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WORLDWIDE LARGE-SCALE FLUCTUATIONS OF SARDINE AND ANCHOVY POPULATIONS

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Decade-scale regimes of sardine *Sardinops sagax* and anchovy *Engraulis* spp. have been observed in the productive coastal waters of the North-Western, North-Eastern and South-Eastern Pacific and the South-Eastern Atlantic. In each of these systems, the two genera fluctuate out of phase with each other. The subdominant genus may initiate a recovery while the other species is still abundant, so population growth is not necessarily a response to a vacant niche. Rather, it appears to be triggered by formation of one or a few powerful year-classes. At high population levels, quality of sardine and their eggs decreased in Japan, leading to decreased production and survival of eggs, poor year-classes and stock collapse. Excessive fishing of strong year-classes early in the recovery stage may prevent a species from assuming dominance, so influencing the natural succession of species. This may greatly alter the structure and functioning of an ecosystem. For example, a mesopelagic forage fish may replace an epipelagic one, with severe repercussions for predators that can only feed in the upper ocean, e.g. some seabirds. Biological factors also may influence the succession of forage fish. For example, off California, peaks in abundance of predatory species such as bonita *Sarda*, and chub mackerel *Scomber*, separate those of the planktivorous sardine and anchovy. In the Pacific Ocean, sardine distribution has change greatly. Compared with its range when scarce, a population at a high level of biomass can extend 1 000–1 800 miles farther along the coast and 400–2 200 miles farther out to sea. In different periods of high biomass, sardine did not always have the same distribution. In the 1930s and 1940s, near simultaneous fluctuations of sardine in the North-Western and North-Eastern Pacific were in phase. In the 1980s and 1990s, sardine in the North-Western and South-Eastern Pacific were fluctuating in phase. However, along the west coast of North America, sardine started their most recent increase later than in other regions of the Pacific Ocean. This increase is continuing, whereas sardine populations in the North-Western and South-Eastern Pacific have decreased both in catch and geographic distribution since the late 1980s. Therefore, the North-Eastern Pacific has moved out of phase with other major Pacific sardine populations. This may be because abundance of sardine in the California Current has not yet reached a level at which density-dependent effects exert a major influence. Sardine and anchovy in the South-Eastern Atlantic have been out of phase with populations in the Pacific Ocean, especially those off Peru and Chile. Over the last 300 years, episodic fisheries for Bohuslän herring *Clupea harengus* in Sweden coincide with periods of high anchovy abundance off California. Near simultaneous fluctuations of fish stocks in widely separated regions support the view that they are sometimes influenced by climate operating at a global scale. Changes of the gyre-scale circulation seem to be major factors in the decadal climate. In Australia, sardine have a wide range, but the less productive waters support a much lower biomass than is found in the other four systems. *Engraulis* occur in some systems from which *Sardinops* are absent, for example, Brazil, where they and *Sardinella* are segregated vertically in the water column.

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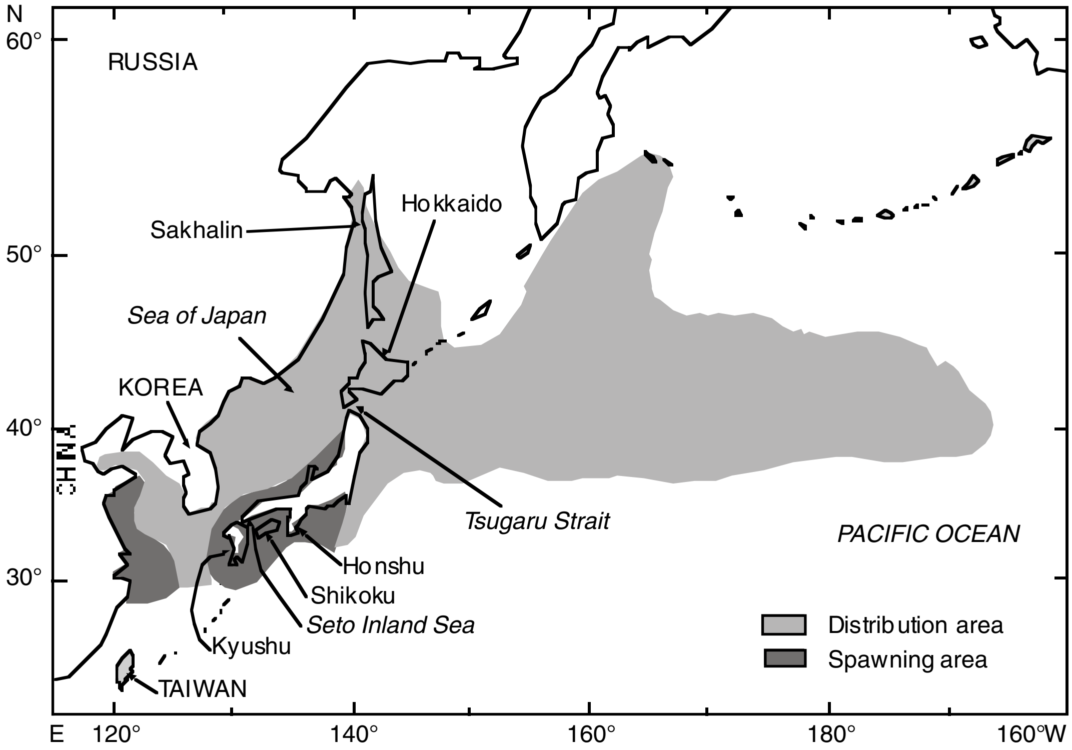

Fig. 1: Distribution of sardine in the North-Western Pacific Ocean, when the population level was very high in the 1980s (after Kuroda 1991). The spawning area is also the area of the population when it is low

In 1993, the Scientific Committee on Oceanic Research (SCOR) established Working Group 98 (WG 98) to investigate "Worldwide Large-scale Fluctuations of Sardine and Anchovy Populations". The first meeting of WG 98 was at Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, Mexico, from 13 to 17 June 1994. WG 98 held its second and final meeting at Scripps Institution of Oceanography, La Jolla, U.S.A., from 20 to 22 October 1997.

Prior to the establishment of WG 98, three workshops were held in La Paz, in 1988, 1990 and 1992, to consider regimes of high and low abundance of sardine *Sardinops sagax* and anchovy *Engraulis* spp. in the five regions where the genera co-occur. Reports of the 1988 and 1990 workshops were published (Lluch-Belda *et al*. 1989, 1992c). This paper summarizes the findings of WG 98.

WG 98 was tasked with collating historical information from the five regions where *Sardinops* have been fished: North-Western, North-Eastern and South-Eastern Pacific, Australasia and South-Eastern Atlantic. Catch data and some other pertinent information are tabulated in the Appendix. Additionally, an overview of fluctuations of sardine and anchovy populations in these five systems is presented in the text. The *Sardinella* fishery of Brazil is also considered, and a section addresses proxy records of sardine and anchovy abundance.

WG 98 was asked to describe the sequence of events at times of major change between sardine and anchovy regimes, to examine evidence for a worldwide cause of the major fluctuations of sardine and anchovy populations, to develop hypotheses regarding causes of these large changes and to consider consequences of such changes for ecosystem functioning. Sections deal with each of these aspects and with implications of regime behaviour for fisheries. Additionally, a brief review of regime changes in other systems is included, and a section considers how climate may operate at a global scale.

Each of the authors made substantial contribution to this report, but none of the authors necessarily agrees with the entire content of it. Throughout its deliberations, members of SCOR WG 98 had utmost respect for each other's views, but there was not always unanimous agreement on all matters.

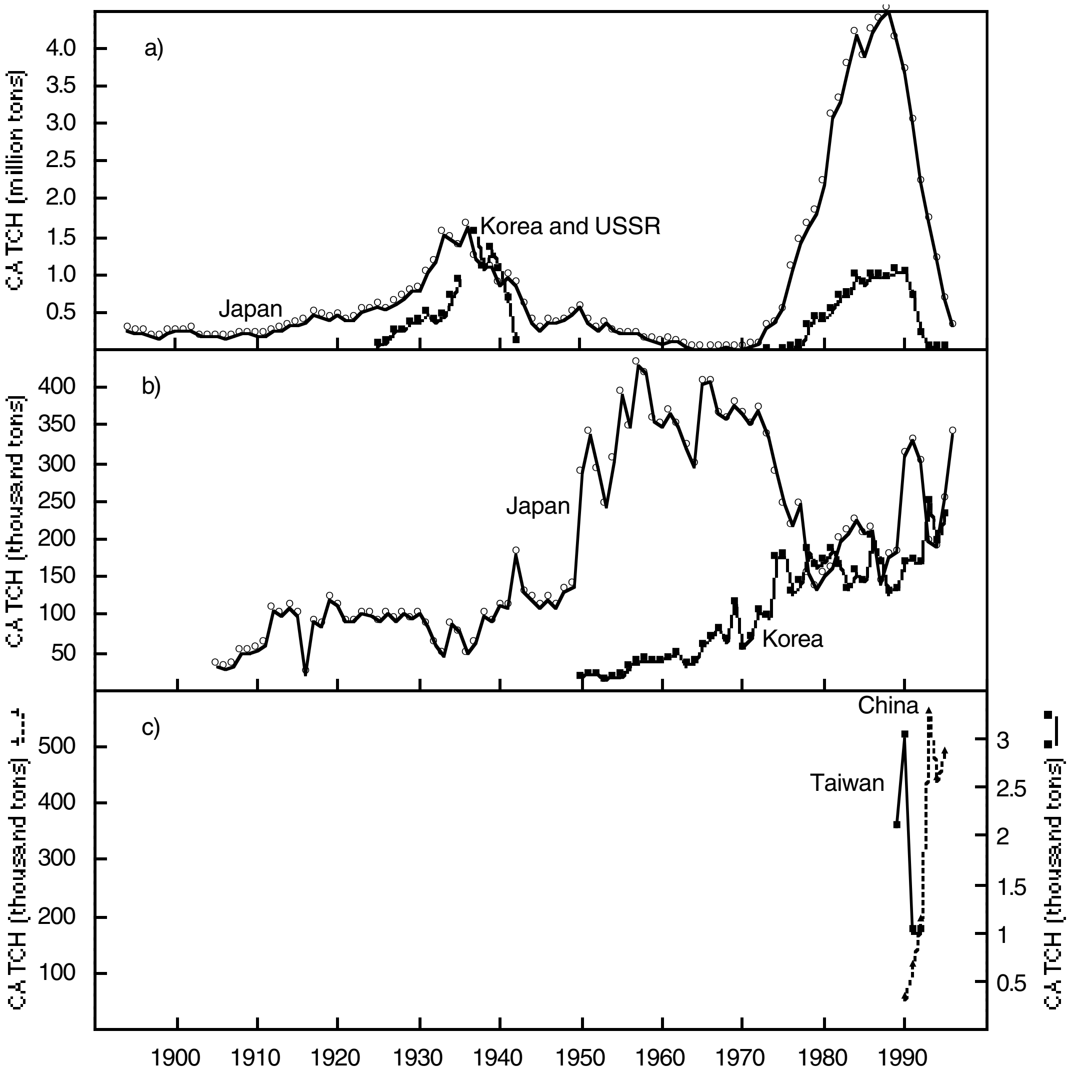

Fig. 2: (a) Trends in the catch of sardine by Japan, and by Korea and the USSR, the latter mostly in the Sea of Japan, 1894–1996, (b) trends in the catch of anchovy by Japan and Korea, 1905–1996, and (c) trends in the catch of anchovy by China and Taiwan, 1989–1996

LARGE-SCALE FLUCTUATIONS OF SARDINE AND ANCHOVY POPULATIONS IN SOME MAJOR OCEAN ECOSYSTEMS

North-Western Pacific

HISTORICAL OVERVIEW

The group of fish that constitutes the largest catches in the Japanese fishery is labeled *iwasi*, which consists of three clupeoid species: sardine *Sardinops sagax*, anchovy *Engraulis* sp. and round herring *Etrumeus* sp. They are harvested not only as adults, but also at the stage of metamorphosis and as post-larvae (Hayasi 1967). Ito (1887) stated that sardine (*Clupea melanosticta* = *S. sagax*) came to open sandy beaches on the east coast of Hokkaido in June and July. At that time, sardine amounted to 8% of the value (in yen) of round herring; anchovy was not listed and landings of each

Table I: Comparison of the lipid levels in adult sardine caught off Japan in 1935 and 1988

Parameter	1935	1988
Months	Early August – early September	Mid August – mid September
Region	Funka Bay off south-western Hokkaido	South-eastern Hokkaido
Average total length (cm)	21.1 – 21.6	22.0 – 22.2
Lipid content (% in flesh)	12.00 – 16.64	20.12 – 22.75

species were not indicated. Sardine, anchovy and round herring are known to have been exploited off Japan since the tenth century. Around 1890, anchovy was one of the most abundant fish (Hayasi 1967). The Japan Bureau of Agriculture (1894, p. 430) stated that sardine was the most important fishery of Japan: "It comes in enormous shoals and is caught almost everywhere along the coast." The fish migrated from south to north in spring and returned to the south in autumn. The greater part of the catch was dried and made into fertilizer and the oil extracted. About 1 200 tons of oil were exported each year (Japan Bureau of Agriculture 1894). Catch data for sardine are available from 1894, and for anchovy from 1905 (Appendix).

Sardine — The Japanese sardine fishery has had a long history since the beginning of the Tokugawa era (1600–1867). There have been six peaks of sardine catches: 1633–1660, 1673–1725, 1817–1843, 1858–1882 (Kikuchi 1958), 1920–1945 and 1975–1995. In the Tokugawa era, sardine were caught primarily by beach seines and eight-angle lift nets set along the shore. Changes in the availability and abundance of sardine caused the development and collapse of various coastal fishing villages.

There are two subpopulations of the Far Eastern sardine. One, the Sea of Japan subpopulation, is distributed in the Sea of Japan and the East China Sea. The second, the Pacific subpopulation, ranges along the Pacific coast of Japan. When the sardine population was small from 1950 to 1970, it was confined to a small coastal area along western and southern Japan. In the 1980s, it was distributed throughout the Sea of Japan (the Sea of Japan subpopulation) and in the Pacific as far east as 165°W (the Pacific subpopulation, Fig. 1).

Trends in sardine catches in the North-Western Pacific between 1894 and 1996 are shown in Figure 2a. There are two peaks in this period, one in the 1930s and the other in the 1980s. In both instances, the increase in catches resulted from an increased stock size, accompanied by an enormous spatial expansion of the range of sardine.

In the 1930s, catches were mainly from the Sea of Japan subpopulation. A large portion of the catch was taken from the north-western Sea of Japan. Part of this subpopulation moved to the Pacific Ocean through the Tsugaru Strait between Hokkaido and Honshu and was caught in Funka Bay off south-western Hokkaido. In the 1980s, the Pacific subpopulation was much larger than that of the Sea of Japan. Most of the catch was from waters south-east of Hokkaido and east of Honshu.

The two subpopulations in the North-Western Pacific can be distinguished from each other by different contents of lipid at the same physiological stage. Table I shows the lipid contents of adult sardine caught just prior to spawning in the two peak years: 1935 (from the Sea of Japan subpopulation) and 1988 (from the Pacific subpopulation). The former had a lower lipid content.

Anchovy — Anchovy has a distribution in the temperate zone of the western North Pacific from southern Sakhalin to Taiwan. The east coast of Japan produced about 75% of the total catch in 1962. This included the Seto Inland Sea between southern Honshu and Shikoku. The northern island of Hokkaido produced <0.5% of the catch on the east coast (Hayasi 1967). Hayasi (1967) reported that the catch peaked in summer and winter and that little is known about the migration of anchovy. The Kuroshio Current transports eggs from southern Kyushu to the Pacific coast of Honshu. Eggs and larvae are found in surface water temperatures of 11–29°C.

The catch from 1905 through 1996 is shown in Figure 2b. The Japanese catch decreased by almost half in the mid 1930s, at the time the sardine catch was high. It then doubled between 1949 and 1950 and continued at this higher level until 1972, when it dropped rapidly through 1979. Since 1979, the trend has been up and down but mostly up. Haysai (1967) reports that the anchovy catch reflected fluctuations in population size and not a preference of the fishers for sardine. Catch data for Taiwan became available in 1989 and for China in 1990 (Fig. 2c). The Chinese catch rapidly increased to 557 000 tons by 1993, whereas the Japanese catch was down to 195 000 tons after a high of 329 000 tons in 1991.

