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Climate Variability and Pacific Sardine Populations and Fisheries

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Abstract.—Pacific sardine *Sardinops sagax* supported the largest fisheries in the world during the 1930s and early 1940s, and again in the 1980s. These peak catches reflected major increases in abundance of three sardine populations: off Japan, off western North America (centered off California), and off western South America (centered off Chile). The dramatic increases and decreases in these stocks were more or less synchronous and have been related to patterns in climate–ocean conditions (i.e., decadal scale regimes). Regime shifts have a multidimensional impact on the organization of ecosystems. Consequently, the North American sardine populations had varying responses (by area) to regime shifts. The changes in sardine abundance, distribution, and behavior provide an example of the need to consider ecosystem changes as distinct reorganizations rather than simply cycles or oscillations.

Introduction

Pacific sardine *Sardinops* spp. constituted the largest fisheries in the world during the 1930s and early 1940s and again in the 1980s, accounting for approximately 13 percent of world fish (and shellfish) production during these time periods (FAOSTAT website: <http://apps.fao.org/page/collections?subset=fisheries>). The major sardine populations, off Japan and the Asian Far East, off Chile and the west coast of South America, and off California and the west coast of North America, fluctuated more or less in synchrony for most of the 20th century (Kawasaki 1991). These fluctuations in abundance have been related to decadal scale patterns in climate–ocean conditions (Beamish et al. 1999), however, the mechanisms responsible for the large fluctuations in sardine abundances and behavior have remained elusive.

The collapse of sardine stocks off the west coast of North America in the late 1940s corresponded to the collapse off Japan. Beginning in the late 1970s, the stocks off Japan, California, and Chile synchronously increased in abundance. Stocks declined off Chile and Japan in the late 1980s and early 1990s, but those off California have not yet declined. These collapses had considerable social and economic impacts. Kondô (1986) relates the prosperity of coastal communities off Japan to the increases and decreases in sardine abundance. It is worth remembering that the California Cooperative Oceanic Fisheries Investigation (CalCOFI) studies were initiated in 1949 in an ongoing attempt to explain the economically devastating collapse of sardine stocks in the late 1940s off the west coast of North America.

Recent studies have shown that climate–ocean and

biological systems are not stable but shift from one state to another (Ebbesmeyer et al. 1991; Polovina et al. 1995; Mantua et al. 1997; Beamish et al. 1999; Overland et al. 2000). In this paper we review the recent and historical changes in sardine distribution, abundance, and fisheries in relation to decadal scale climate–ocean changes and examine possible mechanisms to show how sardine respond to climate variability and ecosystem change.

Distribution

Pacific sardine are a coastal pelagic species inhabiting the coastal regions of the whole Pacific Ocean. They are capable of long migrations (more than 2,000 km), although these migrations generally occur only when abundance is high. Sardine of the north- and southeastern Pacific and western Pacific have often been differentiated into three distinct species: *S. sagax* in the southeast Pacific off the west coasts of Peru and Chile; *S. caeruleus* in the northeast Pacific off the west coasts of North America from southern Alaska to the southern tip of Baja California, Mexico, and in the Gulf of Califor-

nia, Mexico; and *S. melanostictus*, a Far Eastern sardine that inhabits the Sea of Japan and Pacific coastal waters of Japan (reviewed in Grant and Bowen 1998). However, recent information (Hedgecock et al. 1989; Parrish et al. 1989; Grant and Bowen 1998) indicates the genus *Sardinops* may be monospecific as a result of population collapses followed by recolonizations. Within the major geographic areas of sardine distribution, regional subpopulations are thought to exist.

Northeast Pacific Ocean

The Pacific or California sardine of the California Current has a range along the coast of North America that extends from southern Alaska (57°N) to the southern tip of Baja California Sur (23°N) and into the Gulf of California (Figure 1) in periods of high abundance and expansive migratory behavior. In years of low abundance, refuge populations of sardine are restricted between southern California (34°N) and Baja California Sur (23°N). This is also the region of the primary spawning grounds. However, eggs and larvae have been observed as far north as Washington, implying a considerable expansion of spawning activity into northern wa-

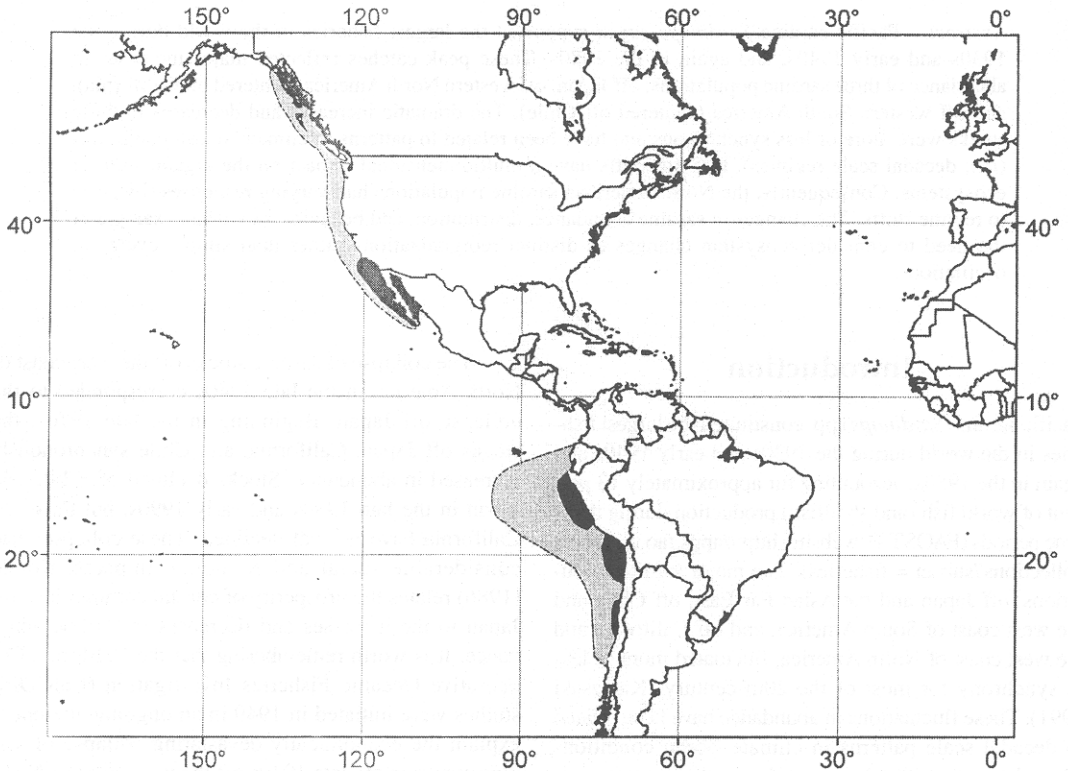


Figure 1. Distribution of sardine in the north and southeastern Pacific Ocean. Black area is occupied when population is at a low level of abundance; gray area indicates range when abundance is high (Modified from Schwartzlose et al. 1999).

ters during periods of high sardine abundance (Walford and Mosher 1941; in Parrish et al. 1989; McFarlane and Beamish 2001; R. Brodeur, National Marine Fisheries Service, personal communication).

Studies on historical and current populations of the sardine of the California Current indicate a significant north-south cline in size at age. The significance of this morphological variation, along with probable correlated life history features such as age at first reproduction, maximum size, and age-specific mortality, has led some authors to propose the existence of three genetically distinct subpopulations or stocks: a northern stock occurring from northern Baja California (30°N) to Alaska (55°N), a southern stock ranging along the Pacific coast of Baja California (23-30°N), and a Gulf of California stock (Parrish et al. 1989). Radovich (1982) proposed a fourth far northern stock consisting of fish in the Pacific Northwest fishery based on meristic and morphometric variations. While the three stocks on the Pacific coast show geographic overlap over time, shifting latitudinally in synchrony, their occurrences at any given time are spatially distinct (Vrooman 1964). Tagging studies suggest that significant intermixing of sardine occurs between northern Baja California and California, and be-

tween California and the Pacific Northwest (Clark and Janssen 1945, in Parrish et al. 1989; Janssen 1948, in Parrish et al. 1989).

Hedgecock et al. (1989) examined a variety of morphological features and protein allozymes in samples taken from five widely separated stocks stretching south from Tomales Bay in central California to Magdalena Bay in southern Baja California Sur and at Guaymas in the Gulf of California. The five populations were considered to be genetically identical at the 32 loci examined. The existence of rare alleles shared by individuals in widely separated locations suggests substantial gene flow (Hedgecock et al. 1989). So, while the sardine of the California Current may be considered to form two and even three fishery stocks, the population as a whole is considered to comprise a single homogeneous gene pool.

