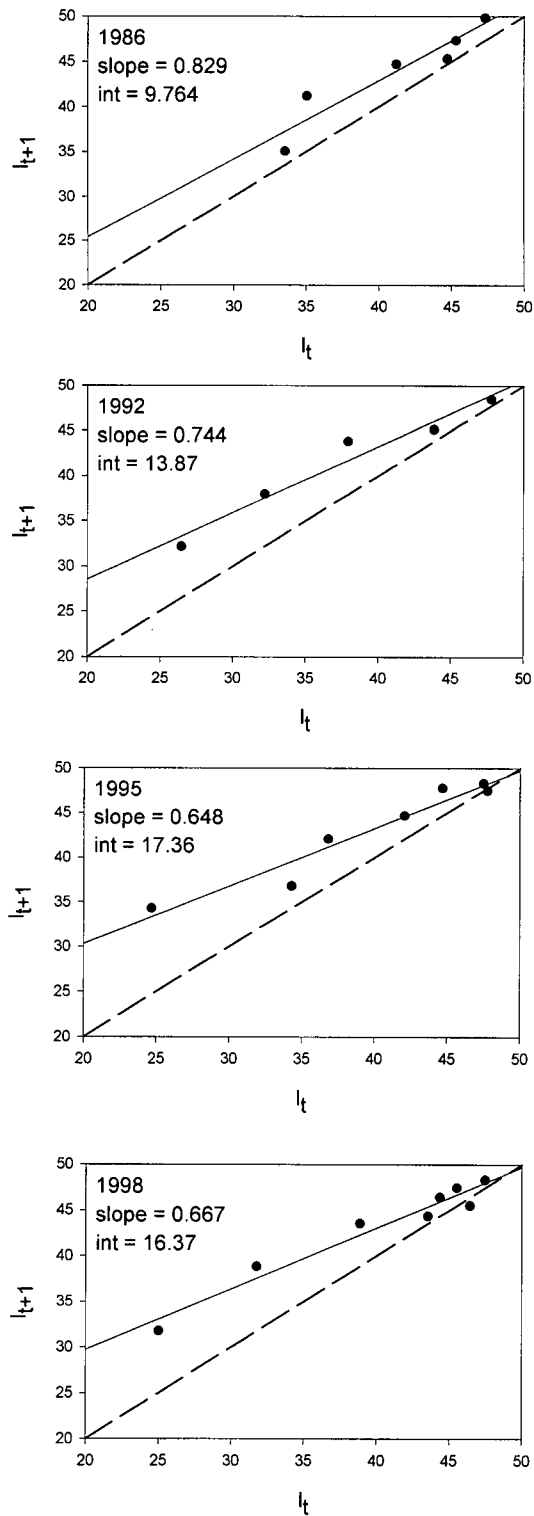


Figure 3.19. Walford plots of unbiased estimates of length-at-age of female hake at ages 2-10 in 1986, and 1-10 in 1992, 1995, and 1998. Dotted line represents 1:1 correspondence.

north (Table 3.1). The ineffectiveness of the method for male hake is somewhat troubling, but because females represent the spawning stock, and the reproductive capacity of female hake is a function of length (McFarlane and Saunders, 1997), growth trends in female hake are more critical than those of males in terms of stock productivity.

Unbiased estimates of the mean length-at-age of female hake in 1986, 1992, 1995 and 1998 are shown in Figure 3.18. A decline in the mean length of females age 8+ between 1986 and the 1990s is evident. A further decline is not evident during the 1990s. The size of females aged 3 and 4 increased over the time period examined. Between 1986 and 1998, the mean length of an age 3 female increased from 35 to 39cm, and age 4 from 41 to 43.5cm.

In all years examined, female growth followed the pattern implied by the VBGF in that the length increments were approximately linear. Walford plots of the size-at-age are shown in Figure 3.19. Estimates of the Walford parameters α and ρ along with the VBGF parameter estimates L_{∞} and K appear in Table 3.5. The analyses were rerun after linear interpolation of the length-at-age of uncommon age classes, which were not represented in the data. The estimates are presented in Table 3.5. Due to the low number of data points available for 1992, the analyses were run using all available data for ages 1-10 and the interpolated values only.