RECENT COLLAPSE OF THE SARDINE POPULATION

Having peaked at 5.43 million tons in 1988, the Japanese catch of Far Eastern sardine declined steeply to 0.3 million tons in 1996. The decrease resulted from a collapse of the sardine population, accompanied by a tremendous reduction of its range. The period between 1977 and 1988 was one of prosperity for sardine with an extended range (Fig. 1), and catches of more than a million tons per year were recorded from the waters south-east of Hokkaido. However, sardine disappeared from around northern Japan in the

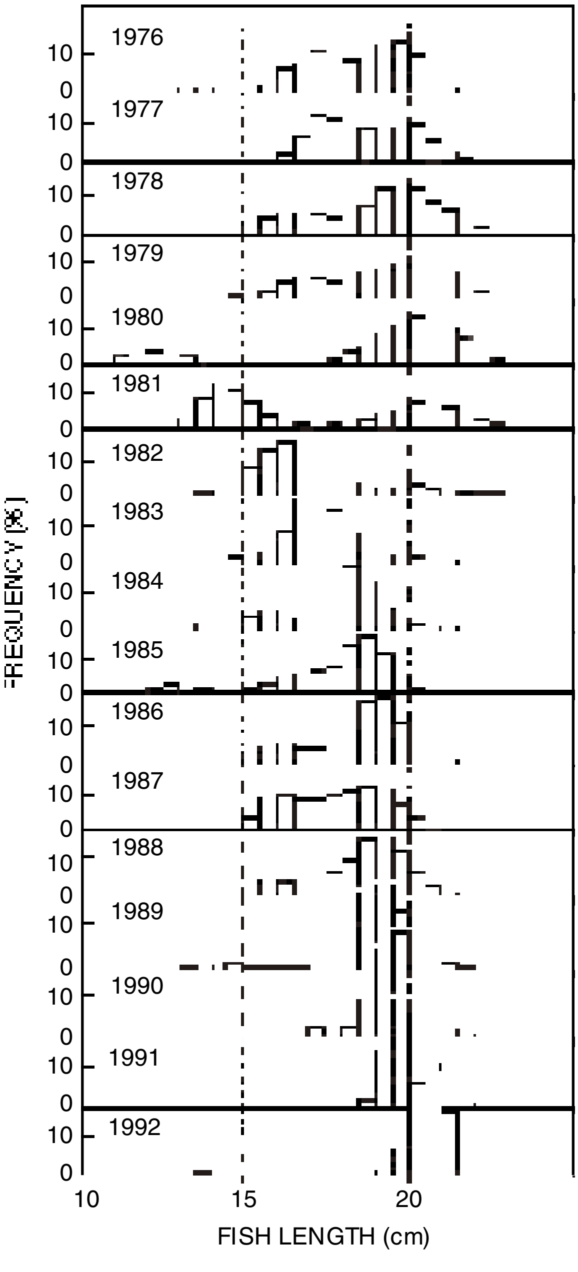

Fig. 3: Annual length frequency distributions of sardine caught by the two-boat, purse-seine operation in waters south-east of Hokkaido, 1976–1992. Data from Hokkaido Kushiro Fisheries Experimental Station

early 1990s, with only a small fraction of the former population remaining in the western Japan Sea by the late 1990s.

Frequency distributions of body lengths (Fig. 3) and a recruitment index (Fig. 4) show that 1-year-old sardine were almost absent off Hokkaido after 1989. Although production of sardine eggs along the Pacific coast of Japan increased from 1984 to 1991, survival of eggs to fish aged one year decreased by an order of magnitude for the 1988 and 1989 year-classes and by two orders of magnitude for the 1990 year-class (Table II). Survival subsequently remained poor. This strongly suggests that the collapse of the sardine population resulted from survival failure, not from overfishing (Kawasaki 1993).

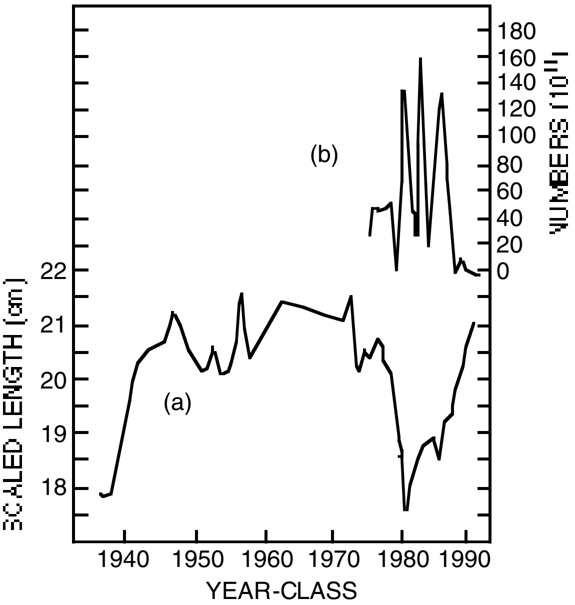

Fig. 4: Annual changes in (a) scaled length of 3-year-old sardine and (b) numbers of 1-year-old recruits south-east of Hokkaido. Sources of data on numbers of recruits: 1976–1984 – Wada (1988); 1985–1994 – Long-term Forecasting on the Distribution and Abundance of the Important Fishery Resources and Related Oceanographic Conditions in the Sea of Chuo Blocs **86** (1991) **93** (1994). From Kawasaki and Omori (1995)

North-Eastern Pacific

In the North-Eastern Pacific, the distribution of sardine and anchovy ranges along the west coast of North America from Baja California to British Columbia, and the Gulf of California. The California Current is the dominant feature along the West Coast, whereas the Gulf is separated by Baja California Peninsula from the California Current. Within this section, the Gulf of California is treated separately, except when comparing it with the West Coast.

The sardine and anchovy fisheries of the California

Table II: Number of eggs produced along the Pacific coast of Japan (A), number of 1-year-old recruits in waters south-east of Hokkaido (B), and the relative survival of eggs to 1-year-old recruits (B/A) for the 1984–1993 sardine year-classes off Japan. Data from National Institute of Fisheries Science, Fishery Agency, Government of Japan

Year-class	Number of eggs ($\times10^{12}$)	Number of recruits ($\times10^{8}$)	Survival ($\times10^{-4}$)
1984	1 854	662	0.357
1985	2 081	1 402	0.623
1986	8 935	7 907	0.880
1987	1 860	1 465	0.778
1988	3 784	116	0.031
1989	3 897	82	0.021
1990	6 528	28	0.004
1991	3 762	27	0.007
1992	1 555	204	0.131
1993	1 591	43	0.027

Current continued their pattern of extreme and unexpected changes into the 1990s. The northern stock of sardine began an extended recovery from its near extinction in the 1970s and currently it is supporting a fishery of more than 100 000 tons. The stock has also recolonized the northern portion of its range between Oregon and Vancouver Island, where it had been commercially extinct for more than 50 years (Hargreaves *et al.* 1994). The Gulf of California sardine fishery rose to more than 270 000 tons annually, collapsed to less than 10 000 tons and then recovered to more than 200 000 tons. The northern anchovy, which was previously absent from the Gulf of California, extended its range to include the Gulf of California. This equatorward colonization occurred during a period of anomalously warm SST, even though northern anchovy *Engraulis mordax* are considered to be more of a cold water species. The far northern stock of anchovy, off Oregon and Washington, has apparently collapsed, even though there was no fishery on this stock.

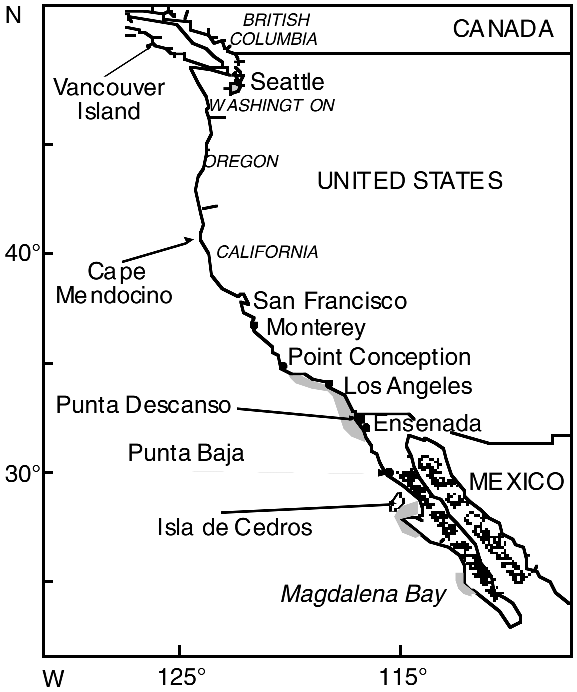

Fig. 5: Range of sardine in the North-Eastern Pacific Ocean. Dashed lines show the area occupied when the population is at a low level of abundance; dots indicate the extreme range when biomass is high. From the late 1960s to the early 1980s, the population was almost entirely south of 30°N. In the 1990s, the population extended from Baja California, Mexico, to British Columbia, Canada

HISTORICAL OVERVIEW

The 1916–1917 seasonal (June–May) catch of sardine in California was 24 975 tons and 241 tons for anchovy, whereas British Columbia reported a sardine catch of 75 tons. In 1935, Washington and Oregon reported their first catches of sardine of 9 and 23 859 tons respectively. Earlier reports of the presence, availability and catch of sardine and anchovy date from the 1850s. Both species were recorded in San Francisco Bay in the early 1850s by Girard (1854) and Lockington (1879). Sardine were not available in the markets from November 1878 through February 1879, were scarce during March and April and reasonably abundant from May through September. Anchovy were reasonably abundant during the entire period. Jordan and Gilbert (1881) reported sardine in San Francisco Bay, Monterey Bay, Port San Luis, Santa Barbara, San Pedro (Los Angeles) and San Diego. They were reported as most common south of Point Conception, especially in San Diego, where they were taken with hook and line from wharves (Jordan and Gilbert 1882). In 1894, it was reported that sardine had been scarce for the past five years in San Francisco (Smith 1895). Canneries were in operation at San Francisco in 1889–1893 and in San Pedro in 1895 (Smith 1895, Anon. 1896). Swan (1894, p. 379) reports "The anchovy come to Puget Sound in enormous quantities, and during their season, from May to November, every bay and inlet is crowded with them." Between 1889 and 1899, the catch in California for sardine ranged from 500 to more than 1 000 tons and for anchovy from 56 to more than 200 tons. These data are available in the State of California Fish Commissioners Reports, and the

Reports and Bulletins of the United States Commission of Fish and Fisheries.

DISTRIBUTION

The geographical distribution of sardine in the California Current is heavily dependent upon its stock size and migratory behaviour (Fig. 5). Its extreme range extends from Alaska (57°N) to Cabo San Lucas (23°N) and around into the Gulf of California. The northern portion of the range is seasonally well below the preferred temperatures for sardine, and it migrates equatorwards to south of about 36°N to overwinter and spawn. Tagging studies indicated that the larger/older fish moved farther north than young adults (Clark and Janssen 1945). During the period of low stock size and generally cold temperatures (1950–1980), sardine were virtually absent from the Oregon-Alaska region and few occurred off central California. Sardine young of the year were found off central California in 1992 for the first time since 1957–58, and spawning concentrations were discovered in 1994. The rapid growth of the population during the 1990s and warm sea surface temperatures have resulted in the stock re-occupying feeding grounds in central California, Oregon, Washington and British Columbia. This expansion was associated with a northward and offshore movement of the principal spawning grounds from Baja California to the region offshore and north of Point Conception (35°N).

In the California Current system, anchovy are distributed from the Queen Charlotte Islands, British Columbia, to Magdalena Bay, Baja California, and they have recently colonized the Gulf of California.

GROWTH, MORTALITY AND SEXUAL MATURITY

Sardine — Pacific sardine have considerable regional variation in growth rates, with average size at age increasing from south to north in the northern stock (Phillips 1948). The bulk of the fish in the historical California fishery were five years or younger. Larger (to 30 cm total length, *TL*) and older (to 13 years of age) fish were the most common in the Canadian fishery. Sardine in southern Baja California and the Gulf of California do not achieve the size of the northern fish. However, size-at-age for younger fish is not markedly different.

Murphy (1966) reported that the natural mortality rate (M) of the northern stock was 0.4 during the peak of the fishery, and that it increased to 0.8 during the period of population decline. MacCall (1979) used a constant mortality rate of $M = 0.4$ for his analyses and Clark and Marr (1955) estimated an M of 0.51. Sardine older than six years are very rare in the southern regions, which suggests that natural mortality may be higher than off California.

Sardine are multiple-batch spawners and their annual fecundity is indeterminate. Relatively little information is available concerning the variation of fecundity with age. Based on comparisons with sardine off South Africa, Butler *et al.* (1993) estimated that 2-year-old sardine spawn on average six times per year, whereas the oldest sardine spawn 40 times per year. Both eggs and larvae are found near the surface. Temperature strongly influences the geographical distribution of sardine. Off southern Baja California, eggs are most abundant at 22–25°C, whereas they are most common at 17–21°C in the Gulf of California and at 14–16°C off California (Lluch-Belda *et al.* 1991b).

Anchovy — In the central anchovy stock, fish as old as seven years and as large as 23 cm *TL* have been recorded, but the majority of the population is <16 cm and less than four years of age. Estimates of M vary from 0.6 to 1.1. There is a great deal of regional variation in age composition and size, with older and larger anchovy found farther offshore and to the north; in the southern stock, fish do not exceed 14 cm (Parrish *et al.* 1985).

Spawning occurs all year, but there is a seasonal peak in late winter and early spring (February–April). In contrast to sardine, anchovy throughout their range have a similar preferred spawning temperature, near 14°C, and eggs are most abundant at temperatures of 12–16°C (Lluch-Belda *et al.* 1991b). Females spawn numerous batches of eggs throughout the spawning season and the annual number of batches and annual fecundity is highly age/size dependent. Females aged four and older produce nearly five times as many eggs per unit body mass as 1-year-old fish. This increased fecundity is primarily achieved by an increased number of spawnings and increased length of the spawning season in older fish (Parrish *et al.* 1986). Spawning of 1-year olds is also dependent upon sea surface temperatures, sexual maturity being depressed at temperatures <13°C (Methot 1989).

STOCK STRUCTURE

Sardine — Two sardine subpopulations occupy the California Current. A northern stock (off northern Baja California to Alaska) and a southern stock (off central and southern Baja California). A separate Gulf of California subpopulation was distinguished on the basis of serological techniques (Vrooman 1964). Biochemical genetic analyses and morphological studies (Hedgecock *et al.* 1989) show extremely little genetic variation among sardine from central and southern California, the Pacific coast of Baja California or the Gulf of California, suggesting that the fish in the various areas may form separate fishery stocks, but not genetic stocks.