Northwest Pacific Ocean

The Far Eastern sardine occurs in the Sea of Japan and off the Pacific Coast of Japan from 29°N in the south to the east coast of the Kamtchatka Peninsula (54°N) in the north (Figure 2), areas influenced primarily by the

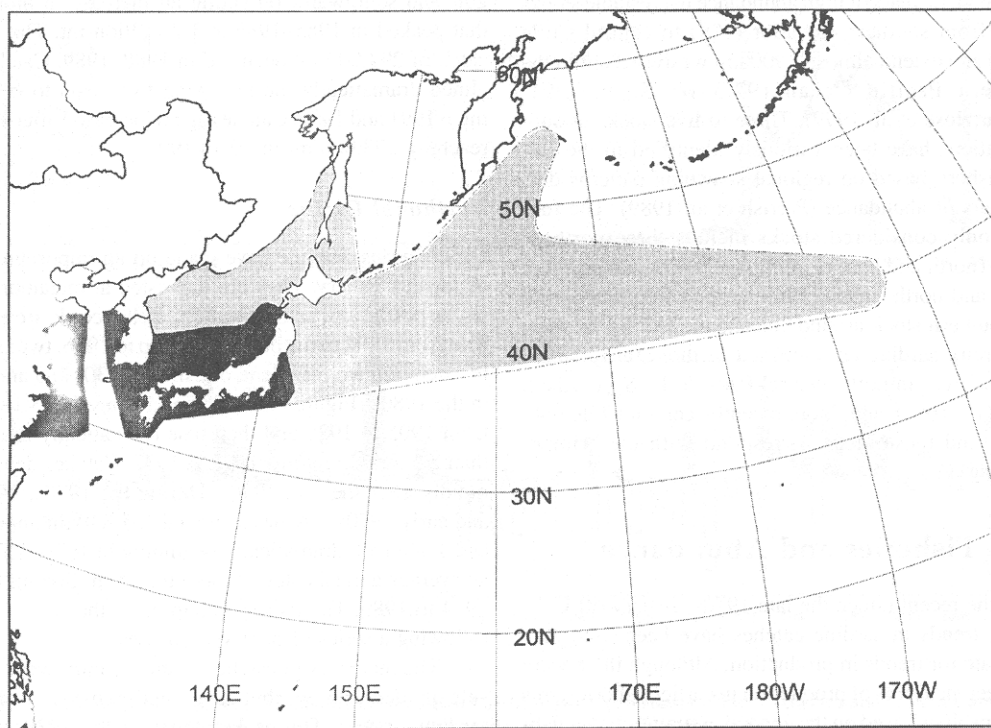


Figure 2. Distribution of sardine in the northwestern Pacific Ocean. Black area is occupied when population is at a low level of abundance; gray area indicates range when abundance is high (Modified from Schwartzlose et al. 1999).

Kuroshio Current and to a lesser extent the colder Oyashio Current (Tokai Regional Fisheries Research Laboratory 1960, in Parrish et al. 1989). Two and possibly four subpopulations or races (Kondô 1986) are defined based on their geographic distribution, particularly during spawning, and phenotypic variation, though genetic differences have not been found (Hiyama et al. 1995; Schwartzlose et al. 1999). In the two-subpopulation scheme, one inhabits the nearshore areas of the Sea of Japan, the East China Sea, and the south coast of Japan, and the species distribution is restricted to these areas in years of low abundance. The second subpopulation, distributed into the northern reaches of the Sea of Japan, along the Pacific coast of Japan, and as far east as 165°W, has a more ephemeral existence but becomes much larger than the one in the Sea of Japan when conditions are favorable (1980s; Schwartzlose et al. 1999). The large Pacific stock is thought to derive from an increase in stock size and expansion of the Sea of Japan northern subpopulation through the straits dividing the islands of Japan.

Southeast Pacific Ocean

The Chilean Sardine inhabits coastal waters off Chile and Peru that are influenced by the Humboldt Current (Figure 1). In years of high abundance harvestable stocks occur from southern Ecuador (1°S) to central Chile (42°S) and extend almost 1,900 km westward out in the southern Pacific Ocean (97.5°W; Serra 1991; Schwartzlose et al. 1999). Three to five stocks or subpopulations have been variously identified in the sardine fishery based on regional spawning patterns during years of abundance (Parrish et al. 1989). The four commonly considered stocks include three northern stocks (north and central Peru, south Peru and northern Chile, and north-central Chile around Coquimbo) and one southern stock around Talcahuano (37°S). In years of scarcity sardine are confined to three fairly small, discreet areas in north-central Peru (5–12°S), northern Chile (18–16°S), and, more recently, central Chile (34–39°S), and these areas correspond with the primary breeding areas.

Fisheries and Abundance

Until the recent (since the late 1970s) fishery off California, trends in sardine catches have been used as a surrogate for trends in production. Although there were no direct measures of production in earlier fisheries, this relationship is based on the general assumption that fishing effort and catches were related to abundance, particularly in a largely unregulated fishery where the individual product value was small.

Northeast Pacific

The catch of sardine in California ranged from 500 metric tons (mt) to more than 1,000 mt during the period 1889–1899 (State of California Fish Commissioners Reports and Reports and Bulletins of the U.S. Commission of Fish and Fisheries, in Schwartzlose et al. 1999). Sardine catches of 65,903 mt and 75 mt were recorded in California and British Columbia (BC), respectively, during the 1917–1918 season.

The fishery off California to British Columbia rose dramatically after 1926, reaching a peak of 726,000 mt in 1935 (Figure 3A), then declined dramatically in the late 1940s. The collapse of the fishery progressed from northern areas (BC and Washington) to California. The fishery was closed and the stock protected in the early 1970s. A slow recovery of this stock became evident in the early 1980s. The fishery began to expand off California and northern Mexico in the early 1990s, and average annual catches have exceeded 100,000 mt since 1997.

A fishery began in the Gulf of California during the late 1960s when declining stocks off the west coast of Baja California sent boats into the gulf after the previously untapped stocks (Figure 3A). Fishing was limited to the central east coast until 1979–1980 when it expanded both into the cooler waters of the northern gulf and southward, reflecting an increase in biomass that peaked in 1985–1986 at 1.2 million mt. The peak catch of 294,000 mt occurred in 1988–1989. Catch declined dramatically the following two years to <7,000 mt in 1991 and 1992. Catches again increased after 1993, reaching 203,000 mt in 1996–1997.

Northwest Pacific

For centuries, sardine have made up an important part of Japan's fishery. They are harvested at metamorphosis, as postlarvae, and as adults. Catch records are available from 1894 to the present, and up to 1996, two peaks in catch size were evident, one in the 1930s and another in the 1980s (Figure 3B). Catches averaged 253,180 mt from 1905 to 1926 and then rose dramatically to more than 2.6 million mt in 1936 and 1937. Catches declined rapidly after the mid 1940s. During the 1950s, 1960s, and early 1970s, catches averaged 131,840 mt annually and again rose dramatically beginning in 1976–1977 to an average annual catch of more than 5 million mt from 1984 to 1989. The fishery collapsed in the early 1990s following a series of poor year classes.

The increases in catches in this century were a result of increases in abundance and expansion of the sardine's range. The peak catches of the 1930s were taken mainly from the Sea of Japan stock, particularly from the northwest. The peak abundance and catches of the 1980s differed from that of the 1930s in that the