Table 3.5. Asymptotic length (L_{∞}) and growth rate constant (K) estimates for female hake in 1986, 1992, 1995, and 1998. Estimates obtained using Walford's method. Standard errors appear in parentheses. Asterisk denotes estimates obtained after linear interpolation of length-at-age for ages that were not well represented in the survey data.

year	ages	N	p value	r^2	ρ	α	var(ρ)	var (α)	K	L_{∞} (cm)
1986	2-10	9	<.001	0.93	0.84	9.23	0.007	13.25	0.17 (1.09)	58.35 (1.65)
1992	1-10	5	0.004	0.95	0.74	13.87	0.008	11.42	0.30 (1.16)	53.35 (1.54)
1995	1-10	7	<.001	0.92	0.65	17.36	0.006	9.58	0.43 (1.24)	49.26 (1.42)
1995	2-10	6	0.003	0.88	0.76	12.56	0.015	26.82	0.28 (1.15)	51.79 (2.18)
1998	1-10	8	<.001	0.94	0.67	16.37	0.004	6.38	0.40 (1.22)	49.14 (1.12)
1998	2-10	7	<.001	0.89	0.54	21.79	0.006	11.34	0.61 (1.36)	47.78 (1.73)
*1986	2-10	9	<0.0001	0.94	0.89	7.25	0.006	12.34	0.11 (1.06)	66.89 (1.97)
*1992	2-10	9	<0.0001	0.94	0.68	16.32	0.004	7.25	0.38 (1.21)	51.48 (1.15)
*1995	2-10	9	<0.0001	0.93	0.77	12.22	0.005	10.65	0.27 (1.14)	52.25 (1.33)
*1998	2-10	9	<0.0001	0.91	0.60	19.83	0.004	8.78	0.51 (1.29)	49.30 (1.40)

The estimates were found to be sensitive to the number of data points used in the regression and, because of this, the estimates generated using the interpolated values may be the most reliable. It is possible that an increase in growth rate occurred in the population (as suggested by the trend in the results), however, an increase in K of 0.40 over a twelve year period is highly unlikely, and given the large variance associated with all estimates, the results are unconvincing.

Density dependent and environmental factors can differentially affect the growth of young and old hake (Smith et al., 1990; Dorn, 1992). The possibility exists that the growth rate of young hake changed, and that due to the variety of factors that affect population length-at-age estimates (data, aging errors, migration, ocean conditions), this change was overlooked. A closer examination of juvenile growth is warranted.

Length frequencies of age 2 and 3 hake sampled between 1990 and 1997 in Canadian waters and on the spawning grounds in the southerly California Current (Monterey, Eureka and Columbia INPFC areas) were compared in order to explore the possibility of differences in growth between the northern and southern spawning grounds. This comparison was conducted only for the 1990s, because as mentioned previously, young hake were seldom sampled off Canada prior to 1990. Because small size limits the migration distance (Francis, 1983; Ware, 1978), it was assumed that the juveniles sampled in Canadian waters were produced in Canadian waters. The length frequency distributions in the U.S. and Canada (Figure 3.20) are all significantly different at the 5% level (Kolmogorov-Smirnov two sample test). A comparison of the combined means shows that age 2 hake are 4cm (or 12%) larger, and age 3 hake are 5cm (or close to 13% larger) in Canadian water than in the south. These results indicate that the juveniles produced in the northern California Current were larger and therefore grew faster than those produced in the southern areas during the 1990s.