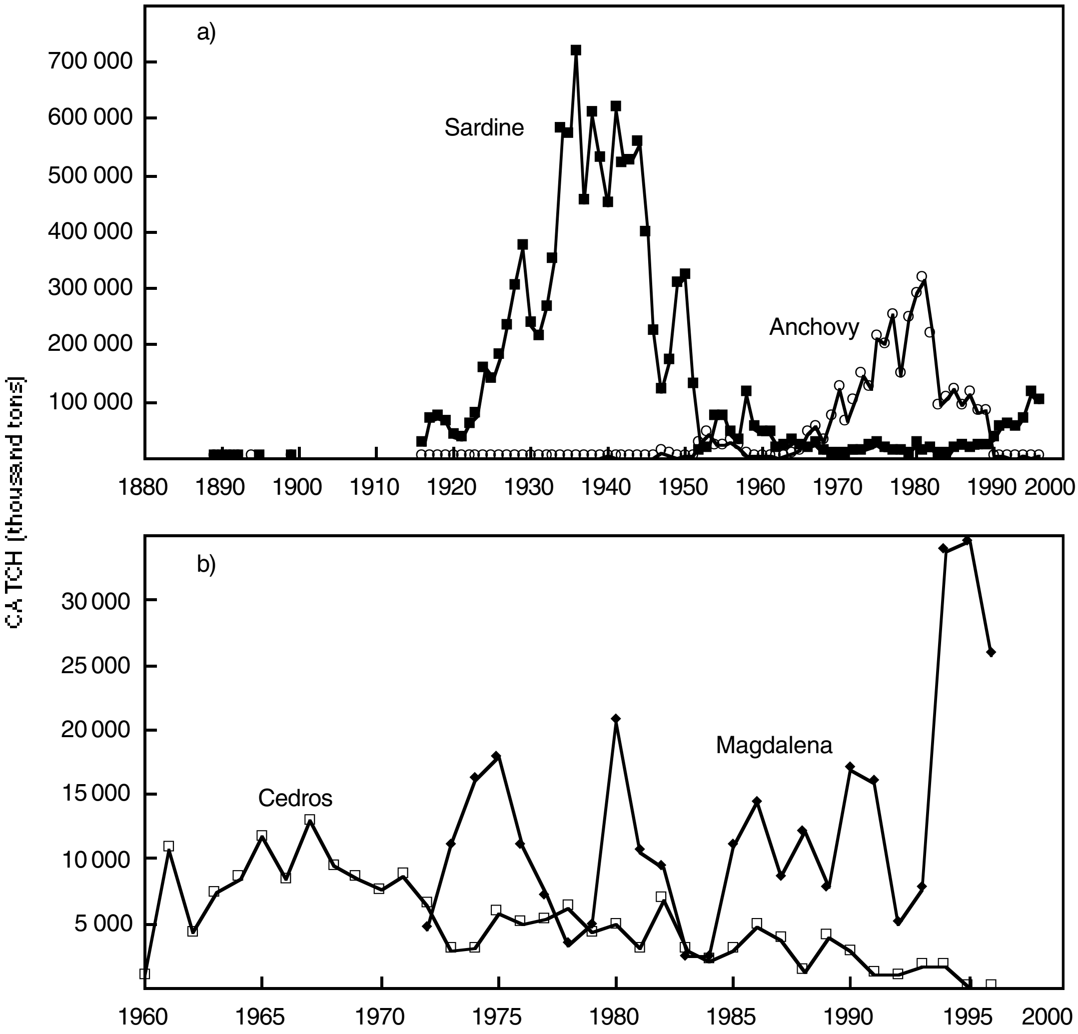

Fig. 6: Trends in catches of (a) sardine and anchovy in the California Current, 1889–1997; seasonal data (July–June) were used from 1916/1917 through 1967/1968, because the British Columbia, Washington and Oregon data are all seasonal data (annual data were used from 1968 through 1996), and (b) catches of sardine at Cedros and Magdelena off southern Baja California, 1960–1996

Anchovy — The anchovy population has traditionally been divided into three fishery stocks (northern, central and southern). However, a fourth fishery stock is probably that in the Gulf of California. The northern subpopulation extends from British Columbia to central California and little information is available for that stock. The central subpopulation, which has supported significant commercial fisheries in the U.S. and Mexico, ranges from central California to Punta Baja, Baja California. The bulk of the central subpopulation is located in the southern California Bight, which extends from Point Conception, California, in the north to Point Descanso, Baja California, in the south. The southern stock resides off the Pacific coast of central and southern Baja California and it supports a small fishery in southern Baja. Anchovy have only recently recolonized the Gulf of California and, since the mid-1980s, small catches have been made there.

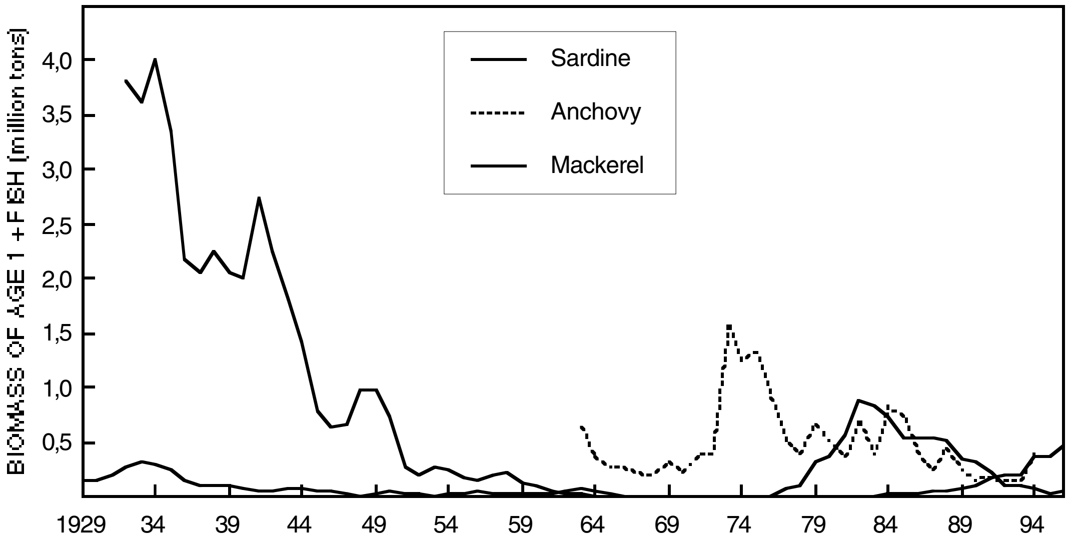

Fig. 7: Trends in the biomass of sardine, anchovy and chub mackerel off California and northern Baja California, 1929–1996

FISHERY (WEST COAST)

Sardine — The California sardine fishery peaked at more than 700 000 tons in the mid 1930s and collapsed in the 1950s, falling from a biomass of just over four million tons to <3 000 tons in the 1970s. The fishery was finally completely protected in the early 1970s, and there was evidence of recovery in the early 1980s. The stock has now expanded to cover its original range and the fishery exceeded 110 000 tons in 1997 (Fig. 6a). The stock in southern Baja California has continued to support a small fishery, but little evidence of a major population has ever been observed there (Fig. 6b).

Anchovy — The central stock in the California Current supported a fishery that averaged more than 200 000 tons from the mid 1970s to the early 1980s. It peaked in 1981 at 310 211 tons, but two years later it had declined by 70%. The fishery again declined sharply in 1990, and it has remained at a low level (Fig. 6a). Few anchovy are harvested in either the southern Baja California region or to the north of Point Conception.

STOCK ASSESSMENT (WEST COAST)

Sardine — Former assessments of the northern sardine stock were based on cohort analyses (Murphy 1966, MacCall 1979), whereas more recent assessments have used an integrated stock synthesis type model (Hill *et al.* 1998). The present geographical expansion of the stock has made estimates rather imprecise, because an unknown proportion of the stock is out of range of many of the monitoring systems utilized in the development of the stock assessment model (Fig. 7). Assessments are not available for the stock off southern Baja California.

Anchovy — The central stock has had major research effort directed towards stock assessment. The most recent biomass estimates (Jacobson *et al.* 1995) show that it peaked at 1.6 million tons in 1973 and has not exceeded 500 000 tons in the past decade (Fig. 7). During the early 1990s, biomass was about 150 000 tons and the most recent estimate is about 400 000 tons. Palaeo-sediment analyses show that this stock is highly variable at longer time-scales (see the section on Proxy Records). Stock assessment work for the other stocks of anchovy in the California Current has been limited and no information is available for anchovy in southern Baja California. An early estimate based on eggs and larvae was made for the northern stock, which suggested it was more than 260 000 tons in 1975 (Richardson 1981). However, more recent information on spawning rates implies that this estimate was too large. The most recent work on the stock suggests that, although it has been virtually unexploited,

Fig. 8: Fishing areas for sardine in the Gulf of California

it has declined to an extremely low level. In contrast, the newly established population in the Gulf of California has been the subject of research and the estimated spawner biomass in 1991 was 110 000 tons (Cotero-Altamirano and Green-Ruiz 1997).

GULF OF CALIFORNIA

Sardine — Sardine were reported in the Gulf of California for many years before fishing started. A few examples are: in 1940 there were sardine north of La Paz (Clark 1947); they were collected near Guaymas in 1951 and 1952 (Walker 1953); they were collected in 1961 and 1962 in the western Gulf, from the lower Gulf to the upper Gulf (Vrooman 1964).

The sardine fishery is the largest of those for small pelagic fish in the Gulf of California. This fishery began in the late 1960s, as the sardine fishery on the west coast of Baja California declined and boats moved to the Gulf. First, small boats, without ice, fished near the port of Guaymas. By 1977, larger boats arrived, fished over a larger area and spent more time fishing before returning to port. Fishing during that time was limited to the central, east coast of the Gulf and from October to May. By 1979/80, the fishing area expanded to the major islands in the northern Gulf and extended to a 12-month fishery. By 1982/83, the fishery also expanded southwards along the east coast of the Gulf (Cisneros-Mata *et al.* 1995, Fig. 8). The peak catch of 294 000 tons was in 1988/89, after which the catch declined by almost two-thirds in one year and then further to 7 000 tons in 1991/92. Since then, the catch increased to 203 000 tons in 1996/97 (Fig. 9). In recent years, there have been some regulations on the fishing season in the Gulf.

Virtual population estimates of sardine biomass showed an increase in the adult stock from 1975/76, with a peak in 1985/86 of about 1.2 million tons. Subsequently, the population decreased. The level of recruitment showed a similar pattern, increasing after the 1974/75 season until 1984/85, and then falling dramatically. The mean length and size at maturity of sardine decreased during the period of increased abundance, then increased as the stock size decreased.

Lluch-Belda *et al.* (1986) concluded that the sardine catch is influenced by the availability of the fish to the fishing fleet and that availability is influenced by the ocean climate. During warmer years, sardine do not move as far south along the east coast of the Gulf, and the fleet has less area to fish. During the coldest years, the fish have been caught as far south as Mazatlan. Overfishing could have influenced the very rapid collapse of the fishery at the time when both biomass and recruitment were declining (Cisneros-Mata *et al.* 1995) .

Anchovy — In 1985, juvenile anchovy were sighted near Guaymas, and during the fishing year 1985/86 they were being caught with sardine schools. This was the first time anchovy had ever been reported in the Gulf (Hammann and Cisneros-Mata 1989), although their earlier presence is known from scales in sediments (see section on Proxy Records). The first appearance of anchovy in the catch was also the year of the beginning of the decrease in sardine biomass. There was an increase in the catch of chub mackerel *Scomber japonicus* that year. The anchovy fishery reached a peak in the 1989/90 fishing season (18 000 tons), then declined to zero during the 1996/97 fishing season (Fig. 9). The spawner biomass was estimated to be 105 000 tons in 1991 (Cotero-Altamirano and Green-Ruiz 1997).

Ichthyoplankton studies, undertaken since 1971, have shown that sardine eggs and larvae occur south of Isla Angel de la Guarda, across the Gulf of California. In 1985, when anchovy were first detected in the Gulf, eggs and larvae of sardine were more abundant than those of anchovy. By 1987, there were approximately equal numbers of eggs and larvae of the two species and the area of their distribution was similar. However,

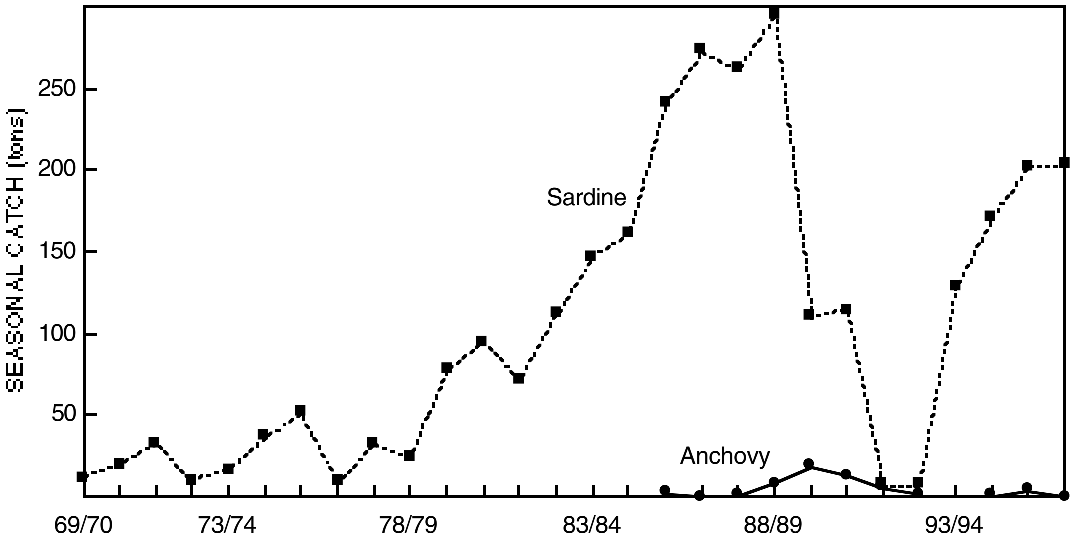

Fig. 9: Trends in catches of sardine and anchovy in the Gulf of California, 1969/70–1996/97

during 1991, 1992 and 1994, young anchovy larvae were much more abundant than sardine larvae. During 1987, 1991 and 1992, anchovy eggs and larvae were found in the vicinity of the large islands in the Gulf, but during 1992 they were restricted to the more northerly, cooler waters, because of the *El Niño* event.

South-Eastern Pacific

The Humboldt Current is the most productive in the world in terms of anchovy and sardine biomass. Catches have been made from Ecuador south to Talcahuano (35°S) in Chile, but mostly from northern Peru to northern Chile (Fig. 10).

The fishing industry began in the 1930s, but it did not develop into large-scale production until about 1955. By 1963, the catch of anchovy in the Humboldt system, for fishmeal production, was more than that of any other fish species in the world (Doucet and Einarsson 1967). Many of the fishmeal processing plants were imported from California, where the sardine catch had collapsed. Since 1959, the combined annual catch of anchovy and sardine in the Humboldt system has never been less than two million tons. Until about 1975, the catch was almost exclusively anchovy. At that time, the sardine biomass and catch began to increase markedly. In 1986, the sardine catch began to decrease and the anchovy catch to increase.

DISTRIBUTION

There are two stocks of anchovy in the Humboldt Current, a northern stock, fished in northern and central Peru, and a southern stock, fished in southern Peru and northern Chile (Fig. 10). There are also four relatively discrete stocks of sardine: a northern stock off north-central Peru, a shared stock off southern Peru and northern Chile, a Coquimbo stock (29°31´S) and a Talcahuano stock (35°38´S, Parrish *et al.* 1989).

For anchovy, there was a larger catch of fish in northern and central Peru than in southern Peru by factors ranging up to 37, except for 1978, 1980, 1981 and 1984, when more fish were caught in southern Peru. During 1983, an *El Niño* year, there were very few anchovy caught in either location, especially southern Peru (366 tons); off north Chile there was no catch. Generally, the ratio of catches off north-central Peru to those in southern Peru and northern Chile fell from 1960 through 1984, and then began to increase again. Overall, it appears that anchovy are more plentiful in north and central Peru than in southern Peru.

When comparing the anchovy catch off southern Peru with that of northern Chile between 1969 and 1985, more fish were consistently caught off southern Peru. In all other years between 1960 and 1996, except 1965, more anchovy were caught off northern Chile than southern Peru (Appendix).