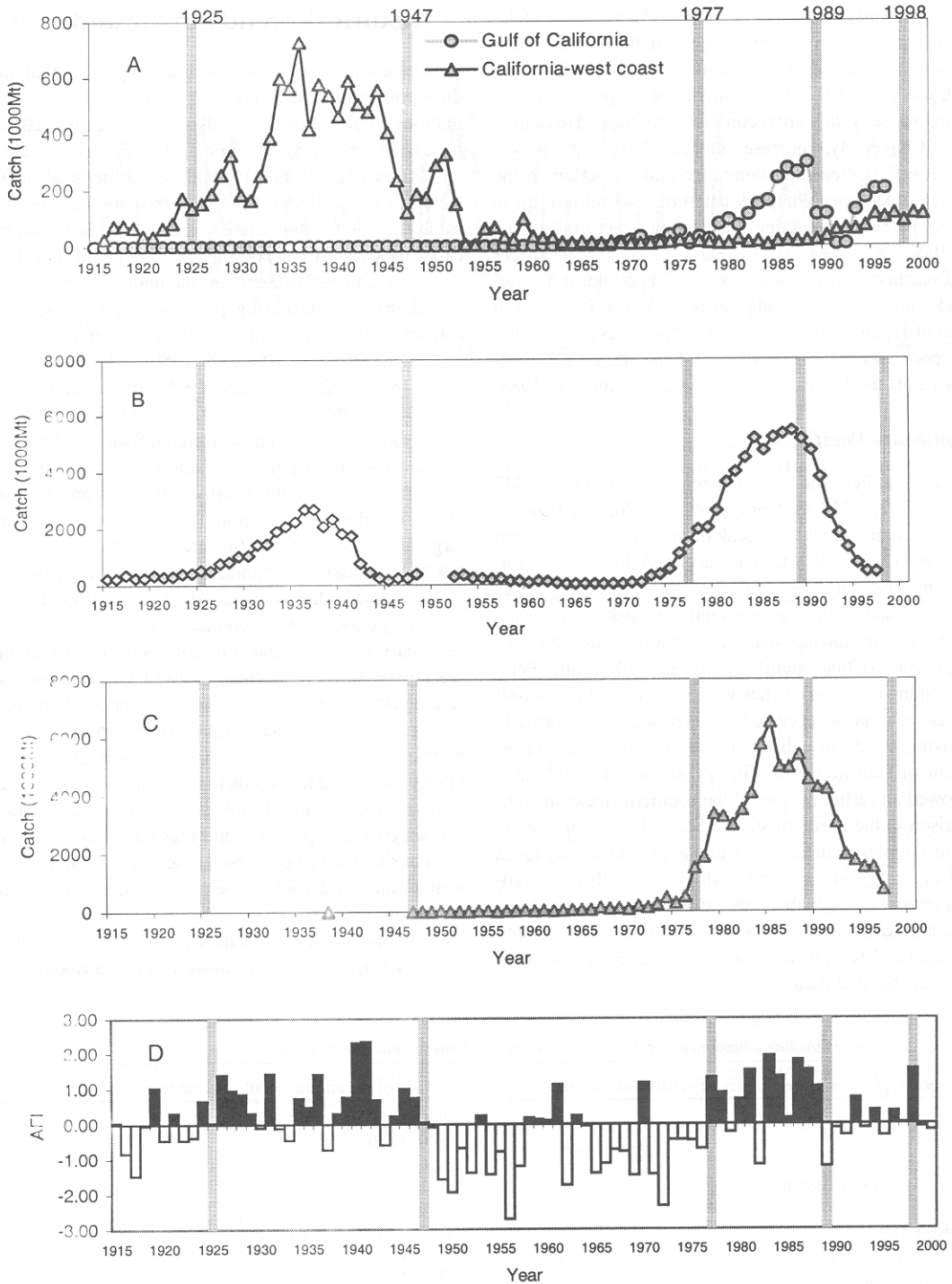


Figure 3. Total catch of sardine, 1915–2000. (A) Northeast Pacific ocean (west coast of North America and Gulf of California). Catch statistics from 1916–1968, Radovich (1982); 1969–1982, FAO yearbooks; 1983–2000, updated from Hill et al. (1999). (B) Northwest Pacific ocean (Japan and surrounding waters). Catch statistics from 1915–1952, Nakai (1960); 1953–2000, FAO yearbooks. (C) Southwest Pacific ocean (Chile and Peru). Catch statistics from 1938–1997, FAO yearbooks. (D) The Atmospheric Forcing Index—lines indicate regime shift years of 1925, 1947, 1977, 1989, and 1998.

range expansion reached far off the Pacific coast of Japan, and the major catches occurred in this Pacific population southeast of Hokkaido and east of Honshu. During the years 1977–1988, catches of more than 1 million tons per year were recorded off southeast Hokkaido.

Conversely, decreases in catch have been associated with decreasing abundance and reduction in the range of sardine. The peak catch of 5.43 million mt in 1988 preceded a decline that saw the catch fall to 0.3 million mt in 1996. By the early 1990s sardine stocks off northern Japan had disappeared, and later in the decade only a small population remained in the western Sea of Japan. This most recent decline was precipitated by poor survival of one-year-old fish (i.e., poor recruitment) off the Pacific coast of Japan beginning in 1988.

Southeast Pacific

Catches off Peru and Chile averaged 19,290 mt from 1947 to 1965, 208,720 mt from 1966 to 1976, and then increased dramatically to a peak of more than 6 million mt in 1985 (Figure 3C). Catches declined dramatically following 1992. Of the four relatively discrete fishing stocks off Peru and Chile, the two southern stocks had consistently smaller catches than the two more northerly stocks off northern Chile–southern Peru and north–central Peru. Declining trends in catches were experienced by all four stocks after peaks occurred in these stocks in a northerly moving trend through the 1980s. The trend in recruitment of sardine to this fishery as two-year-olds also showed an earlier decline of the southern stocks in comparison to the northern stocks. Scale deposition rates in core samples (which reflect trends in abundance) taken off Peru suggest that sardine stocks were also undergoing periods of high abundance during the 1930s and low abundance in the early 1900s and from the 1940s through the mid 1970s (Schwartzlose et al. 1999; Baumgartner et al., unpublished data).

Historical Trends in Abundance

Evidence continues to accumulate suggesting that sardine populations have not only undergone large fluctuations in abundance, but also that these fluctuations have been synchronous around the Pacific Ocean (Soutar and Isaacs 1974; Kondô 1986; Baumgartner et al. 1992; Beamish et al. 1999). Kondô (1986) summarized the catch records for the Japanese sardine fishery from the early 1600s until the present and concluded that there has been a history of extreme fluctuation in abundance. He identified alternating periods of good and poor catches starting in the mid-1600s. Peak catches of sardine occurred from 1640–1660, 1680–1730, 1815–1840, 1860–1885, 1920–1945, and 1975–1995 (Table 1).

Baumgartner et al. (1992) analyzed fish scale deposition rates in core samples from the Santa Barbara Basin and identified periods of increased sardine scale deposition from about 1820–1880 and from 1900 to 1950. The Baumgartner et al. (1992) data did not show large abundances of Pacific sardine in the early 1600s but do show that the abundance was high from 1670 to 1750, similar to Japanese records (Kondô 1986). In general, the periods of the good and poor catches of Japanese sardine show some similarity between strong and weak periods off California (Table 1). Of more interest, Baumgartner et al. (1992) show that large abundance fluctuations were characteristic of the dynamics of the populations as far back as the year 360. Beamish et al. (1999) compared the trends in abundance of Pacific sardine to trends in abundance of Pacific salmon *Onchorynchus* spp. and found that they were synchronous during the last century. These trends in abundance were related to decadal scale patterns in climate–ocean conditions.

An updated version of the Baumgartner et al. (1992) analysis (Figure 4), using more recent sediment sam-

Table 1. Records of sardine abundances off Japan and California (from Beamish et al. 1999).

Historic reports of large catches of sardine off Japan	Periods of accumulation of sardine scales off California
1920–1945	1900–1950
1860–1885	1840–1870
1815–1840	1820–1840
No record of large catches	
1680–1730	1670–1750
1640–1665	No record of large catches
	1510–1540
	1330–1370
	1240–1280
	1150–1190
	915–1040
	680–705
	460–630
	360–400

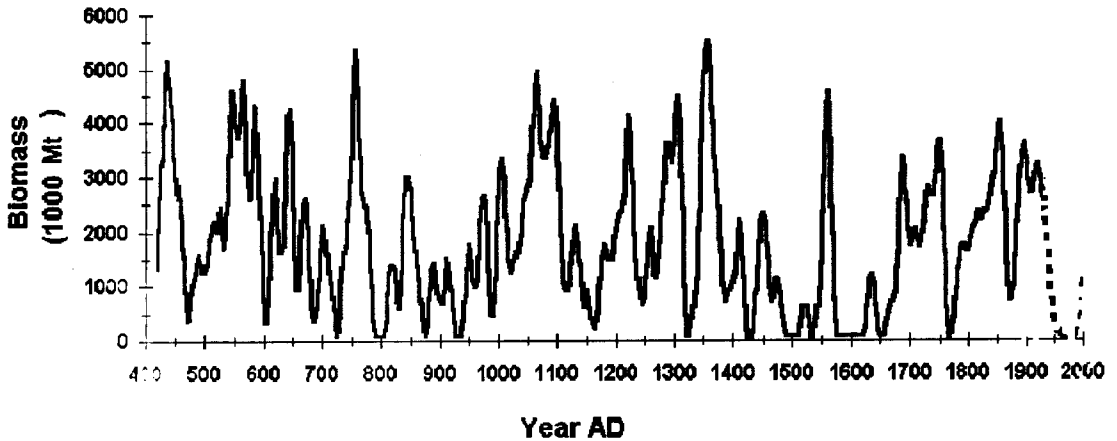


Figure 4. Hindcast of sardine biomass from scale-deposition rates in Santa Barbara Basin off southern California (heavy black curve). Biomass estimates of California fishery stock shown by superimposed dashed curve (Baumgartner et al., in preparation).

pling and calibrating to virtual population analysis biomass estimates provides a reconstruction of the sardine population biomass in the region from northern California to north-central Baja California (Baumgartner et al., unpublished data). The reconstructed biomass data represent five-year averages from AD 420–1975 and are smoothed with a 15-year filter. This figure emphasizes the differences in the information content regarding the dominant time-scales of variability that can be discerned from the fisheries data and more recent biological surveys that span the last 50–75 years compared with the fish scale–deposition data that span the past 1,600 years. The biomass estimates of the modern population cover only a portion of one realization of a multidecadal oscillation in abundance, whereas the scale–deposition record contains more than 25 realizations (Baumgartner et al. 1992). The fish scale record of Figure 4 also shows that there are important multicentennial-scale changes in the past 1,600 years that must interact in some way with the multidecadal variability. Similar relationships between multidecadal and multicentennial variability is seen in paleoclimate proxy records from the Santa Barbara Basin (Field and Baumgartner 2000).