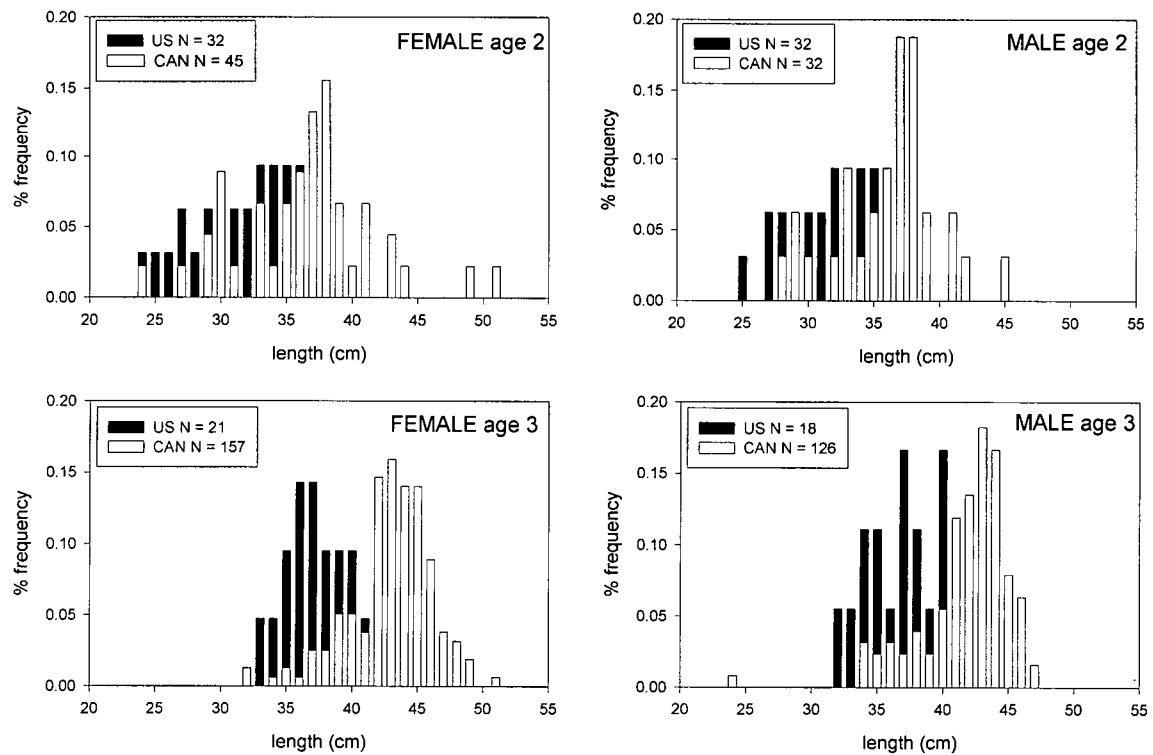


Figure 3.20. Length frequency comparisons of age 2 and 3 male and female juvenile hake produced in Canadian waters with those produced in U.S. waters during the 1990s. Figures show that juveniles produced in northern areas were larger than those produced in the southern areas.

3.4 DISCUSSION

3.4.1 Upwelling and Climate

Most major surface currents are created by the drag of the wind on the surface of the ocean, and the winds are caused by differential heating of the surface of the spinning earth (Mann and Lazier, 1996). Along the equator in the inter-tropical convergence zone, warm air rises and is replaced by cold, equatorward flowing air from the north and south. The air is warmed and rises as it flows toward the equator, and cooled as it flows to the higher latitudes and descends in the subtropical highs (around 30°N). This meridional (north-south) circulation is called Hadley circulation (Mann and Lazier, 1996). In addition, the air near the equator moves faster than air at the higher latitudes and is deflected to the west by the Coriolis force, creating the easterly tradewinds. As the air moves westward along the equator it is warmed. Air in the western Pacific rises as it warms, creating a low pressure system. As the air rises it is cooled. The cool air moves eastward and descends over the eastern Pacific, creating a high pressure system. This convective circulation is called Walker circulation. Variability in the east-west pressure gradient across the Pacific is measured by the Southern Oscillation Index (SOI) (Walker, 1924), which emphasizes zonal (east-west) sea level pressure variability.

A recently developed index, the extra-tropical Northern Oscillation Index (NOIx) (Schwing et al. 2000), represents the differences between the sea level pressure anomalies at the North Pacific High, located at 35°N in the northeast Pacific, and the low pressure system near Darwin, Australia. The NOIx is an index of meridional (Hadley) as well as zonal atmospheric patterns and as such, it summarizes the atmospheric forcing of climate change in the northeast Pacific (Schwing et al. 2000). Like the other climate-ocean indices, the NOIx is characterized by positive and negative phases. The negative phase is associated with strong oceanographic and atmospheric El Niño-like anomalies in the northeast Pacific, while positive values are associated

with La Nina conditions. The average NOIx over the summer (April-September) and winter (October-March) periods during 1977-1998 is shown in Figure 3.21. The data are available online at:

<http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html>.