Catches of sardine were always greater off north-central Peru and northern Chile than off southern

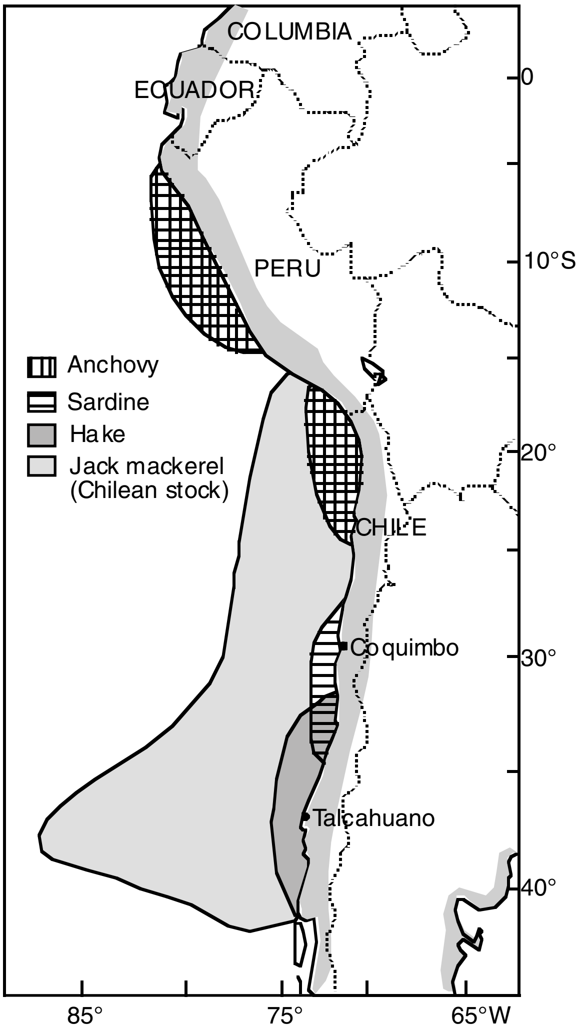

Fig. 10: Generalized locations of the fisheries for anchovy, sardine, hake and jack mackerel in the South-Eastern Pacific Ocean. When biomass of sardine was high, they were found up to 1 200 miles from the coast

Peru (Appendix).

Information is available that, when sardine biomass off Chile was high in 1983/84, sardine extended westwards nearly 1 200 miles into the south Pacific Ocean, to 97.5°W. During the 1982–83 *El Niño*, there was a large geographical displacement of sardine, as shown by tagging recoveries and hydro-acoustic surveys. During that *El Niño*, the Ecuadorian sardine fishery was much reduced as the fish moved south into Peruvian waters, possibly to avoid high water temperatures. Sardine also appeared to move into southern Peru and Chile. Maximum movement was from about 9 to 30°S. There is considerable evidence for intermixing of sardine from central Peru to Coquimbo, Chile (Parrish *et al.* 1989).

Russian investigations were undertaken at a distance of more than 200 miles from the coast of Peru and Chile from 1978 to 1985. These showed seasonal and interannual variations in the distribution of sardine. Most sardine were found in surface temperatures of 17–20°C. The distributions of eggs and larvae were patchy. Batch fecundity varied between 35 and 150 thousand eggs in female sardine of 20.7–31.5 cm (fork length, *FL*). The timing and location of spawning varied among years. During the season before the 1982/83 *El Niño*, and during that *El Niño*, eggs were relatively scarce. Anchovy spawned in water temperatures of 16–18°C, whereas sardine spawned in temperatures of 19–21°C (KVS, pers. obs.).

LANDINGS

Anchovy — Trends in landings of anchovy off Peru and Chile are shown in Figure 11. The catch rose steeply from 1956 to 1970, peaking at nearly 13 million tons. It then dropped to less than two million tons in 1973. At that time, the sardine catch began to increase. The anchovy catch oscillated up and down until 1984, when it reached its smallest catch of 25 084 tons. The catch then rose to almost 12 million tons in 1994. In 1995 and 1996 the anchovy catch was about eight million tons.

The catches from each of the two anchovy stocks are in phase, ascending or descending together in most years (Fig. 12). The largest catches are from the northern stock. In 1970, when the highest catch was recorded, the catch from the northern stock was 5.5 times that from the southern stock. In 1994, the peak of the recent anchovy boom, there was a three-fold difference in catches from the two stocks. When the catch was at its lowest, in 1984, the catch from the northern stock (2 403 tons) was smaller than that from the southern stock (24 818 tons). That year followed the 1982–83 *El Niño*, and there may have been a southern displacement of the catch.

There is some exchange of anchovy between regions. In 1970, tagging of anchovy off Peru showed fish there to be mainly a single population, but there were some tags recovered in Chile (IMARPE 1972, Yañez 1991).

Sardine — Catches of sardine off Peru began in 1951 with 1 000 tons. In 1952 and 1953, some 400 and 100 tons were caught respectively. There are no reported catches from 1954 through 1957. Then in 1958, the catch was 2 000 tons. From 1959 through 1972 the

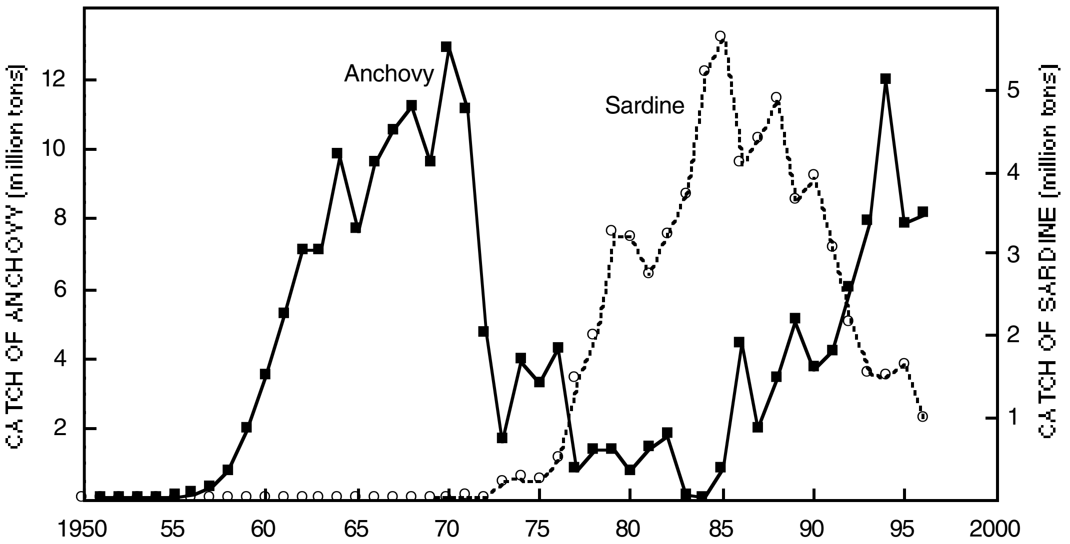

Fig. 11: Trends in catches of sardine and anchovy in the Humboldt Current, 1950–1996

largest catch in any year was 10 000 tons, but mostly annual catches ranged between 1 000 and 4 000 tons. Catches off northern Chile began in 1965 (3 800 tons), but only from 1970 are data recorded separately for all four stocks.

Catches from the three northern stocks began to increase in the early 1970s, and from the southern Talcahuano stock in the late 1970s. Catches off northern-central Peru peaked around 3.4 million tons in 1988, and then decreased (Fig. 13). Off southern Peru and northern Chile, catches peaked in 1985 at a level of three million tons, and then steadily decreased. The pattern

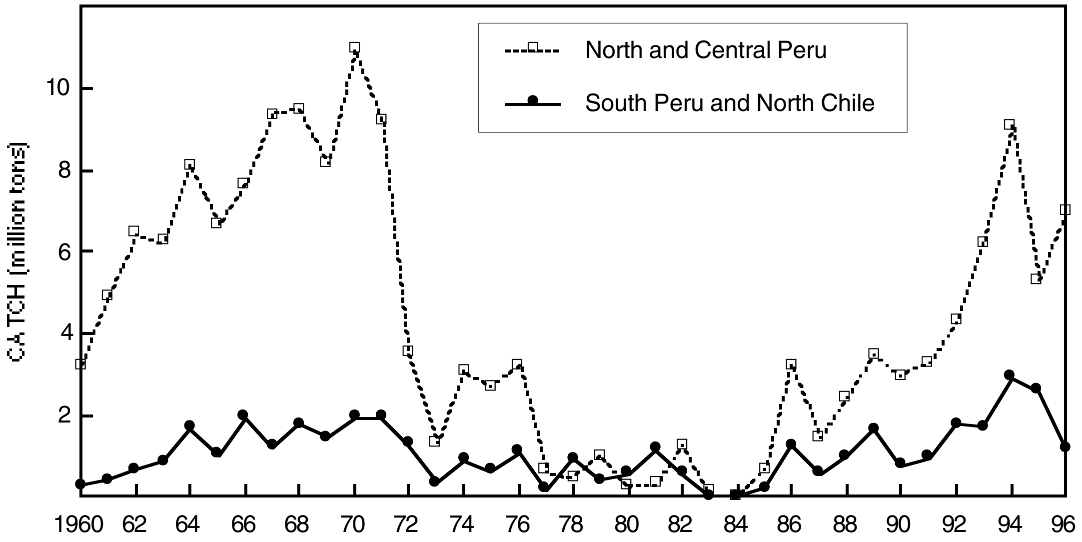

Fig. 12: Trends in catches of anchovy from the stock off northern and central Peru, and from that off southern Peru and northern Chile, 1960–1996

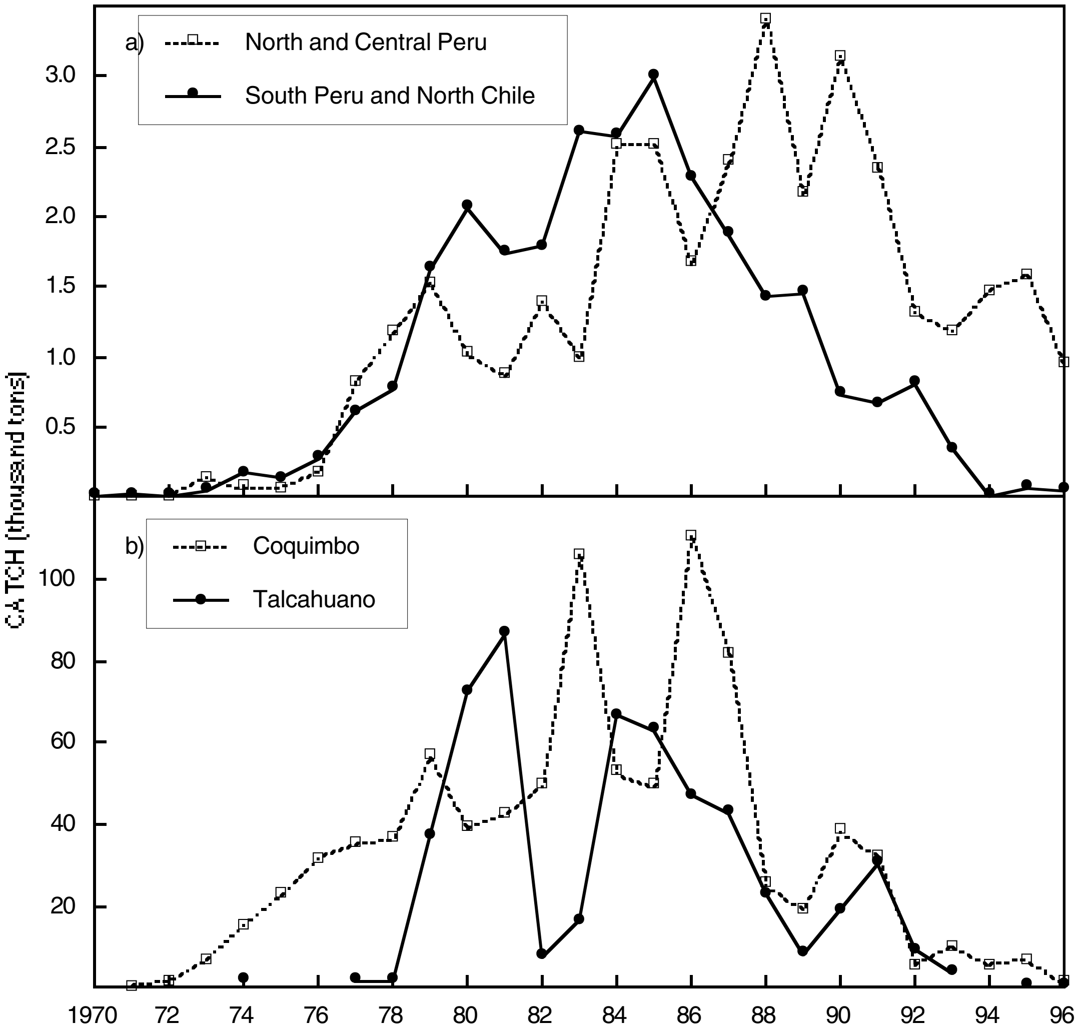

Fig. 13: Trends in catches of sardine from the four stocks in the Humboldt Current – those off (a) northern and central Peru and off southern Peru and northern Chile, and (b) off Coquimbo and off Talcahuano, 1971–1996

off Coquimbo was similar, but at Talcahuano the catch peaked in 1981 (Fig. 13). In 1996, landings in Peru amounted to about one million tons, but those from stocks along the Chilean coast were <50 000 tons.

ABUNDANCE

Trends in biomass of anchovy and sardine, for both adults and recruits, are shown in Figure 14. Those for adults suggest that both the anchovy decline and the sardine increase were initiated in the early 1970s. Biomass of adult sardine off north-central Peru peaked in 1987, whereas off south Peru/north Chile the peak was in 1980. Biomass of anchovy off north-central Peru began to recover after 1983.

More exact dates of the initial change from a regime of anchovy to one of sardine, and the subsequent reversal to an anchovy-dominated system, can be deduced from estimates of recruit biomass (Fig. 14b). Anchovy recruitment fell in 1970, coinciding with the period when the composition of the ichthyoplankton community off northern Chile changed (Loeb and

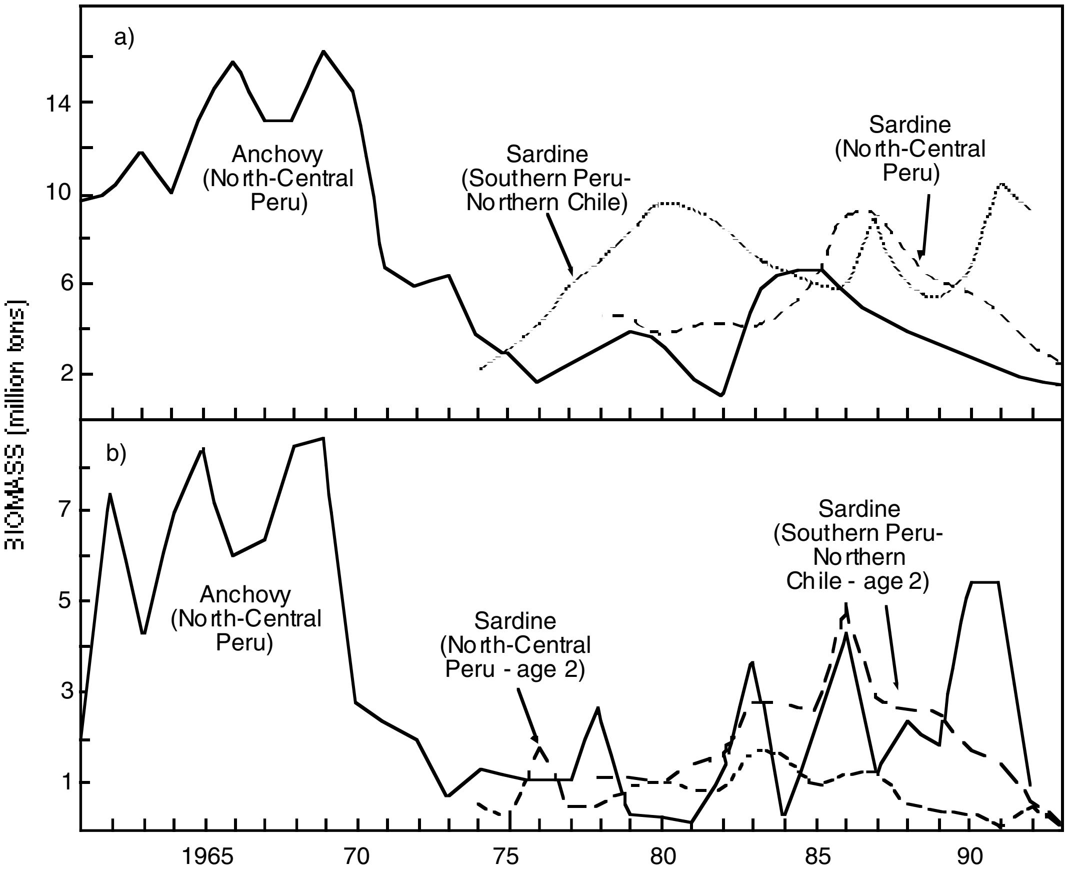

Fig. 14: Estimates of the biomass of (a) the adult component of stocks of sardine and anchovy in the Humboldt Current and (b) recruitment to those stocks, 1961–1993. Sardine recruits are aged two years, those of anchovy are young of the year

Rojas 1988). Recruitment of sardine increased from the early 1970s, fluctuated around a high level, and started to decrease again from about 1988–1990. As sardine recruits are 2 years old, this means that poor year-classes originated two years earlier. Trends of sardine recruits support the conclusion of an earlier decline of the Chilean stocks than that off north-central Peru.