Relationship With Climate

A number of recent studies have related large-scale climate changes to fluctuations in fish abundance (Beamish et al. 1999; Hare and Mantua 2000; McFarlane et al. 2000; Zhang et al. 2000). For the North Pacific, these large-scale climate changes have been characterized by changes in the Aleutian Low Pressure system, atmospheric circulation patterns, and spatial sea surface tem-

peratures. In general, the intensity and position of the Aleutian Low determines atmospheric circulation patterns. Atmospheric circulation patterns drive oceanic circulation (mid-ocean and coastal current patterns), which determines the amount of Ekman pumping and spatial distribution of sea surface temperatures. McFarlane et al. (2000) used indices that measured these three climate–ocean conditions (Aleutian Low Pressure Index, Pacific Circulation Index, and Pacific Interdecadal Index) to produce one composite index, the Atmospheric Forcing Index (AFI; Figure 5). A positive AFI score corresponds to an intense Aleutian Low, above-average frequency of southwesterly and westerly atmospheric circulation, a winter warm phase of the Pacific Decadal Oscillation, which has a pattern of general cooling in the central North Pacific and warming in the coastal areas. Abrupt changes in AFI in the early 1920s, late 1940s, mid 1970s, and late 1980s coincide with climate regime shifts of 1925, 1947, 1977, and 1989 (Mantua et al. 1997; Minobe 1997; Beamish et al. 1999; Hare and Mantua 2000; McFarlane et al. 2000). The extreme positive AFI value for 1998 may indicate the onset of a new climate regime (McFarlane et al. 2000).

To illustrate the basin-wide responses of sardine to climate regime shifts, the catch (mt) of Japan, Chile, and California stocks were combined by averaging the standard deviates (Ebbesmeyer et al. 1991) of each catch series. Initially, each series was detrended by subtracting the long-term mean. The averaged standard deviates of sardine catch changed systematically across regime shift years (Figure 6). Typically, positive AFI values (i.e., strong Aleutian Lows, above average southwesterly and westerly atmospheric flow, and cooler sea

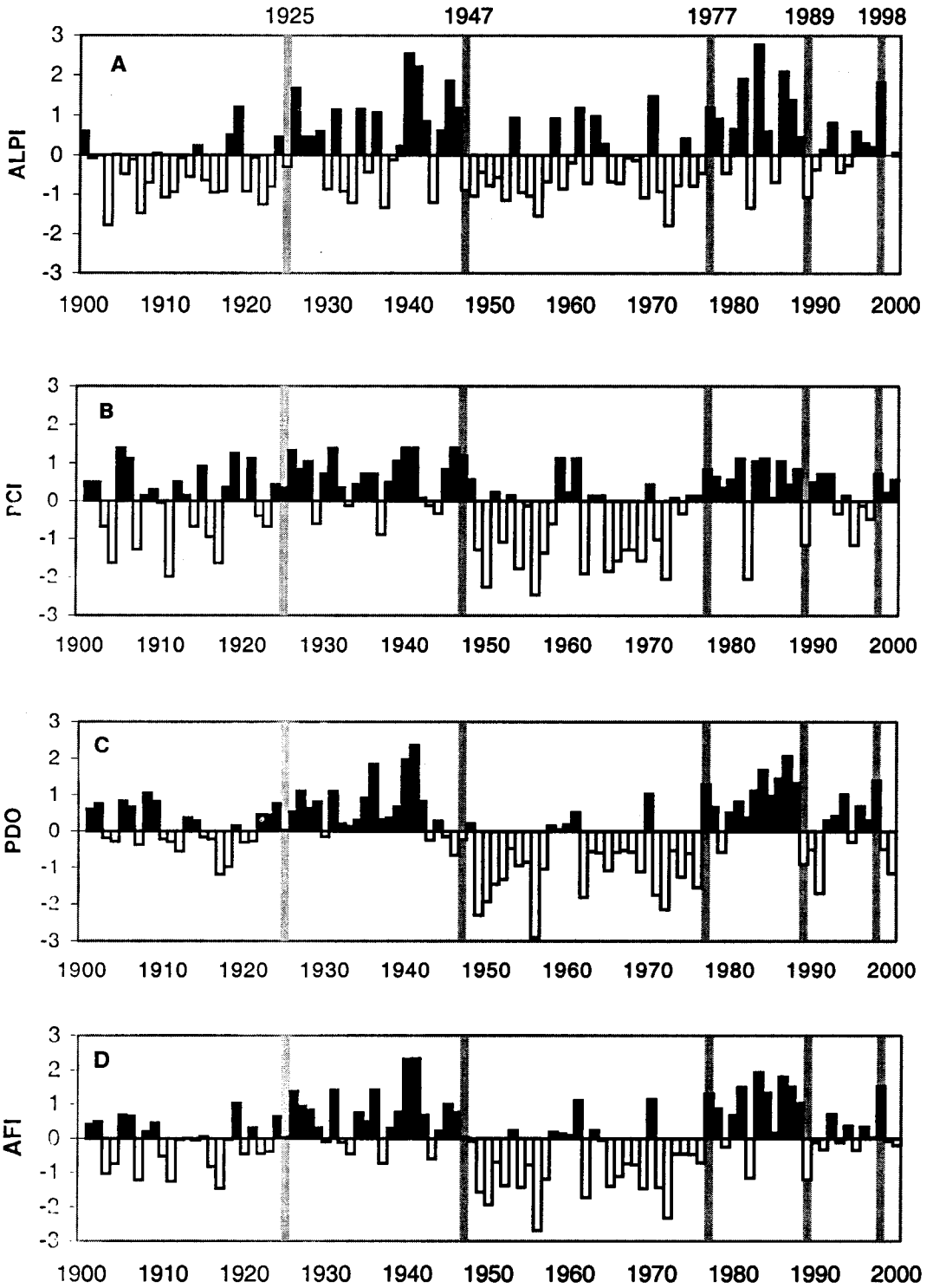


Figure 5. Indices of climate change. (A) Aleutian Low Pressure Index. (B) Pacific Circulation Index. (C) Pacific Interdecadal Index. (D) Atmospheric Forcing Index, developed from the three indices as represented by standardized scores along the first principal component (from McFarlane et al. 2000).