The NOIx was generally negative between 1977 and 1983, positive between 1984 and 1991, and negative again between 1992 and 1998. The change to negative values of the NOIx after 1992 coincides with, and may be related to, the switch to negative upwelling anomalies observed along the coast of California during the same period (Figure 3.5b). A weakened gradient between the eastern high pressure system and the low pressure system in the west will result in a less intense westerly flow. Weaker trade winds are associated with less intense equatorward (Hadley) flow, which in turn results in weaker upwelling-favorable winds along the coast of North America. This connection between large scale changes in atmospheric circulation and upwelling points to atmospheric variability as the ultimate cause of the observed changes in hake distribution.

3.4.2 Upwelling and Euphausiids

The northern extent of hake migration is related to large-scale atmospheric and oceanographic changes, but the mechanism underlying the change in distribution has yet to be identified. There are two mechanisms that directly influence the distribution of marine species: active swimming and advection. Although hake (like all other highly migratory, nektonic species) are strong swimmers, the northward migration can be expected to be either impeded or assisted by changes in the current speed and direction (Dorn, 1995). Hake exhibit schooling behavior, and it has been suggested that migration evolved in schooling species as a consequence of the need to expand the foraging area due to localized depletion of resources by large schools

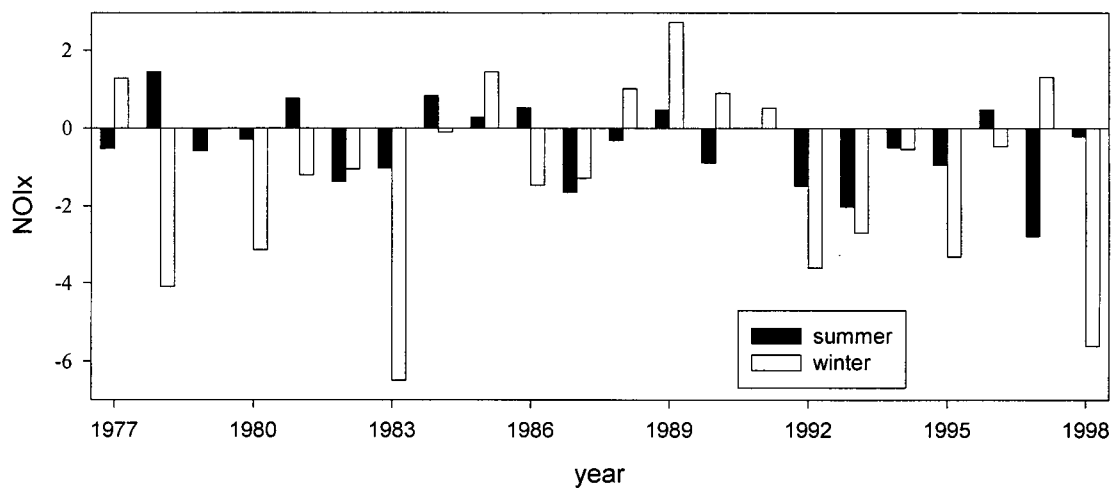


Figure 3.21. Average summer (April-September) and winter (October-March) NO_x values over the period 1977-1998. The NO_x was predominately negative between 1977 and 1983, positive from 1984-1991, and shifted to predominately negative after 1991.

of fish (Roff, 1988). Migration requires tradeoffs, because traveling long distances is energetically costly and can affect the amount of energy allocated for reproduction. In order to offset the high energetic cost of migration (and to maximize the fitness gained during the feeding migration) it is reasonable to assume that hake survived because of their ability to take advantage of favorable coastal currents during migration. Therefore, it is possible that weaker southward and/or stronger poleward currents promote the transport of more hake north to the feeding grounds during warmer than average conditions in the California Current, as Dorn (1995) suggested.