South-Australia Pacific

BACKGROUND

The coastal and oceanic waters off Australia are relatively unproductive, with both the east and west coasts of the continent dominated by south-flowing, warm, oligotrophic, tropical waters (Pearce 1991). The strengths of these currents are strongly correlated with variations in the Southern Oscillation Index. One of the major impacts of these currents, particularly off the west coast of Australia, is to inhibit almost completely any upwelling. Therefore, the eastern boundary current off Western Australia (WA) is unique in the world.

There are two additional factors that influence the potential size of the pelagic fish resources of Australia. First, the continental shelf in most southern areas of Australia is relatively narrow. Second, with most of the continent being arid, there is relatively little input from river systems providing terrestrial sources of nutrients. This is especially the case in the western half of the continent, where the majority of the land is desert.

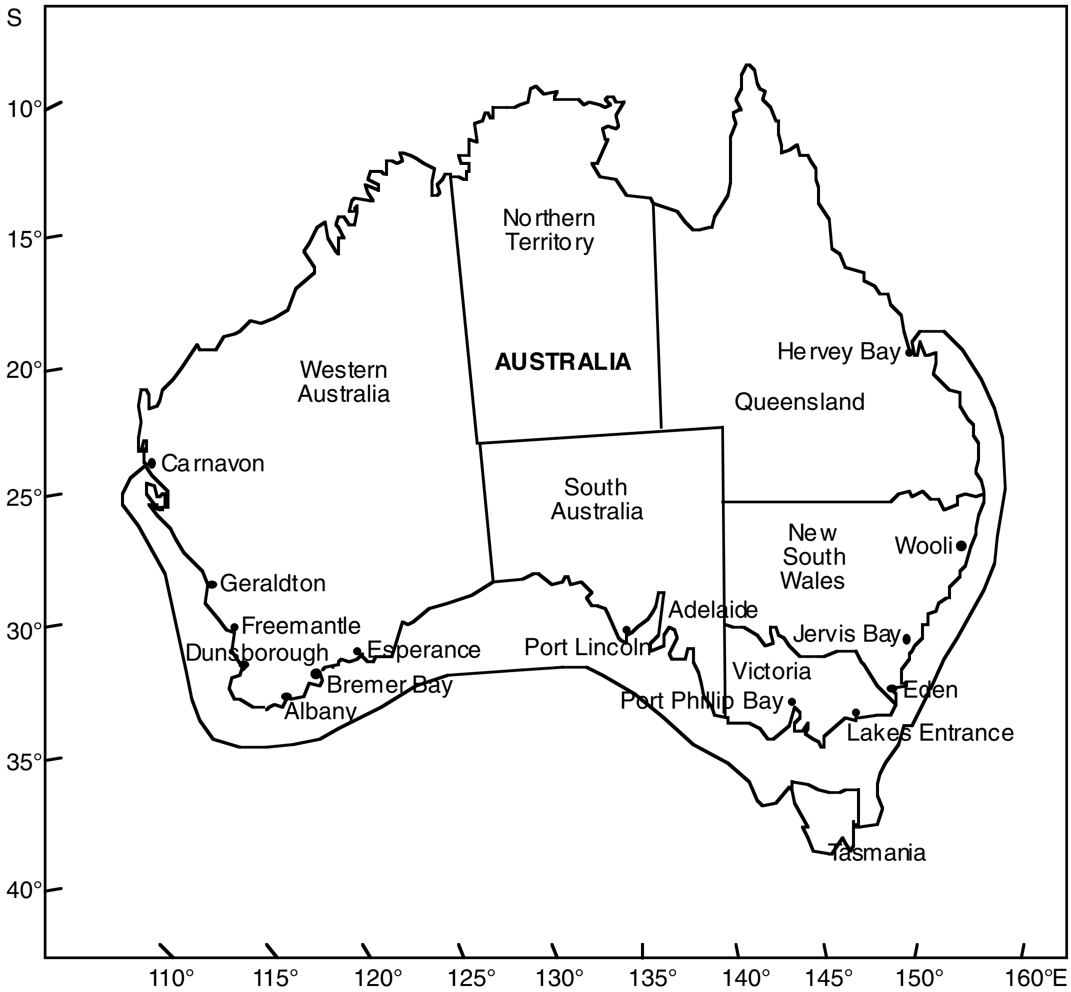

Fig. 15: Distribution of sardine off Australia. Except for Carnarvon and Hervey Bay, which are at the extremes of the range, the other locations shown are fishing ports for sardine

DISTRIBUTION

Sardine — The distribution of sardine (or pilchard as they are locally known) in Australia extends across the entire lower half of the continent, from Red Bluff near Sharks Bay in Western Australia (WA), down and across the southern WA coastline, the Great Australian Bight (GAB), South Australia (SA), Victoria (Vic) and northern Tasmania and up the New South Wales (NSW) coast to Hervey Bay in southern Queensland (Fletcher 1990, Fig. 15). This is a total of 6 700 km, which makes it the largest range, in terms of linear distance, of all *Sardinops* populations. *Sardinops* also are distributed around the coasts of New Zealand.

Trawl surveys and plankton studies have shown that, within Australian waters, sardine are almost totally restricted to waters of the continental shelf (e.g. Fletcher 1990, 1994). Furthermore, although larvae have sometimes been found in estuarine environments (Gaughan *et al.* 1990), extensive sampling has found neither juveniles nor adults within these locations in WA. Sardine have, however, been caught in oceanic regions along the south coast of WA, particularly near Esperance. On the east coast of Australia, Blackburn (1949, 1950) concluded that juvenile sardine inhabited sheltered bays and inlets, albeit with little supporting evidence (Fletcher 1990).

Anchovy — The Australian anchovy *Engraulis aus-*

tralis also has a distribution that spans most of southern Australia. However, it generally inhabits only sheltered bays, inlets and estuarine areas, being rarely found in oceanic waters, and is therefore not found in the GAB. There is little information available for this species and there is no consistent fishery for it.

STOCK STRUCTURE

A large amount of work has been devoted to studying the stock structure of sardine in Australia, particularly in WA, and has shown that separation can be seen at a number of different levels.

Spawning times — Spawning seasons vary greatly among localities. Therefore, in the eastern region of WA and into the GAB, the main time for spawning by sardine is April–July (Blackburn 1950, Fletcher *et al.* 1996b). At Bremer Bay, there is also only one main spawning period per year, during June and July (Fletcher *et al.* 1994), whereas at Albany there are two periods of spawning, one in July and the other December/ January (Fletcher *et al.* 1994). There are also two periods of spawning on the west coast of WA, one in August and the other in February–March (Fletcher *et al.* 1996b).

Elsewhere in Australia, sardine spawn from February to March (SA) and November (Vic), whereas in NSW the season in the south begins during summer and moves later in the year with increasing distance up the NSW coast (Fletcher 1990).

Age structure — The rates of total mortality measured for a number of areas in WA appear to be related to the different levels of fishing exploitation. Therefore, at Albany, the total mortality rate is high ($Z > 0.8$), which correlates with the long history of heavy fishing in that region. At Bremer Bay, where exploitation has been much lower, mortality is lower, whereas at Esperance, where exploitation has only just begun, the curves appear to merely reflect natural mortality ($Z = 0.43$). Such differences are inconsistent with a freely mixing adult stock.

Plankton — Plankton surveys completed in summer and winter on the south coast of WA for the years 1991–1995 have confirmed that there are a number of discrete spawning areas, which are consistent in space and time, but the products of these are often mixed as a result of transport by the Leeuwin Current (Fletcher *et al.* 1994, 1996b). Furthermore, there has always been a large gap between spawning areas on the South and West coasts. There has also been surprisingly little evidence of movement of material from the West Coast to the South Coast, despite the presence of the strong, south-flowing Leeuwin Current.

Morphological studies — Studies of variation in morphological features have found significant differences among regions. An eastern group (NSW), a south-eastern group (Vic), a south-western group (southern WA) and a western group (west coast of WA, Blackburn 1951, Syahailatua 1992).

Electrophoresis — Dixon *et al.* (1993) completed an allozyme study of the genetic structure of sardine throughout Australia and concluded that there was "a series of contiguous quasi-independent pilchard sub populations". Those authors delineated western, south-western, south-eastern and eastern populations, the boundaries of which possibly shift in response to variations in environmental conditions, particularly the Leeuwin Current. However, this separation was not shown to be complete.

Minor and trace elements — Results of a relatively new technique of examining the composition of minor and trace elements in otoliths as a method of stock delineation were initially promising for sardine. They showed clear separation among sites on the South Coast, but no separation between West Coast sites (Edmonds *et al.* 1995). Repeated sampling on the South Coast showed that the level of temporal variation was similar to the level of spatial variation. However, there appear to be at least two South Coast stocks, the positions of which may vary with time. There is some overlapping of stocks, at least on a small scale.

$O^{16/18}$ isotope analyses — Sampling of sardine otoliths from different locations revealed very clear differences in isotope ratios among sites, which were sustained over a full year of sampling (Edmonds and Fletcher 1997). Otoliths from West Coast sardine had ratios suggesting that they lived in water that, on average, was 1.5°C warmer than South Coast sardine. Those from Esperance indicated a temperature about 0.5°C cooler than at Albany and Bremer Bay. Both these results are consistent with average differences in temperatures among sites. These data support the notion that there is little movement between the South and West coasts by adult sardine, and that there is even restricted movement along the South Coast by adults.

Conclusions — In WA, there appear to be two separate spawning stocks, those on the West Coast and the South Coast, with recruits functionally separated. Along the South Coast there also seems to be a finer level of separation, with at least two and probably three adult stocks in that region. The position of these stocks is variable and there is evidence for major flow between areas during the juvenile phases (<3 years of age), but only minor movement as adults. In terms of fisheries management, the three South Coast areas are treated separately. By contrast, none

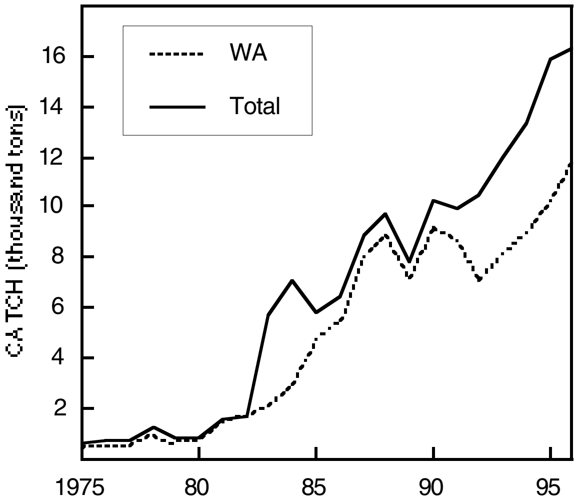

Fig. 16: Trends of catches of sardine in Western Australia and overall in Australia (Total), 1975–1996

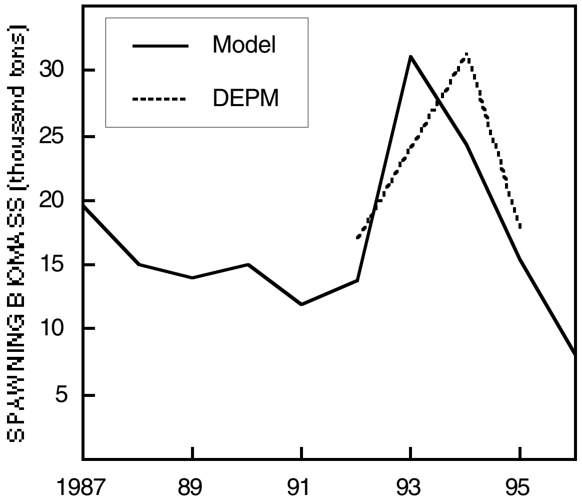

Fig. 17: Estimates of spawner biomass of sardine in the Albany region of Western Australia from a simulation model (Model) and the daily egg production method (DEPM), 1987–1996

of the data collected on the West Coast have indicated any finer level of stock separation, and consequently this area is treated as one stock.

GROWTH AND SEXUAL MATURITY

The size of individual sardine is much smaller in Australia than at the other locations around the world where the species is located. The average and maximum sizes in WA are 160 and 205 mm *FL* (40–100 g) respectively (Fletcher and Blight 1996). Despite the difference in sizes attained, the pattern of growth appears to be relatively similar to other *Sardinops* populations (Fletcher 1990). For the WA population, sexual maturity is attained during the second year, at approximately 120–130 mm *FL*, and sardine live to a maximum of nine years (Fletcher 1995, Fletcher and Blight 1996). Females grow to larger lengths than males (L_∞ of the Von Bertalanffy equation is 174 and 164 mm respectively), with the change in growth trajectories occurring after age two (Fletcher 1995, Fletcher and Blight 1996).

FISHERY

The fisheries for sardine and anchovy in Australia are small in comparison to the other regions of the world where these species are found. The maximum annual catch for these two species combined from Australian waters has been only around 16 000 tons. The composition of the catch is dominated by sardine, with the fishery for anchovy largely restricted to one or two embayment areas in Victoria on the south-eastern coast of Australia.

The largest sardine fishery is in WA (Fletcher 1991). There, fishing for sardine began during the 1950s, expanding during the 1970s and especially the 1980s in both the areas of fishing and the level of catches (Fig. 16). There are at present seven management zones for sardine fishing in WA; all either already have a Total Allowable Catch (*TAC*) or a *TAC* that is being determined. A total of more than 40 boats has endorsements to use purse-seine gear within these zones and the catch during the past five years has averaged approximately 9 000 tons. This makes up more than 75% of the total sardine catch from Australian waters. Catches in other locations around Australia have increased recently, particularly in SA. The Australian catch of sardine exceeded 10 000 tons in 1990 and during the period 1992–1996.

ABUNDANCE

Estimates of the size of sardine stocks in Australia have only recently been available. A computer simulation model, based on catch and effort information for the WA south coast fishery, was created in 1991 (Fletcher 1992). This estimated that the stock size of sardine in the Albany region was between 10 000 and 35 000 tons. Subsequent use of the model in conjunction with catch-at-age information, which has been collected yearly since 1989, has refined these estimates. The size

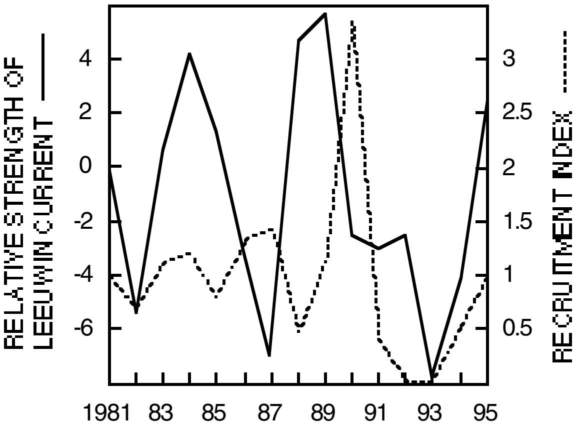

Fig. 18: Comparison between a recruitment index for sardine in the Albany region of Western Australia, and the relative strength of the Leeuwin Current as measured by sea level at Freemantle, 1981–1995

of the spawning stock at Albany during this period varied between 8 000 and 25 000 tons (Fig. 17), because of fluctuations in recruitment (Fig. 18, Fletcher 1994, 1995).