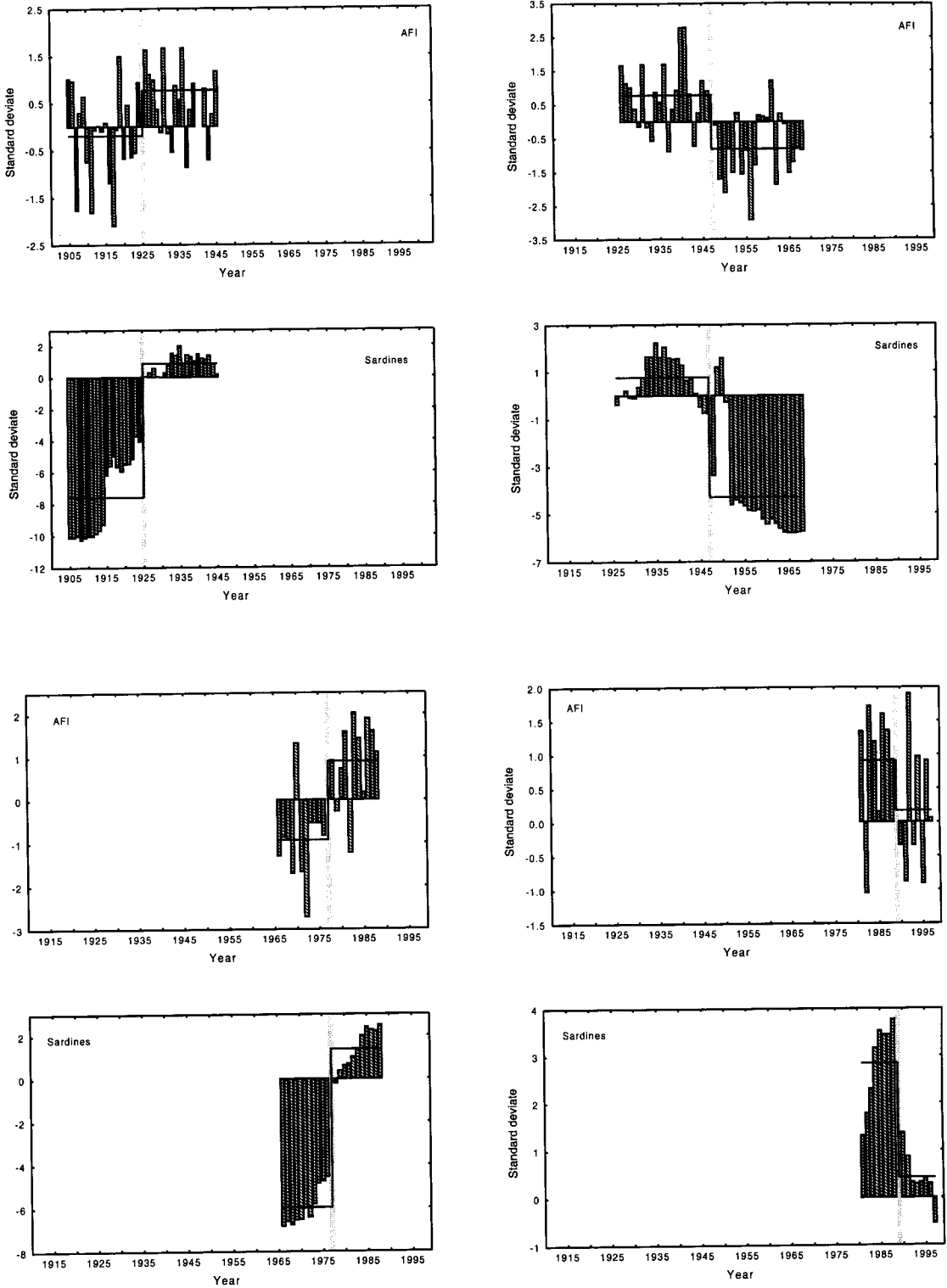


Figure 6. The mean standard deviates of the Atmospheric Forcing Index (upper panels) and total sardine catches (lower panels) time series illustrating the synchrony of moving and decreasing sardine abundance and climate/ocean changes.

surface temperatures in the central Pacific) correspond to higher sardine abundance. It is clear that on a global scale (Japan, Chile, and California) there is a strong relationship between sardine abundance and changes in climate-ocean conditions (Figure 6). On a regional scale, previous authors have shown that the response of sardine to climate conditions may vary. For example, the increased abundance of the Japanese sardine occurred mainly in the Sea of Japan in the 1930s and early 1940s and off the Pacific coast of Japan in the 1980s. Off California (and the rest of the west coast of North America) the increase in abundance occurred in the Pacific coast stock in the 1920s, 1930s, and 1940s and in the Gulf of California stock in the late 1970s and 1980s (Figure 3A). This stock has provided relatively large catches up to the present time (with the exception of the early 1990s). The increase in the Pacific coast stock was delayed by ten years or more, and the fishery did not expand until the early 1990s (Figure 3A). It should be noted that although there were varying regional responses in sardine dynamics, the timing of these responses still did correspond to decadal scale shifts.

Factors Affecting Recruitment Success

While it is clear that sardine dynamics in the Pacific Ocean correspond to climate-ocean dynamics, the underlying mechanisms controlling their abundance have yet to be identified. We reviewed a number of mechanisms, both biological and physical, that have been advanced (Table 2) as factors controlling year-class success (recruitment). Emphasis has been placed on temperature changes as a causal agent, although no direct cause and effect relationships can be found. Temperature has been linked to timing of spawning events; quality of eggs produced; expansion of spawning range; larval and juvenile growth; and food abundance, availability, and type (all linked to temperature through changes in current patterns, mixing, and advection of larvae to favorable areas; Table 2). Although temperature is not a direct mechanism controlling recruitment, it does appear to be useful as a surrogate for a whole suite of possible mechanisms regulating sardine distribution and abundance. For example, a relationship between temperature and the southward movement of the center of concentration of biomass during the decline of the Pacific sardine off California can be seen in Figure 7. This figure shows the shifts from year to year in biomass concentration as inferred from the ratios of the catch per unit effort (CPUE) of the central California fishery stock and the southern California stock between 1932 and 1951. The CPUE data are from Marr (1960, his Table 2), and the temperature data are the an-

nual averages of the ocean temperature measured at Scripps Pier, La Jolla, California. The CPUEs provide regional estimates of density based on the nonlinear dependence of fishing success to abundance and availability of the stock (MacCall 1976). The relationship between the north-south ratios of CPUE and ocean temperature off southern California provides further evidence that the observed declining productivity of the sardine population was associated with a southward contraction of favorable habitat (Baumgartner, unpublished data). There were interannual changes in the ratios from 1934 to 1944, but the biomass center in that period generally remained concentrated off central California (ratios >1). A persistent shift occurred from 1945 onwards with all the ratios less than 1, indicating that the reduced biomass was centered off southern California. Ware and Thomson (1991) identified a widespread change in production in the northeast Pacific Ocean as a cause for the long-term changes in Pacific sardine (among other fishes). They suggest decreased coastal upwelling on the multidecade scale as the driving factor.

While the sardine population expanded in warm years in the Humboldt system, Serra et al. (1998) could not determine a relationship between sardine recruitment and temperature. However, they did determine an optimal environmental window for the formulation of year-classes by developing an index of upwelling as a measure of the environment. They suggested that a change in oceanographic conditions (upwelling) in the late 1960s off of northern Chile, indicated by a change in species composition of the ichthyoplankton, created conditions favorable for sardine.

Most recently, McFarlane and Beamish (2001) examined sardine off the west coast of British Columbia, Canada. They found no significant relationship between sea surface temperature and sardine presence or absence off the west coast of Vancouver Island. They concluded that the expansion of sardine into Canadian waters since the early 1990s was a response to an assemblage of factors (atmospheric pressure systems driving North Pacific wind patterns resulting in changes to ocean currents) that characterized an ecosystem reorganization during the 1990s. They suggested that the 1989 regime shift resulted in conditions favorable for sardine by increasing the productivity of diatoms. Crawford et al. (1991) examined the possible mechanisms linking the fluctuations in sardine catches in the Pacific and concluded that temperature was not the direct cause. Bakun (1997) summed up the relationship of sardine abundance and temperature as follows: "...it seems unlikely that temperature alone could be the major causal agent, since the sea temperatures on the eastern and western sides of the Pacific Ocean tend to vary out of phase rather than in phase."

Table 2. Factors Affecting Recruitment Success

Factor	Mechanism	Reference
BIOLOGICAL		
Spawning Biomass	Biomass/recruit relationships	Jacobson and MacCall 1995
Condition	Small number of high quality eggs produced by high quality adults (larger body size, high lipid and EPA levels)	Kawasaki and Omori 1995
Competition	Co-occurrence with hake, jack mackerel, and chub mackerel and some overlap in food items main competitor for food is anchovy	Marr 1960; Ahlstrom 1960
	Anchovy population increases as sardine population decreases; greater access to food	Murphy 1966; Silliman 1969, in Radovich 1982
	Competition with anchovy other than for food Density independent growth	Kawasaki 1993 Yamaguchi and Kawabata 1992
Food	Faster larval growth means less size dependent predation	Cowan et al. 1996, in Logerwell and Smith 2001
	Adequate nutrition for larvae and juveniles	Marr 1960; Arthur 1976; Lasker 1975, 1981; Watanabe and Saito 1998
	Adults spawn in areas rich in larval food (nauplii of small copepods)	Lasker 1975; Kondô 1986
Disease	Change in food availability	Kawasaki 1993
	Intra- and interspecific (chub mackerel)	Kishida and Matsuda 1993
	Predation of eggs and larva Cannibalism of eggs and larvae	Ahlstrom 1960 Davies 1957 in Murphy 1966
PHYSICAL		
Temperature	Indicator of a complex set of favourable environmental conditions	Sette 1960 in Marr 1960; Naganuma 1992
	Affects gonadal maturation cycle, timing of spawning, and access by larvae to favourable conditions	Marr 1960
	Increasing SST may reflect increased solar radiation that would enhance 1° productivity	Kawasaki and Omori 1988
	Mixing of cooler, nutrient rich waters of the Oyashio Current with the warmer Kuroshio leads to lower SST and increased post-larva to age 1 survival	Noto and Yasuda 1999; Yasuda et al. 1999
	Cooler temperatures correlated with recruitment to age 1 in the Sea of Japan	Hiyama et al. 1995
	High abundance associated with global warm periods related to shifts in major ocean gyres and reduction in subpolar input to eastern boundary currents	Lluch-Belda et al. 1992
	Currents and Eddies	Upwelling limited to wind speeds of 7–8 m/s associated with enhanced larval survival (or 5–6 m/s)
Increased local upwellings within the Kuroshio Current related to 1° and 2° productivity and larval survival		Nakata et al. 1994
Storms can disrupt concentrations of larval food		Lasker 1975
Increased offshore transport of eggs and larvae lead to higher mortality		Parrish et al. 1983
Greater abundance of larval food (copepod larvae) within the Kuroshio Current		Kondô 1986; Nakata et al. 1995; Hara and Watanabe 1989
Ecosystem Reorganization	Higher productivity in the form of larval food in eddies off California	Sette 1960, in Marr 1960; Logerwell and Smith 2001
	Linkage between sardines and climate regime shifts specific to an assemblage of factors that characterize ecosystem change	McFarlane and Beamish 2001
	Changes in properties of coastal flow in both eastern and western Pacific ocean. Linked to improved productivity.	MacCall 2002