Variability in the strength of the prevailing currents may not fully explain the observed changes in hake distribution, because the impetus for the summer migration is food. If food concentration and/or feeding conditions were equal throughout the entire California Current ecosystem, it is improbable that hake would undertake such an extensive (>1000km) migration. Summer feeding migrations of pelagic fish are initiated for several reasons, all of which are related to food (Nottestad et al., 1999). Foremost is the availability of local food resources, which is affected by competition between and within species, and when depleted, drives fish to migrate in search of food (Roff, 1988). Smaller fish will reach satiation at lower food concentrations than larger fish and will not migrate as far (Nottestad et al., 1999). Feeding migrations in the northern hemisphere are directed northwards during the spring and summer, because primary and secondary production propagates from south to north and prompts the fish to follow (Mann and Lazier, 1996). A further reason the fish move north to feed is that, in boreal latitudes, day length increases throughout the summer, thereby increasing the time visual feeders such as hake can spend feeding, and increasing the energy intake and overall fitness (Suthers and Sundby, 1996). As discussed in Chapter 1, changes in climate can affect primary and secondary

production and species interactions. A change in any of these factors might result in changes in the extent of the summer feeding migration of hake.

That climate affects the distribution of marine fishes is nothing new - there is an extensive body of work on the effects of water temperature on fish distribution. For example, Smith (1985) documented a northward shift in the distribution of many fish species in the California Current between 1955 and 1959, during the onset and transition to an El Niño event. It was unclear whether the change in distribution was directly related to temperature, or related to the effects that warming had on food availability and quality. More recently, a study showed that the distribution of Pacific salmon in the North Pacific is limited by thermal barriers (Welch et al., 1993). However, in spite of the close link between temperature and fish distribution, the distribution of key fish species in the California Current changed dramatically after 1989 (Chapter 1), while no temperature index (e.g. the PDO and coastal SST) exhibited a significant shift.

McFarlane and Beamish (2001) examined the northward shift in the distribution of Pacific sardine (*Sardinops sagax*) along the west coast of North America during the 1990s. No relationship between SST and the northward extension of sardine distribution could be identified. Instead, the authors suggest that the California Current ecosystem underwent a reorganization with the 1989 regime shift that improved the production of diatoms (a key food item), and created an environment favorable for sardine.

The distribution of sardine in the California Current is closely linked with abundance (McFarlane and Beamish, 2001) – in high abundance years the range expands. Therefore, improved primary production may lead to increased survival and abundance, and ultimately to range expansion. Unlike sardine, the change in distribution of hake does not appear to be closely linked to abundance. Therefore, regime shifts can affect dominant species differently. During the

1990s, as the hake moved farther north, there was no concurrent increase in abundance. This is an indication that the change in hake distribution was density-independent.

In order to explore hake feeding migration dynamics fully, information on their primary prey item, euphausiids, is required. Significant evidence has accumulated that hake distribution is closely linked to the presence of euphausiids (a review may be found in Chapter 2), but the converse might not be true. For example, there was no observed effect on euphausiid biomass in the California Current after the initiation of the foreign joint-venture fishery along the west coast of North America, which removed sizable amounts of hake, a major predator on euphausiids (Mullin and Conversi, 1989). If food is an important factor in hake migration as Nottestad et al. (1999) suggest, the fact that hake have not been shown to negatively affect euphausiid abundance on a large scale is further evidence that the change in hake distribution in the 1990s was unrelated to hake biomass.

Several lines of evidence indicate that euphausiid distribution is greatly affected by variable current patterns. For example, in the Barents Sea, *Thysanoessa* spp. distribution varies interannually and seasonally due to variations in the intensity of the North Atlantic Current (Siegel, 2000). Miller et al. (1985) tracked changes in the zooplankton community off the west coast of Oregon during the 1983 El Niño and showed that the zooplankton community was dominated by more southerly species, and that the relative abundance of the usually dominant euphausiid, *Thysanoessa spinifera* was lower than usual. Observations that weak upwelling is related to higher diversity of the zooplankton community have been made throughout the California Current ecosystem (Siegel, 2000; Mackas et al., 2001). During El Niño or El Niño-like years, the change can be attributed to the intrusion of southern zooplankton species as the result of weakened upwelling and a northward shift in the Subarctic Boundary (Siegel, 2000a). An invasion of smaller, southerly zooplankton species during weak upwelling years would reflect a shift to less desirable prey, because hake prefer larger euphausiid species such as *T.*

spinifera (Tanasichuk, 1998). A change in the relative abundance of larger prey due to a southerly invasion will occur first in the southern California Current and, if conditions persist, propagate northward. No published data are available on the relative abundance of large and small zooplankton off California in the 1980s versus the 1990s, but the possibility exists that a change in the zooplankton community composition off California induced hake to move farther north in the 1990s.