The daily egg production method (DEPM) for calculating biomass, which is independent of fishery information, was used in the Albany area from the period 1991–1995 and in 1997 (Fletcher *et al.* 1996a). These estimates, based on plankton tow data and adult spawning parameters, have varied between 15 000 and 32 000 tons, in good agreement with model estimates.

The pattern of recruitment at this site has seen large cohorts of 2-year-old fish derived from spawning during 1989 and 1990 entering the fishery. This was followed by a period of four years of greatly reduced recruitment that resulted in substantial declines in stock size, and a reduction of the quota from 5 500 to 3 500 tons per annum. These variations in recruitment may possibly be linked with variations in the strength of the Leeuwin Current, which in turn is influenced by *El Niño* Southern Oscillation (ENSO) events (Fig. 18). The Leeuwin Current directly influences temperatures and transport (Fletcher *et al.* 1996b). Many other species are affected by these fluctuations (Caputi *et al.*1996). There was no expansion of anchovy in this region during the period of reduced sardine abundance.

The stock at Bremer Bay has been assessed using yearly catch-at-age information since 1989 and DEPM surveys in 1992 and 1993. Both indicate that the biomass is about 20 000 tons. Estimates of biomass for the other areas in WA are too preliminary to place much confidence in them.

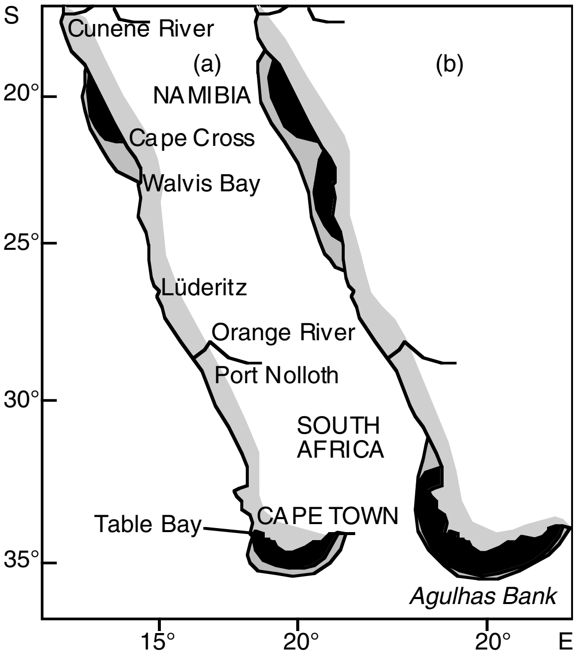

Fig. 19: Major fishing (hatched) and spawning (black) grounds of sardine in the South-Eastern Atlantic during periods of (a) low and (b) high abundance (after Lluch-Belda *et al.* 1989)

Estimates of biomass of sardine off SA using DEPM were 56 000 tons in 1995 and 18 000 tons in 1996. During those years, the *TAC* for the region was between 1 500 and 3 000 tons.

In Vic, the catch in the Port Philip Bay region has averaged approximately 1 000 tons for the past few years. This fishery catches mostly young-of-the-year (<11cm); almost no mature individuals are taken.

Off the NSW coast, fisheries for sardine have existed for a number of decades but the level of catches has been small (<500 tons and usually <100 tons). Although no formal estimate of stock size is available for the region, a substantial amount of dead sardine was seen off the coast during the period of mass mortalities. Hence, it is possible that the stock there may be bigger than has been assumed.

Conclusions — Until recently, variations in the biomass of sardine off Australia have been mostly short-term (2–5 years) fluctuations, more similar to those of tropical species such as *Sardinella* of Brazil than to those of *Sardinops* off Japan, southern Africa and Peru/Chile. However, sustained poor recruitment of sardine off many areas of WA during the 1990s suggest that long-term cycles may be possible.

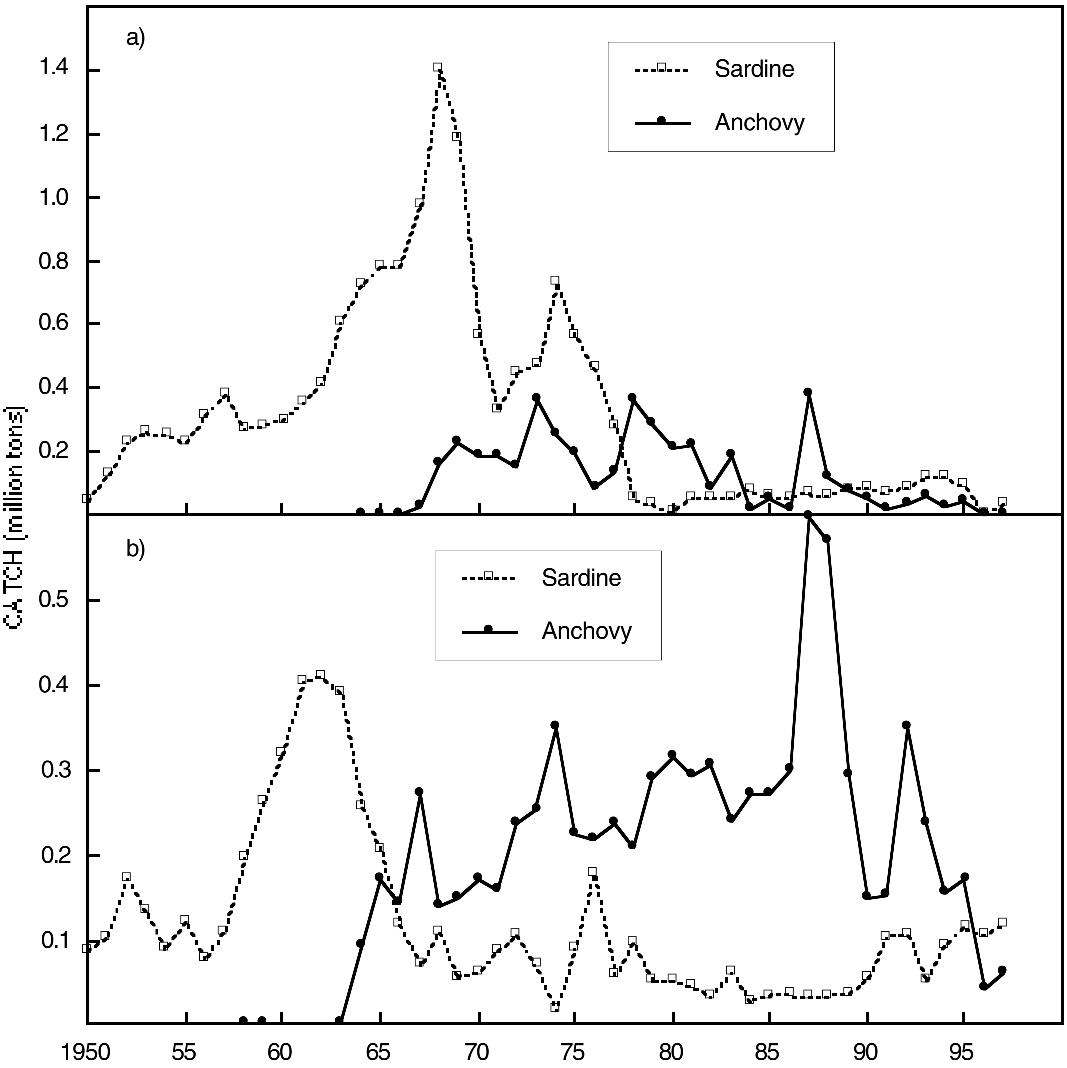

Fig. 20: Trends in catches of sardine and anchovy off (a) Namibia and (b) South Africa, 1950–1996

The very restricted distribution of anchovy in Australia results in there being almost no direct interaction with sardine. There are few reports of anchovy having a wider distribution at any time in the past. Therefore, there is no evidence that there has been a period when anchovy has dominated over sardine. Consequently, the fluctuations of stocks of sardine and anchovy in Australia do not yet exhibit characteristics observed in other regions of the world. This may result from the Australian ecosystems being considerably less productive than those elsewhere, and may also reflect the relatively short duration of the Australian time-series.

South-Eastern Atlantic

DISTRIBUTION

There are two relatively independent stocks of sardine and anchovy off southern Africa, one each north and south of an area of intensive upwelling in the vicinity

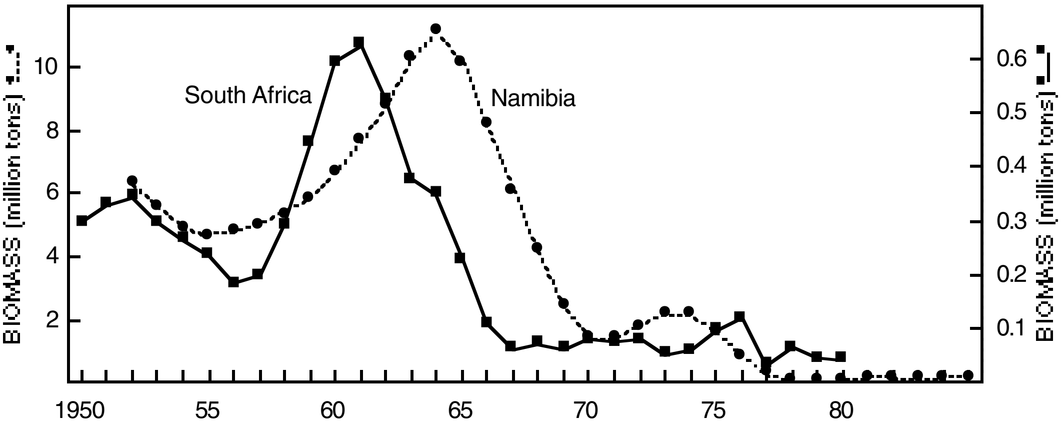

Fig. 21: Estimates from virtual population analysis of spawner biomass of sardine off Namibia and South Africa, 1950–1985

of Lüderitz (26°38´S, 15°09´E), Namibia (Fig. 19).

When sardine were at a high level of abundance, adults were plentiful north of Cape Town and south of Walvis Bay. As the stocks collapsed, the distribution of older sardine contracted and they spawned mainly in the north off Namibia and in the south off South Africa (Fig. 19). Adult anchovy tend to remain north of Walvis Bay, and on the western and central Agulhas Bank off South Africa (Hampton 1992, Barange *et al.* 1999). They generally did not colonize the region between Lüderitz and Table Bay that had been occupied by adult sardine.

Young-of-the-year of both sardine and anchovy are found from Walvis Bay northwards and south of the Orange River (Crawford *et al.* 1987, Hampton 1992, Barange *et al.* 1999). Off South Africa, they migrate southwards to the Agulhas Bank, and are only abundant off the West Coast seasonally.

Histories of the fisheries up to1985 have been reviewed by Crawford *et al.* (1987). Regimes of sardine and anchovy in southern Africa since 1950 have been described by Crawford (1998).

FISHERIES

Sardine — In the 1950s and 1960s, 13.5 million tons of sardine were harvested by the purse-seine fisheries, 3.7 million tons off South Africa and 9.8 million tons off Namibia. The South African sardine fishery collapsed in the mid 1960s, ahead of that off Namibia, which decreased in the early 1970s (Fig. 20, Crawford *et al.* 1987). In the following two decades, from 1970 to 1989, the sardine catch totaled 5.7 million tons, of which 1.2 million tons were from South Africa and 4.5 million tons from Namibia. The annual South African catch peaked at 0.41 million tons in 1962 and the lowest catch of 16 000 tons was recorded in 1974. Off Namibia, 1.4 million tons were caught in 1968, but only 12 000 tons in 1980. The Angolan fishery has also exploited the northern stock of sardine.

Virtual population estimates of the spawner biomass of sardine off South Africa peaked at 0.63 million tons in 1961, falling to 0.03 million tons in 1977 (Fig. 21). Off Namibia, overall sardine biomass was estimated to have been more than 11 million tons in 1964, but just 0.05 million tons in 1979. For both South Africa and Namibia, the estimates are considered to reflect only large-scale trends in abundance because there are several limitations, including uncertainties concerning terminal fishing mortalities and the contributions of older age-classes in the initial period of the fishery (Armstrong *et al.* 1983, 1985, Thomas 1986).

Acoustic surveys to estimate sardine abundance were initiated off South Africa in 1984 (Hampton 1987). The spawner biomass of sardine was then 0.03 million tons, but it increased steadily to 0.77 million tons in 1997 (Hampton 1992, Barange *et al.* 1999). Off western South Africa, the increase is confirmed by the contribution of sardine to the diet of Cape gannets *Morus capensis*, which rose from <10% by mass in each year between 1978 and 1984 to almost 60% by 1990 (Crawford and Dyer 1995). A relatively strong sardine year-class was formed off South Africa in 1983 (Berruti and Colclough 1987), probably triggering subsequent growth of the resource. Acoustic surveys for sardine have recently been undertaken off Namibia, where more than 0.5 million tons were recorded in both 1991 and 1992 (Boyer 1994).

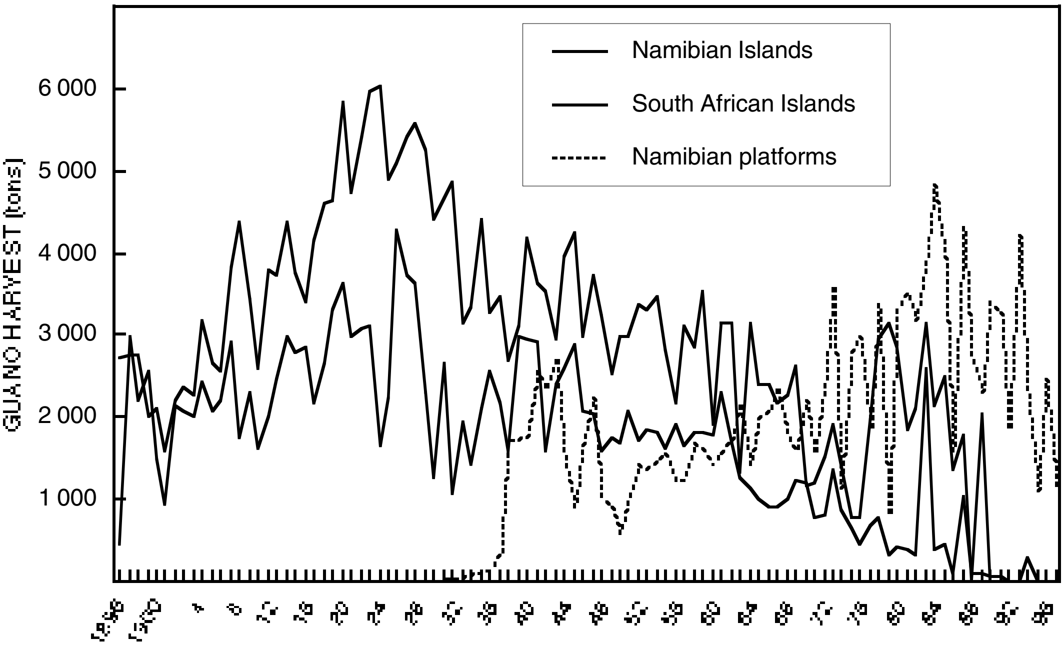

Fig. 22: Trends in harvests of seabird guano at islands off Namibia and South Africa, and at platforms off Namibia, 1896–1995

Anchovy — In the 1950s, anchovy was probably at a low level of abundance off South Africa. A large majority of fishers held that anchovy increased in abundance after the mid 1950s, most believing that the increase took place during the early 1960s (Crawford and Kriel 1985). In research catches of juvenile fish off western South Africa, anchovy contributed an annual average of 4% of total numbers of fish caught between 1955 and 1959. This proportion rose to 30% between 1960 and 1965. Equivalent values for sardine were 25 and 10% (Crawford *et al.* 1987). An especially good research catch of juvenile anchovy was recorded in 1962 (Crawford *et al.* 1990a). From 1953 to 1956, anchovy constituted 9–20% of the mass of the food eaten by Cape gannets off western South Africa (Davies 1955, 1956, Rand 1959). From 1978 to 1988, it formed 37–64% by mass of the food eaten by Cape gannets (Berruti *et al.* 1993, Appendix).