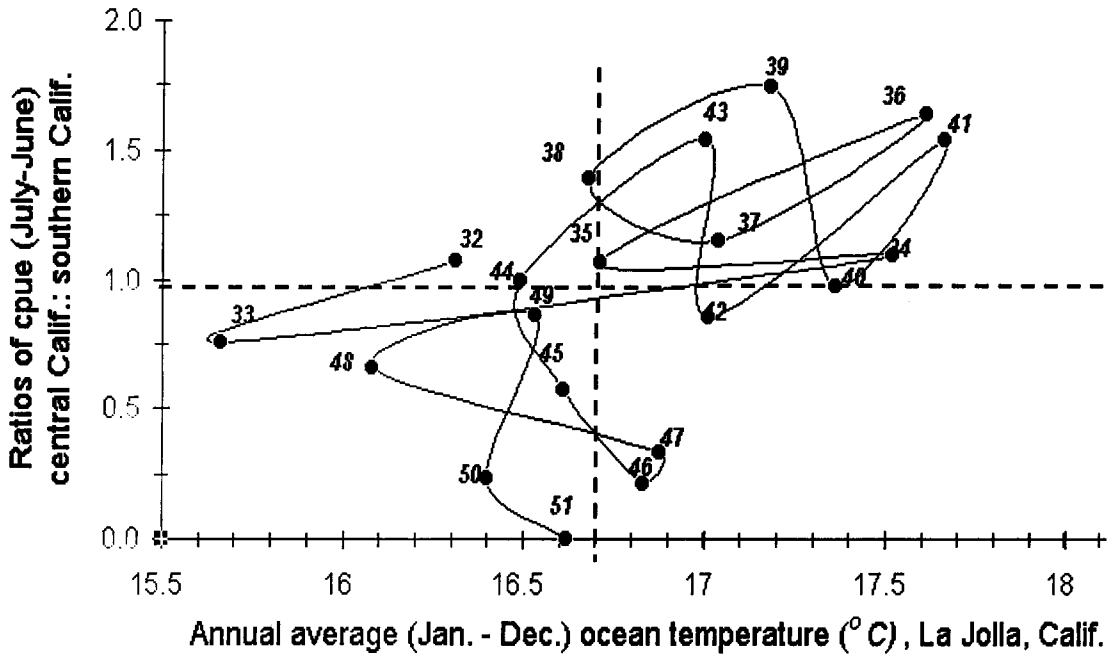


Figure 7. Year-to-year shifts in biomass concentration of the California sardine stock in relation to coastal ocean temperatures measured at Scripps Pier in La Jolla, California. The shifts in biomass are inferred from the ratios of the catch-per-unit-effort (CPUE) of the historical stock on the fishing grounds off central California to the CPUE from southern California between 1932 and 1950 (CPUE data are from Marr 1960; Table 2). The CPUEs provide regional estimates of density based on the nonlinear dependence of fishing success to abundance and variability of the stock.

In summary, we still do not understand the underlying mechanisms controlling year-class success in sardine. Studies examining these mechanisms on a regional level remain a research focus in many laboratories throughout the Pacific. It will be necessary for investigators to continue to examine these regional responses on a broader (Pacific-wide) scale in the context of decadal-scale changes in ocean conditions (regimes) if we hope to understand the recruitment dynamics of this species. Recently, MacCall (2002) suggested a flow hypothesis regime shift synthesis based on the recent history of the sardine populations off Japan, North America, and South America, which supports the ecosystem reorganization hypothesis of McFarlane and Beamish (2001). MacCall (2002) resolves the cooling favorable to Japanese sardines and the warming favorable to the North American sardines. When the Kuroshio flow is strong and warm it is unfavorable for the Japanese sardine, and when the California Current is strong and cold, it is unfavorable for the North American sardine. The meanders and fronts in all three systems are more elaborate when the flow is minimal. Consequently, sardine may have a larger habitat in the offshore regions of the boundary currents. Presumably these changes in

flow pattern are reflected in changes in zooplankton abundance that would serve as forage. This hypothesis is consistent with trends in both eastern and western stocks.

What Caused the Decline and Recovery of the California Sardine, Fishery or Environment?

Historically, declines (even collapses) of stocks have been attributed to fishing (for example, see Hillborn and Walters 1992). Although the work described earlier in this report suggests dramatic increases and decreases in sardine abundance have occurred for the last 1,800 years, fishing has still been examined as a possible controlling factor. Hiyama et al. (1995) examined stock size and recruitment (Figure 8) of sardine in the Sea of Japan and adjacent waters and found that years of successive poor year-classes preceded the decline of the exploitable stock and concluded recruitment failure (not fishing) led to the rapid decrease in stock size. While fishing effects are important and undoubtedly exacerbate any declines, most fisheries scientists now believe that

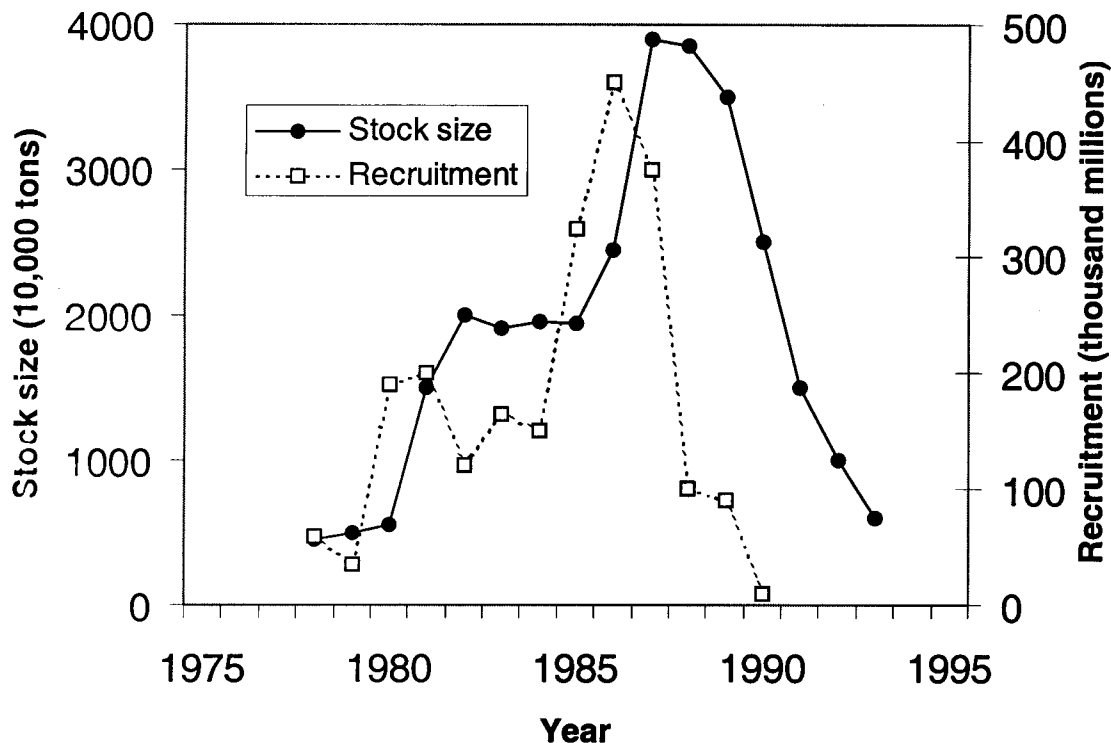


Figure 8. Stock size and recruitment in the Sea of Japan and adjacent waters (from Hiyama et al. 1995).

a fish's environment and changes to that environment play a more important role.

One possible cause of decline of the California sardine population in the 1940s was a reduction in the age composition of the stock from about ten reproductive year-classes to two reproductive year-classes (Murphy 1966) as a result of poor recruitment compounded by fishing. He suggested this reduced number of year-classes prevented the necessary trophic advantages of long northern migrations into rich feeding grounds (i.e., the fishery impacted population resilience to changes in the habitat [ecosystem]).

When the fisheries were closed for economic and conservation reasons, the stock began to recuperate. A regime shift in the mid-1970s coincided with these fishery conservation actions, and the population increased by about 30% annually after 1977 from the low levels of the 1970s. A dramatic increase occurred in the early 1990s, following the 1989 regime shift. While the evolutionary and demographic parts of this explanation have been widely accepted (Roff 1992), two hypotheses have been developed to explain variability of year-class success in the California Current region.