Substantial changes in euphausiid biomass have also been linked to changes in upwelling. Brodeur and Pearcy (1992) examined fish diets off the coast of Washington and Oregon and found that euphausiids dominated the diets during strong upwelling years. This result implies a positive relationship between euphausiid biomass and upwelling. More direct evidence was found by Smith (1985), who showed that euphausiid displacement volume (proxy for biomass) decreased off the coast of California during El Niño years, and by Gomez (1995) who showed that *Nyctiphanes simplex* occurs in high densities off Baja California in strong upwelling years. The change in abundance might be linked to changes in distribution as discussed above, but Smiles and Pearcy (1971) argue that off Oregon and California, recruitment success (production) is determined by strong upwelling because the onset of upwelling determines the amount and quantity of phytoplankton available to euphausiid larvae.

Synchronous with a weakening of summer upwelling-favorable winds in the early 1990s, both *E. pacifica* and *T. spinifera* increased in abundance off the WCVI (Mackas et al., 2001). These results are rather surprising, given the previous discussion. Mackas et al. suggested that during periods of below average upwelling or downwelling, euphausiid recruitment is high because the larvae are maintained on the food-rich continental shelf and not flushed offshore into relatively food-poor oceanic waters by strong Ekman transport, which occurs during strong upwelling events.

The fact that weaker than average upwelling affects euphausiids in the northern and southern California Current differently adds to the argument that the summer distribution of hake changed in the 1990s in relation to food. Based on the previous discussion, smaller tropical euphausiid species would be expected to be present off the coast of North America during periods of weak upwelling-favorable winds, and as mentioned previously, hake prefer the larger species. A shift in dominance to smaller species with the intrusion of southern water may have induced hake to move north in search of larger species. Additionally, recruitment and subsequent abundance of euphausiids in the southern California Current may have declined somewhat or remained stable from the 1980s to the 1990s in the 1990s, while in the north, the abundance increased dramatically (Mackas et al., 2001). Although data are unavailable for the southern California Current, the results of Mackas et al. alone imply the formation or intensification of a north-south gradient in food availability in the 1990s. Less desirable or less abundant (or a combination of both) prey in the south would induce hake to forage farther north. This response, combined with the migration theory of Nottestad et al. (1999) may provide a reasonable explanation for the observed changes in hake distribution.

3.4.3 Growth

A change in the relative abundance of food throughout the ecosystem, coupled with warmer waters and changed migration distance were expected to affect hake growth. Unfortunately, the results of growth analysis were inconclusive. As with any study, the results are only as good as the data. Fish growth studies that are performed in a relatively closed system such as a lake and/or within a resident marine population can be expected to yield reasonable results because a cohort present in one year will be present in the next. On the other hand, when examining a highly migratory stock whose availability to the fishing gear depends on geography, oceanography, time of year, and age, it is more difficult to study growth. The fish must be

sampled throughout their range, especially when the geographic distribution depends on size, and all efforts must be made to sample fish at every age. The U.S. triennial surveys meet the requirement of sampling throughout the geographic distribution, however, because the spawning grounds were located offshore and southward, the youngest ages were less available to the surveys prior to the 1990s. The biology of hake further complicates the analysis. The three year cycle of strong recruitment means that the less abundant age groups are not sampled adequately, and when the sample size is small, as in the present case, the uncommon age groups are sometimes not sampled at all. Literal interpretation of the results is therefore not appropriate. The question of whether the decrease in size of the largest fish sampled (and therefore the predicted L_{∞}) is the result of a change in growth rate remains unanswered, in part because of the very real possibility that the decrease is related to length selective mortality from the fishery (Smith et al., 1990).