Between 1957 and 1959, anchovy contributed <2% to the diet of each of African penguins *Spheniscus demersus*, Cape gannets and Cape cormorants *Phalacrocorax capensis* near Walvis Bay, Namibia (Matthews 1961, Matthews and Berruti 1983). By contrast, from 1978 to 1982 anchovy formed 53% of the food of Cape gannets at Namibian islands south of Walvis Bay (Crawford *et al.* 1985). Newman (1970, p. 12) wrote of 1963 "... during this year the anchovy abundance was extremely low, and negligible catches were recorded." In that year, only 600 tons were caught off Namibia, leading Thomas (1985) to conclude that the Namibian anchovy resource was then small. There-fore, off Namibia, anchovy was uncommon in the late 1950s and early 1960s.

Anchovy was first exploited by the southern African purse-seine fisheries in the 1960s. By 1966, it contributed more than any other species to the South African purse-seine catch, and it continued to dominate the fishery for 30 years, up to and including 1995. Sardine regained dominance in 1996 and 1997. The anchovy catch dropped from 170 000 in 1995 to 40 000 tons in 1996 (Fig. 20).

Off South Africa, the spawner biomass of anchovy, estimated acoustically, was between 0.97 and 1.75 million tons from 1984 to 1988. It fell to about 0.5 million tons in 1989 and 1990, was above 1.5 million tons in 1991 and 1992, but fell again to <0.5 million tons in 1994 and 1995 (Hampton 1996). It was <0.2 million tons in 1996 and 0.8 million tons in 1997 (Barange *et al.* 1999).

Off Namibia, anchovy was first caught in 1964. Catches were small until 1968, when 0.16 million tons were landed. In 1978, when the catch was 0.36 million

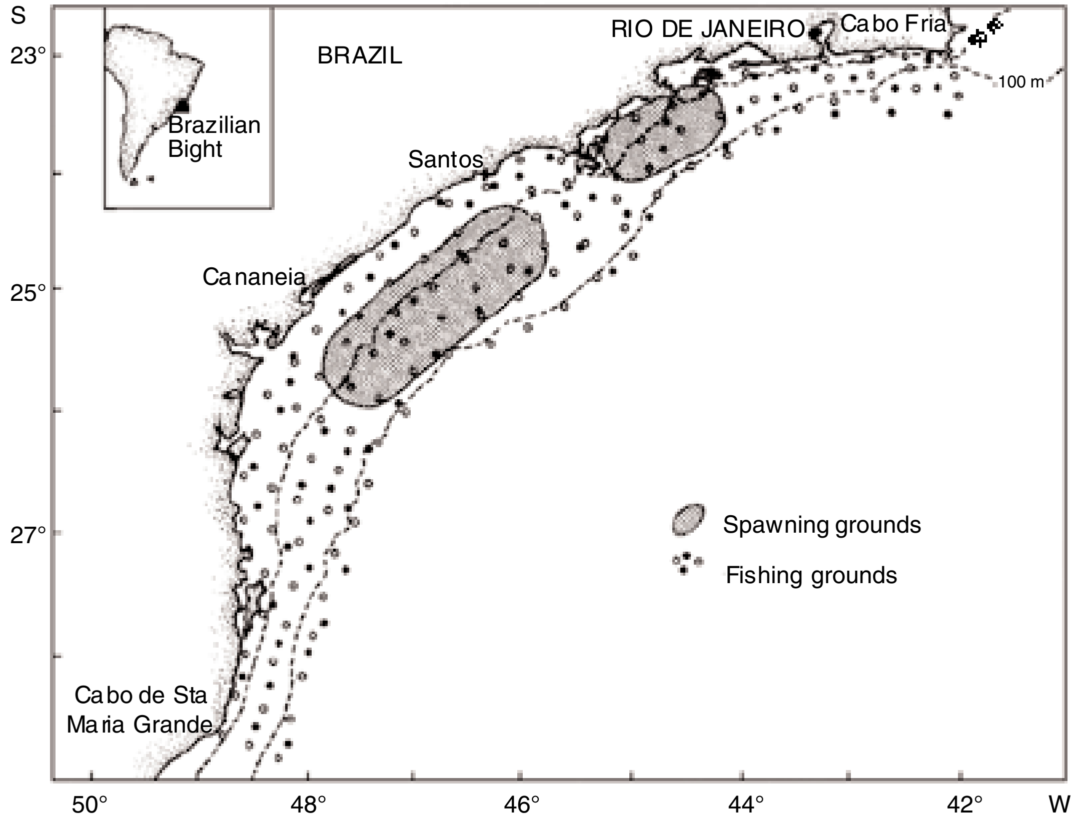

Fig. 23: Spawning and fishing grounds for *Sardinella* in the Brazilian Bight, Brazil

tons, anchovy became the most important contributor to the Namibian purse-seine fishery. This situation continued until 1984, when <17 000 tons of anchovy were caught. Poor catches continued in 1985 and 1986. In those three years, sardine dominated the landings. In 1987, the anchovy catch off Namibia was the highest yet recorded, 0.38 million tons. Thereafter, annual catches rapidly plummeted, and by 1997, were just 1 000 tons. From 1990 to 1996, sardine regained dominance of the Namibian purse-seine catch.

The contributions by mass of sardine and anchovy to the diet of Cape gannets off western South Africa are available for 1978–1997 (Appendix). They correlate well with survey estimates of spawner biomass for the period when both sets of information are available – sardine ($r = 0.63$, $p = 0.05$, $n = 10$, unpublished), anchovy ($r = 0.80$, $p < 0.01$, $n = 10$ – Crawford and Dyer (1995). The diet time-series may be used as surrogate indices of abundance of sardine and particularly anchovy off South Africa.

LONGER TERM TRENDS

Records of harvests of seabird guano at islands and platforms off Namibia and South Africa are available for the years 1896–1995 (Fig. 22). The seabirds producing guano eat mainly sardine and anchovy. Fluctuations in the quantity of guano produced reflect fluctuations in the availability of sardine and anchovy to the seabirds (Hutchinson 1950, Crawford and Shelton 1978). For example, the collapse of sardine off South Africa in the 1960s led to greatly reduced yields of guano at islands. Pre-whitened residuals for these two time-series over the period 1950–1975 indicate a significant relationship between guano yield and the biomass of sardine one year earlier ($r = 0.39$, $p < 0.05$, $n = 26$).

Cape cormorants are most numerous when anchovy abundance is high (Crawford and Dyer 1995, Crawford 1999). They decreased throughout the early 1930s, so probably anchovy were decreasing in that period and

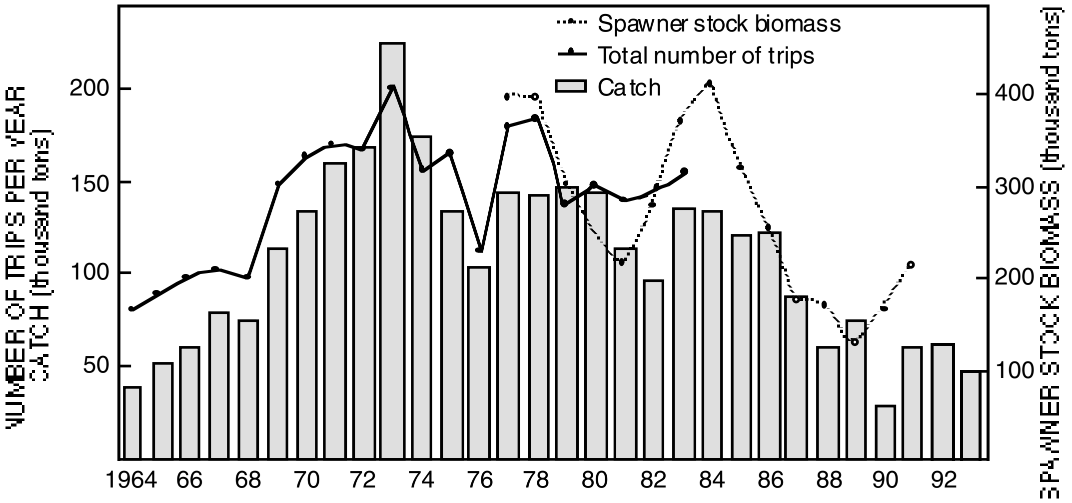

Fig. 24: Trends in catch, biomass of the spawner stock and fishing effort (number of trips per year) for *Sardinella* in the Brazilian Bight, 1964–1993

responsible for the high guano yields in the 1920s (Crawford and Jahncke 1999). Guano harvests were also high in the 1940s, but it is not possible to speculate as to which forage fish was abundant prior to powerful year-classes of horse mackerel *Trachurus trachurus* (=*T. t. capensis*) that were formed in 1946, 1947 and 1948 (Geldenhuys 1973).

More than two million measurements of sea surface temperature (SST) collected between 1910 and 1990 have been analysed for 88 areas in the South Atlantic and South Indian oceans (0–50°S, 25°W–50°E, Villacastin-Herrero *et al.* 1996). After accounting for biases in the data, the model indicates an average warming of 0.52°C over the region investigated between 1910 and 1990. Coherence in residuals (obtained by subtracting modelled results from observed data) indicates that several large areas of the oceans, often conforming with known oceanographic features, are influenced similarly. Therefore, there may be remote forcing of the southern African marine environment and its fish stocks.

South-Western Atlantic

The Brazilian sardinella *Sardinella brasiliensis* and south-west Atlantic anchovy *E. anchoita* share the same habitat in the south-eastern Brazilian Bight, but segregate vertically. The former occupies the upper mixed layer, whereas the latter occurs in the bottom layer inshore of cool South Atlantic Central Water (SACW). The Brazilian sardinella stock has been exploited by purse-seiners since the late 1950s and is an important commercial resource. Conversely, although anchovy has a relatively large biomass, there is no commercial fishery for it in the Brazilian Bight. The Brazilian sardinella population is confined to the Bight. It does not migrate extensively, and its abundance is limited by the productivity of the region between 22 and 29°S (Fig. 23). This may explain why the biomass of sardinella in the Bight has not exceeded a level of about one million tons (Cergole 1995), with a maximum catch of 243 000 tons in 1973.

The Brazilian sardinella increased coincidentally with the recent increases of sardine in the Pacific and anchovy off South Africa, and also decreased in the late 1980s as the same resources decreased. The increased landings of Brazilian sardinella in the late 1960s resulted from greater fishing effort (Fig. 24). Thereafter, the fluctuations in landings appear to have been driven by the failure of some year-classes. Because the Brazilian sardinella matures when one year old and 84% of commercially caught sardinellas are fish aged one or two years, the failure of one year-class results in a drastic reduction of the spawner biomass and catch.

The fluctuations of the Brazilian sardinella population have been influenced by a low-frequency oceanographic anomaly, which seems to be induced by weather perturbations during the spawning season. The known failures of two year-classes (1975 and 1987) are attributed to a lack of intrusion of SACW to the coastal region, which probably caused high mortality of sardinella larvae (Matsuura 1996). Following the 1987 recruitment failure, sardinella biomass decreased drastically, resulting in a minimum catch of 31 000 tons in 1990. After the 1993 spawning season, the sardinella population began a recovery phase. Total catch increased to 84 000 tons in 1994 and exceeded 100 000 tons in 1997.

PROXY RECORDS OF LONG-TERM CHANGES IN SARDINE AND ANCHOVY POPULATIONS

There are several means by which the long-term histories in abundance of sardine and anchovy may be documented. These are the anecdotal records of catch sizes of the Japanese sardine; the records kept of harvests of seabird guano off Peru as well as off Namibia and South Africa; and the sedimentary records of fish-scale accumulation off the west coasts of the United States and Mexico, and off Peru and Namibia. Careful examination of relationships among these various series provides the only way to begin to answer the question of whether these populations exhibited global synchroneity prior to the introduction of industrial-scale purse-seine fisheries.

The record for the Japanese sardine begins soon after AD 1600 as qualitative indices of good or poor catches in certain areas (Kikuchi 1958). These data need to be used with caution and should be interpreted in light of the spatial-temporal variability in feeding and spawning locations of modern populations.

Records of the annual harvests of seabird guano collected off Peru and Namibia/South Africa are available for about the last 100 years. The harvests are influenced by various factors, such as collecting effort and rainfall, and require careful interpretation. However, there is evidence that major signals often reflect pelagic fish production in the two systems (e.g. Crawford and Shelton 1978, Crawford and Jahncke 1999).

Some systems offer the possibility of extending the historical records by reconstructing variability of populations of the small pelagic fish species and their environment through application of marine paleoecology. This information is contained in the natural archives of marine sediments found in rare locations of suboxic deposition associated with eastern boundary currents of the North and South Pacific as well as the South Atlantic. These sites provide windows into the nature of large-scale variability over a hierarchy of time-scales from interannual through interdecadal and centennial.

So far, the longest and most reliable records are available from the Santa Barbara Basin (Southern California Bight) of the California Current, where sampling and analysis completed in the 1970s (Soutar and Isaacs 1969, 1974) is now augmented by additional information. This is one of the best sites for reconstructing a detailed chronology from the annual layering (varves) of the sediments. Recent work on existing data has produced a composite time-series from approximately AD 300 to 1970 for the Santa Barbara Basin. These data have been analysed to determine signal-to-noise characteristics and principal time-scales of variability by spectral analyses. A new sampling programme has begun for the Santa Barbara Basin, with a major objective being the development of as reliable and "robust" time-series as possible over the past 2 000 years for sardine and anchovy. These new time-series will provide higher resolution (five-year sample blocks) than the existing series based on 10-year averages of annual scale-deposition rates published by Baumgartner *et al*. (1992).

A second known site in the California Current is the Soledad Basin, lying just north of Bahia Magdalena, Baja California Sur, Mexico. Previous work at this site has provided a record of five-year averages of fish-scale deposition from approximately the years 1810–1970 (Soutar and Isaacs 1974), even though the sediments are not well varved. The site is important because it lies within the boundary of the southern subpopulations of sardine and anchovy of the California Current. Therefore, plans are being developed to resample the Soledad Basin for reconstruction of series comparable to those of the Santa Barbara Basin, which will perhaps reach back 2 000 years and provide a resolution of roughly 10 years.

Recent work has shown that sardine and anchovy records can be reconstructed from the varved sediments of the Gulf of California. This opens the possibility of developing comparisons of the subpopulation histories in the California Current with subpopulations in the Gulf of California to determine the relative timing of their major periods of growth and decline. So far, the reconstructed record in the Gulf of California extends over the approximate period 1740–1970 and is resolved into 10-year blocks of scale-deposition rates. This record shows anchovy scales more frequent, over time, than sardine. Also in the record are scales of chub mackerel and hake *Merluccius* spp. (Holmgren-Urba and Baumgartner 1993).