In the first hypothesis, year-class success has been attributed to the assembly and maintenance of meso-

scale eddies between the California Current and the Southern California Bight, which provide conditions favorable to offshore survival and growth of larvae and juveniles (Sette 1960; Smith 2000; Logerwell and Smith 2001). Logerwell et al. (2001) suggest that eddies, rather than meanders and fronts as proposed by MacCall (2002), sustain the multiseason retention and production of late-larval and possibly juvenile sardines. There had been a perception that the major habitat of the sardine population was coastal and that offshore habitat was not important. However, in contrast to this perception are high seas observations of juvenile sardine in albacore stomachs (Ahlstrom 1960), the occurrence of sardine eggs more than 161.3 km (100 mi) offshore in 1920–1932 and 1939 (Smith 1990), and adult sardine found more than 483.9 km (300 nautical mi) outside of the CalCOFI pattern (Macewicz and Abramenkoff 1993). Egg distribution maps (Checkley et al. 2000) of the recovering sardine population and recent surveys (Figure 9) show a change in egg distribution north and offshore of the more traditional area off San Diego (approximately 23°N). This distribution may be related to an abrupt change in available food for spawning adults related to the presence of a recurrent anticyclonic eddy southwest of Point Conception (Haury et al. 1986; Pelaez and McGowan 1986).

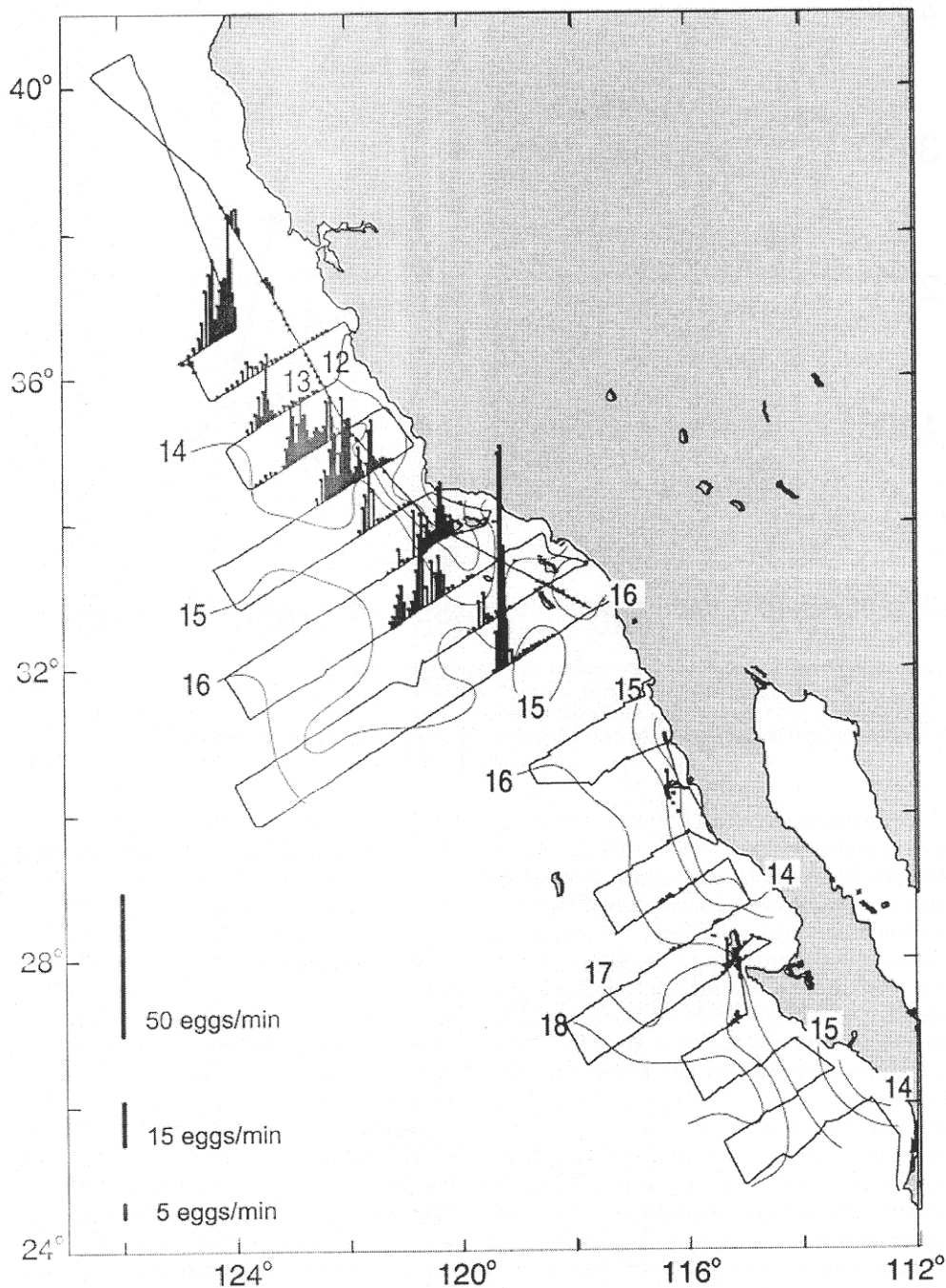


Figure 9. The spring (April) 2000 distribution of sardine eggs in the California Current from combined Cufes surveys of the CalCOFI and IMECOCAL (Investigaciones Mexicanas de la Corriente de California) programs. Units of concentrations are given in eggs/min measured by the pumping and collection systems that are similar on the two vessels used (research vessels *David Starr Jordan* and *Francisco de Ulloa*). Eggs were distributed from just south of Punta Eugenia (approximately 27°N) to the waters offshore of San Francisco just north of 38°N. Note the striking contrast in abundance/concentration and distance offshore of the sardine eggs in the CalCOFI region (southern California Bight to Morterey, California) compared with the southern IMECOCAL region off Baja California. Temperatures at 10 m are plotted with the egg concentrations.

Marr (1960) suggested a second hypothesis in which cooler coastal waters delayed sardine spawning time, resulting in reduced larval survival and subsequent recruitment. A recent increase of sardine spawning area occurred within the southern California Bight between 1978 and 1991. Figure 10 shows the distribution of sardine egg abundances for the year 1949 for the months April through July. This was in the period after the persistent decline in

productivity and shift in the center of concentration of the sardine biomass associated with the cooler ocean temperatures indicated in Figure 7. Comparison of the 1949 distributions with the April 2000 data in Figure 9 indicates that after 1945, the months of June and July were more equivalent to April of the recent period represented in Figure 9. This suggests that onset of spawning in the region off southern and central California was delayed