The comparison of the size of juveniles produced in Canadian waters with those produced in the southern areas of the California Current indicates that the growth rate of juveniles differed in the two areas in the 1990s. Juveniles reared in northern waters were larger, and therefore grew faster than juveniles reared in the traditional, southern nursery area. When this result is considered along with the results of Mackas et al. (2001), it suggests that during the 1990s, feeding conditions in the northern California Current were better than those in the southern areas, and that increased food availability facilitated the faster growth of juveniles produced off Canada.

3.4.4 Relevance of the Results

The wisdom of using predictions based on simple environmental correlations has been reviewed and criticized extensively in the literature (e.g. Drinkwater and Myers, 1987; Walters and Collie, 1988). The criticisms are most often directed at attempts to predict recruitment using a suite of (but in many cases just one) environmental variables that may or may not directly

affect fish production. In general, the simple correlative relationships do not stand the test of time. However, environment-fish studies have been quite successful at predicting fish distribution, because distribution reflects fish preference, while recruitment is a function of survival at several stages in early life, and in general, only one of the stages is related to the environmental variable selected for analysis (Walters and Collie, 1988). In order for predictive models to be useful to management, and to direct future research, the identification of key processes by which the environment influences fish population dynamics is required (Hollowed, 1992).

A promising relationship exists between upwelling, hake distribution, and food availability. The results of the present study indicate that future research on hake distribution should include work on the relative availability of euphausiids throughout the feeding distribution. In addition, the results could be useful to managers of the Canadian fishery if used in the 'report card' manner of King et al. (2001): provided with information on the present environmental conditions, and a knowledge of the manner in which ocean conditions are likely to affect a fish population, a manager is armed with information that can guide harvest recommendations within a given regime.

3.5 CONCLUSIONS

The aim of this study was to explore changes in spatial distribution of Pacific hake in the 1990s, to develop a predictive index of the migratory proportion of the stock that migrates into Canadian waters, on both interannual and decadal scales, and to explore the possibility that the change in distribution corresponded with a change in growth. The conclusions are:

3.5.1 Abundance

- Increased population size is not a factor in the northward shift in hake distribution in the 1990s.
- The single best predictor of the proportion of mature hake biomass in Canadian waters is the average Bakun upwelling index anomaly over April, May and June at 33°N. This can be taken as an indicator of ocean conditions in the southern part of hake distribution, at the time that hake begin their northward feeding migration.
- The Bakun upwelling index is related to winds and is therefore related to, and a better indicator of large-scale circulation than is sea surface temperature.
- Although hake distribution is related to physical indicators of ocean conditions, evidence is provided that the change in distribution is a function of a change in the availability of the key food item - euphausiids.

3.5.2 Growth

- The migratory distribution was maintained in the 1990s, in that the largest fish continued to move the farthest north.
- The size of fish sampled at the northern limit of the distribution declined as the northern limit extended to higher latitudes. This in itself is suggestive of a decline in the size of the largest fish in the population.
- The results of growth analysis of adult hake are inconclusive.
- Juveniles aged 2 and 3 produced in Canadian waters during the 1990s were on average 12 and 13% larger, respectively than fish of the same age produced in the southern California Current. This suggests that hake produced in Canada grew faster than those produced in more southerly regions, and can be explained by the difference in availability of euphausiids in the two areas.

3.6 FURTHER WORK

The results of this study point to euphausiids as the key to understanding the distribution and growth patterns of Pacific hake. Future studies on the effects of environmental conditions on hake distribution and growth should therefore focus on the relationship between upwelling and euphausiid species composition and abundance throughout the entire California Current ecosystem, and on the relative availability of food in the northern and southern areas of hake distribution.

It was not possible to present conclusive evidence that the changes in atmosphere-ocean conditions subsequent to the 1989 regime shift affected hake growth in this study. The main problems were small sample size and the triennial nature of the coastwide surveys. In order to improve the examination of hake growth, increased sample size and sampling frequency are required. Annual samples of hake size-at-age from California to British Columbia might enable a detailed examination of changes in growth rate. Length-stratified samples should be collected in order to ensure adequate sampling of the smallest (youngest) size classes.

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