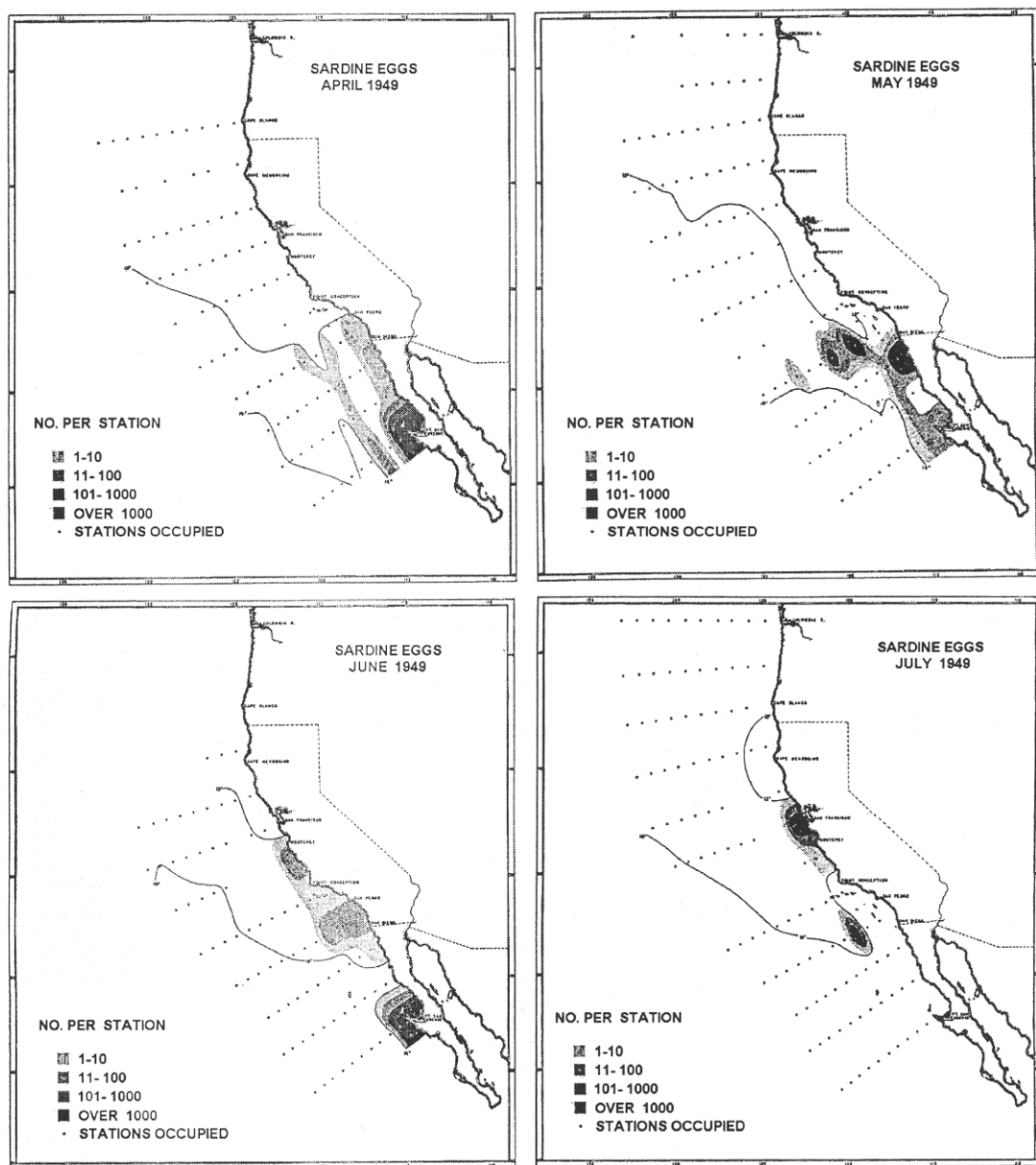


Figure 10. Distribution and relative abundances of sardine eggs from April through July 1949, with the 13°C and 16°C isotherms plotted (from Ahlstrom 1954).

in the period after 1945, whereas in the current regime, spawning is well underway off California by March and April and extends far north of Point Conception, a region of abundant food. Since 1991, the central California coast and offshore waters have been covered with sardine spawning concentrations (Figure 11).

Since 1992, sardine have also increased in abundance in waters off Oregon, Washington (R. Brodeur, personal communication), and British Columbia and are now once again a dominant species in the surface waters (McFarlane and Beamish 2001). This unexpectedly large increase in the abundance of sardine off Canada has radically changed our ideas about the causes of the collapse of sardine populations in the 1940s. The traditional explanation of over-fishing being the principal cause for the collapse is no longer tenable and needs to be reexamined. The spawning of sardine in Canadian waters in 1997 and 1998 represents a radical change in their behavior (McFarlane and Beamish 2001). It is now clear that large-scale fluctuations in oceanic conditions affected both their distribution and their survival. While the coast-wide, decadal-scale research efforts needed to explain the mechanisms controlling the expansion and contraction of sardines above the Pacific coast of North America have not yet been conducted, the population dynamics of sardine appear related to shifts in climate-ocean physics (Figures 3 and 6). These regime shifts create ecosystem conditions that are favorable or unfav-

orable for sardines on decadal time frames. In recent history fishing pressure undoubtedly may have affected the rate of change, but the population dynamics were a reflection of the new dynamics of their ecosystem.

Response to Global Climate Change

The clupeids in general, and sardine in particular, undergo large fluctuations in abundance and changes in distribution that have been related to the ocean environment (Cole and McGlade 1998). The fluctuations in abundance and changes in distribution of Pacific sardine have also been related to changes in other fish species. For example, the migration patterns of northern bluefin tuna *Thunnus thynnus* changed after the 1977 regime shift (Polovina 1996) and those of albacore *T. alalunga* have been affected by the same decadal-scale climate patterns (Kimura et al. 1997). Alternating patterns in the abundance and distribution of Atlantic herring *Clupea harengus* and sardine in relation to the North Atlantic Oscillation have been documented (Alheit and Hagen 1997). In the Pacific, alternating changes in abundance of sardine and anchovy populations (Murphy 1966) are a classic example of changes in dominance in response to regime shift changes. However, as stated, the underlying mechanisms remain to be discovered.

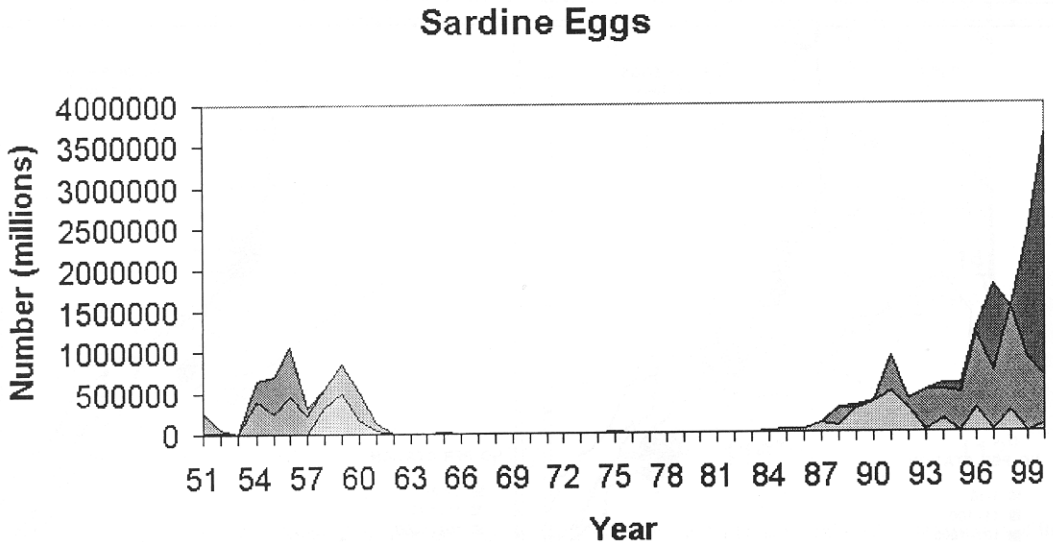


Figure 11. Census estimates of sardine eggs in winter-spring plankton tows, 1951–2000. The light gray shading represents the standing crop of sardine eggs over the continental shelf. The darker shading represents the standing crop of sardine eggs over the continental slope. The black area represents the standing crop of sardine eggs beyond the continental slope in an area called California Current Core and Eddies. The contemporary expansion of sardine spawning started over the continental shelf in the 1980s and expanded offshore in 1991 and northerly by 1994.

There is little doubt that sardine populations throughout the Pacific Ocean respond to decadal scale changes in climate-ocean conditions, although regional responses may vary depending on the reorganization of the local ecosystems. For example, McFarlane and Beamish (2001) hypothesized that the fluctuations in sardine abundance off Canada were related to changes in the species composition and abundances of phytoplankton, particularly diatoms. When a regime favors phytoplankton growth, sardine abundance increases. Ware (2000), using data from Marr (1960) and CalCOFI Progress Report 1 (California Department of Fish and Game 1953), reported a relationship in the California Current system between year-class success in sardine (from 1927 to 43 and 1950–52) and the abundance of diatoms. We are unable directly to observe similar changes in recent years, but we can point out that there have been changes in species composition of zooplankton and an increase in abundance of key dietary species off the west coast of Vancouver Island and Oregon (Mackas et al. 2001). A cumulative shift in the zooplankton fauna off southern Vancouver Island occurred during 1990–1998 to a more southerly assemblage of copepods and chaetognaths with an order of magnitude increase in species endemic to the California Current and converse decreases in some endemic Northeast Pacific continental shelf species. This shift in species composition reversed itself in 2000.

Whatever mechanism or mechanisms are involved in the response of sardine to regime changes, it is likely they will continue. However, we expect that superimposing global warming onto these decadal scale regime patterns will lead to even more profound responses by sardine and other migratory pelagics. Although it is not possible at this time to fully integrate fish population dynamic models with global climate models, the most recent report of the Intergovernmental Panel on Climate Change (2001) does present a number of scenarios that examine likely changes to physical parameters such as temperature, precipitation, winds, currents, sea level, salinity, and upwelling. All of these parameters will likely impact the ecosystem(s) in which sardine live. As indicated, many of these parameters have been linked to sardine productivity through food abundance, availability, and composition. This suggests that sardine may be one of the best indicators of climate change, as their surface water environment is more directly influenced by atmospheric and ocean variability. Since variability on a decadal-scale can be large, one consideration regarding superimposing global warming on this natural variation will be to closely monitor changes in the decadal-scale variability (i.e., more frequent regime shifts), as Shuter and Post (1990) suggested for northern freshwater systems. The historical fluctuations in sardine abundance

and behavior provide an excellent and well-documented case study of how ecosystem changes need to be considered as distinct reorganizations rather than simple interactions between cycles and oscillations. Because climate change affects ecosystems and not just populations, these climate-related ecosystem reorganizations need to be incorporated in our management strategies.

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