The record of fish-scale deposition off Peru/Chile is less well known than off California. The only published reference so far is that of De Vries and Pearcy (1982), who met with considerable difficulty in constructing a continuous chronology of deposition from an approximately 3-m long core from the upper slope off Peru. More recent work by Baumgartner *et al*. (in prep. b) shows the scale-deposition rates

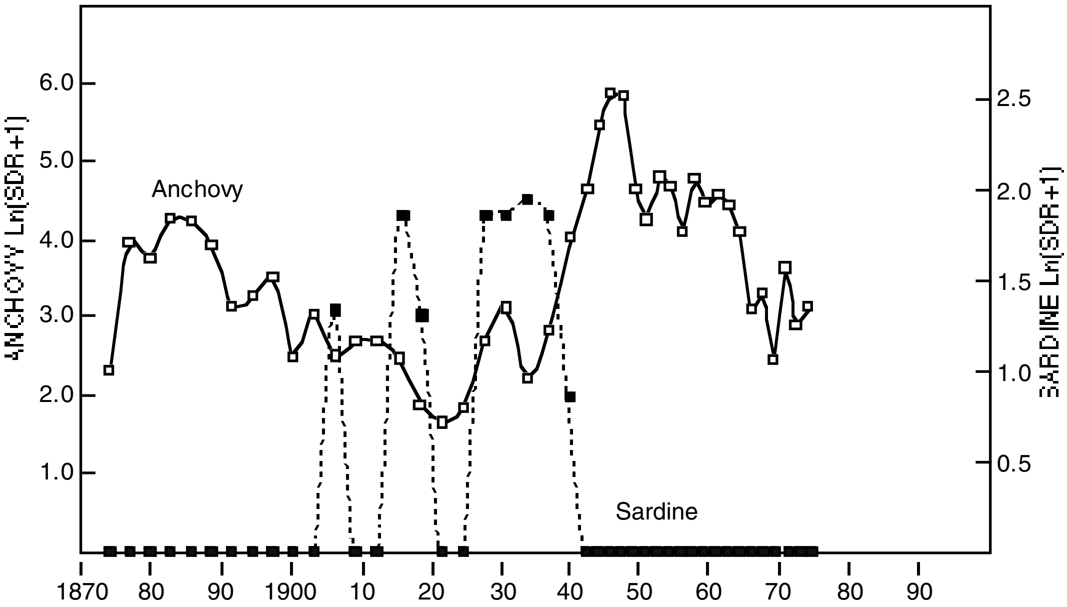

Fig. 25: Deposition of sardine and anchovy scales off Callao, Peru, measured from varved sediments from a single core. SDR = Scale Deposition Rate

(SDR) for sardine and anchovy off Peru, at a site on the outer shelf off Callao at a depth of 194 m (Fig. 25). Although this core does not exhibit continuous annual layers (varves), the chronology of deposition has been undisturbed by bioturbation or physical disruption and therefore can be reconstructed through the use of radiometric dating by the decay of the isotope ^{210}Pb and ^{228}Th/^{232}Th. The core provides a record of the relative abundance of Peru's sardine and anchovy from 1875 through 1974 with a sampling resolution of less than two years. Analyses of these data show that the anchovy record is highly correlated with the decreasing population of guanay cormorants *P. bougainvillii* between the early 1950s and the mid 1970s. The scale deposition of anchovy off Callao also appears to be a good estimator for the difference in biomass between the VPA estimates and landings (Baumgartner *et al.* in prep. b). Note that the relationship between sardine and anchovy in Figure 25 suggests the presence of alternating regimes prior to the development of industrial-scale fishing off Peru.

The third major region known for deposition of fish scales is off Namibia, along the continental shelf. Serious work on these sediments was begun by Shackleton (1987). However, as a result of difficulties with dating the sediments because of the discontinuous nature of the varve formation, the author was not able to provide a chronology of fish-scale deposition that could be used to reconstruct histories of the fish populations. Recently, examination of other cores taken during the 1980s has begun, with the hope of developing a continuous record for the past millennium or more. Eventually it should be possible, with the development of techniques resulting from the work off California, to provide dates for the sediments off Namibia.

Effingham Inlet, located on the west coast of Vancouver Island, Canada, was discovered to be a suitable site for deposits of scales of small pelagic fish in December 1995. It can be used to compare with the Santa Barbara site and the Soledad site, so giving the distribution and abundance over time for the entire range of anchovy and sardine in the California Current (Baumgartner *et al.* in prep. a). The identification and development of sites in the Peru-Chile system lags behind that in the California Current, but near-coastal sites with exceptional records have already been identified off central and southern Peru, and there are potentially important sites off northern and central Chile and in the fjords of southern Chile.

The use of multiple sites is a new phase in the study of fish-scale deposition. Hopefully, it will reveal the distribution/movement as well as abundance of sardine and anchovy throughout their potential habitats.

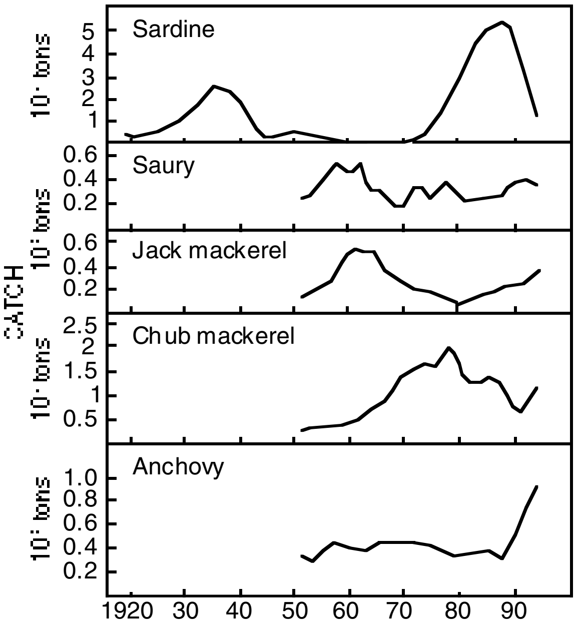

Fig. 26: Changes in catches, expressed as the three-year running mean, of five species of small pelagic fish in the North-Western Pacific, 1920–1996

This is necessary because sardine do not always have the same distribution in different periods of high abundance. Once the geographic coverage of data has been expanded, there will be considerably more information from which to examine synchrony of historical fluctuations in sardine and anchovy populations within the same and between different regions.

SEQUENCE OF EVENTS AT TIMES OF MAJOR CHANGE

Characteristics of change between regimes of anchovy and sardine

Geographic characteristics of change from regimes dominated by sardine to those dominated by anchovy and vice versa have been described (Lluch-Belda e*t al.* 1992c). When anchovy is replacing sardine, a contraction in the range of sardine may be an early indication of change, as off Japan and Chile.

It appears that the subdominant species frequently begins to increase while the dominant one is abundant, as in the recent replacement of sardine by anchovy in the South-Eastern Pacific. The prior decrease of anchovy and increase of sardine in that system appeared to take place more or less simultaneously. Off South Africa, the recent increase of sardine was initiated by a powerful 1983 year-class, formed while anchovy was still abundant. Earlier, anchovy had increased in the early 1960s while sardine biomass was high. However, off Namibia, anchovy has been at a low level of abundance since 1987, and sardine is not yet abundant. Probably, adverse environmental conditions have precluded steady growth of sardine in Namibia.

Species successions

An orderly succession of dominant (i.e. exhibiting a peak in abundance) pelagic species has been observed in the Japanese and California current systems (MacCall 1996), in the Humboldt system and off South Africa.

Off Japan, the succession was: *Sardinops* (1930s and 1940s), followed by a mix of *Trachurus*, saury *Cololabis* and *Engraulis* (1950s and early 1960s), then *Scomber* (late 1960s, early 1970s), then *Sardinops* (late 1970s, 1980s – MacCall 1996). As sardine biomass decreased in the late 1980s, catches of *Trachurus*, *Cololabis* and *Engraulis* rose immediately, and those of *Scomber* began to increase in the 1990s (Fig. 26).

Off California the succession was: *Scomber* (peak 1932), *Sardinops* (peaks 1934, 1941), *Trachurus*, bonito *Sarda* (peak 1960–64), *Engraulis* (peak 1973–75), *Scomber* (peak 1983) and *Sardinops*, which is still increasing (MacCall 1996). In the California system, the only recent period without a clear dominant lies between the years 1945 and 1955, but increased catch levels of jack mackerel *T. symmetricus* suggest that that species may have been unusually productive at that time. MacCall (1996) was hesitant to draw conclusions from jack mackerel catches, because the fishing industry was also seeking alternatives to the severely declining sardine catches during the late 1940s.

Further examination of the historical information on jack mackerel provides confirmation that the period 1945–1955 was indeed unusually productive for that species in California. A collection of length frequencies of jack mackerel was compiled by MacCall and Stauffer (1983) as part of the basis for developing management recommendations. Length frequencies from purse-seine catches of jack mackerel off southern California in the late 1940s and early 1950s consisted mostly of 20–35 cm fish, with a mean age of three years. In later years, the purse-seine fishery has rarely caught other than one-year-old fish. Another set of length frequency data was compiled from night-light surveys conducted offshore of central California during the period 1957–1968. This length frequency contained a strong mode of larger fish of 48–55 cm. The growth curves imply probable ages of 13–20 years, indicating that these fish were originally produced around 1950. Another length frequency was taken from jack mackerel caught in the foreign trawl fishery for hake in 1977. These fish were larger (52–58 cm), suggesting probable ages of 18–30 years, which again is consistent with an origin around 1950. The length frequencies indicate that there was an unusual production of jack mackerel in California around 1950, and confirm the position of jack mackerel in the succession of California's pelagic fish species.

In the Peru-Chile system, the collapse of the *Engraulis* fishery in the early 1970s was followed by a large *Sardinops* fishery in the 1980s, with *Engraulis* again dominating in the 1990s. Jack mackerel increased at the same time as sardine, but remained at a high level of abundance when sardine decreased. *Sarda* catches were high when *Engraulis* was abundant in the 1960s, decreased following the collapse of *Engraulis* in the early 1970s, were low through the early 1980s, and started to increase again as *Engraulis* biomass increased after the mid 1980s (Cury *et al.* in press).

Off western South Africa, the succession was *Trachurus* (1940s, early 1950s), *Sardinops* (late 1950s, early 1960s), *Scomber* (late 1960s), *Engraulis* (1970s and 1980s) and *Sardinops* in the mid 1990s (Crawford *et al.* 1987, Crawford 1998). Additionally, based on guano harvests and numbers of Cape cormorants, *Engraulis* was probably abundant in the 1920s, decreasing in the early 1930s (Crawford and Jahncke 1999).

Off Namibia, a large biomass of *Sardinops* in the 1960s was followed by a mix of *Trachurus* and goby *Sufflogobius bibarbatus* in the late 1970s and early 1980s (Crawford *et al.* 1985, 1987). *Engraulis* also increased following the collapse of *Sardinops* (Crawford *et al.* 1987), but its replacement of *Sardinops* was of shorter duration and less apparent off than South Africa (Crawford 1999). A large year-class of *Scomber* was formed off Namibia in 1977 and persisted in the fishery through 1981 (Crawford and de Villiers 1984).

The ordering of the succession may be influenced by biological interactions. For example, off California, peaks in abundance of more predatory species (*Sarda* and *Scomber*) separate those of the planktivorous sardine and anchovy (MacCall 1996). Similarly, off South Africa, *Scomber* was abundant in the late 1960s, between periods of high biomass of *Sardinops* and *Engraulis*. Also off South Africa, guano harvests were substantially reduced in the 1930s (Appendix), although the demand for guano has always exceeded supply. This perhaps suggests that a more piscivorous species than sardine or anchovy dominated at that time, between likely regimes of *Engraulis* in the 1920s (Crawford and Jahncke 1999) and *Trachurus* in the 1940s.

Of considerable interest is that, from 1983 to about 1989, there was good recruitment of both sardine and anchovy in the Humboldt Current, i.e. the recovery of anchovy began before the decline of sardine. In 1991 and 1992, recruitment of sardine decreased, but there were powerful anchovy year-classes (Fig. 14b). Off South Africa, estimates of recruitment of sardine and anchovy obtained by acoustic survey are significantly positively related for the years 1989–1997 ($r = 0.715$, $p < 0.05$, $n = 9$), a period in which biomass of sardine increased. Anchovy decreased from 1.7 million tons in 1991 to 0.8 million tons in 1997 (Appendix).

EVIDENCE FOR A WORLDWIDE CAUSE OF THE MAJOR FLUCTUATIONS OF SARDINE AND ANCHOVY

Synchrony of the catch trends

Kawasaki (1983, 1991) postulated that the abundance of sardine was being influenced by global climate in three well-separated regions of the Pacific Ocean; off Japan, in the California system and in the Humboldt system. This was based on the observation that, up to the time of his analysis, catches of sardine in all three regions had risen, been sustained and fallen more or less in synchrony. Subsequently, it has become apparent that sardine have continued to increase in the North-Eastern Pacific, while they have been decreasing in the North-Western and South-Eastern Pacific.

Californian sardine were intensively fished as they decreased in the 1950s and 1960s. By the late 1960s, it was difficult to find sardine along the California coast, but sardine were still being caught off Baja California. In 1967, an almost full moratorium on fishing for sardine was introduced off California. In 1973, California legislation permitted a catch of 1 000 tons as soon as the spawner biomass exceeded 20 000 tons. However, it was not until 1986 that a small fishery was allowed (Wolf 1992). Biomass of sardine off California has been increasing at 20–30% per year, and in 1998 was estimated to be 1.78 million tons between Ensenada, Mexico, and British Columbia, Canada (Anon. 1999).

Common regime changes may be linked to global climate change, which in turn may be associated with an interdecadal cycle of dislocation of the convergence area in the North Atlantic where thermohyaline circulation starts (Kawasaki 1994). According to Rahmstorf

(1997), the recent increase in emissions of greenhouse gases weakens, even halts, overturning in the North Atlantic, so radically altering the regional climate. A rapid rise in the concentration of greenhouse gases could disrupt the thermohaline circulation. This could have a serious impact on global climate, and on regimes of sardine, anchovy and other small pelagic fish species in the future. However, as global warming is a recent possibility, it cannot account for the changes in population sizes in the past.

Empirical observations

When Box-Jenkins techniques (Box and Jenkins 1976) were applied to the catch series of sardine in the three regions of the Pacific Ocean up until 1986, to remove systematic time-series effects, there was strong positive correlation between all three series at lags similar to ages at which sardines recruit to the various fisheries (Crawford *et al.* 1991). This finding supported the hypothesis of global forcing. The significant correlations were driven by particular years (Crawford *et al.* 1991). For example, 1980 appeared to have been a favourable year in all three regions, and 1984 unfavourable. An exceptionally strong sardine year-class was formed off Japan in 1980, whereas in 1984 there was poor survival of larvae (Kawasaki 1993).

Further evidence in support of global climate influencing marine ecosystems is provided by the observation that oceanographic anomalies in different regions of the world occur repeatedly at the same time (Harris *et al.* 1992, Crawford *et al.* 1995a). Off Japan, during the period 1955–1985, anomalous southward intrusions of the Oyashio Current (ASIOs) along the east coast of Japan took place in 1963, 1974, 1981 and 1984 (Sekine 1991). The average southward limit of Oyashio water in the boreal spring is approximately 39°–39°30´N, but in anomalous years it intrudes to about 36°N (Sekine 1991). Off Tasmania, periods of low zonal westerly winds (LZWWs) cause a form of Tasmanian "*El Niño*", during which sea surface temperature rises, nutrients become scarce in surface waters, and productivity decreases. There were LZWWs over Tasmania during the periods 1949–50, 1960–63, 1973–74 and 1984–85 (Harris *et al.* 1992). In the South-Eastern Atlantic, Benguela *Niños* advect warm, more saline water from the north onto the Namibian shelf. This water may intrude about 600 km farther south than normal. Such events have been reported for the years 1934, 1949–50, 1963, 1974 and 1984 (Shannon *et al.* 1986) and 1995 (Gammelsrød *et al.*1998).

There is clear correspondence between the four periods of LZWWs off Tasmania and the four Benguela *Niños* off Namibia between 1949 and 1984. Information on ASIOs off Japan is only available since 1955, but ASIOs occurred in each subsequent period of LZWWs off Tasmania and Benguela *Niños* off Namibia. Of particular interest is the year 1984, when oceanographic anomalies were recorded off Japan, Tasmania and Namibia, and when the environment was apparently unfavourable for sardine in the Japan, California and Humboldt systems (Crawford *et al.* 1991).

Prewhitened residuals of guano harvests off Peru and southern Africa are significantly negatively related for the period 1920–1953, i.e. prior to development of intensive fisheries for sardine and anchovy, suggesting that the out-of-phase nature between sardine and anchovy in the two systems (Crawford *et al.* 1991) has been in operation since at least 1920 (Crawford and Jahncke 1999).

More precise definition of dates when increases or decreases in pelagic fish populations were initiated will assist in determining if climate operating at a global scale is influencing populations and, if so, how. Examination of historical databases may allow such dates to be established. A case study of the Japanese fishery for the different pelagic species would be especially beneficial. Japan has many stations collecting biological and fisheries data and oceanographic information. Its comprehensive research programme has lasted many years and continues today. A difficulty is that many of the data, especially historical information, may not have been collated into a central database.

Teleconnections

The existence of teleconnections among the low-frequency fluctuations of coastal pelagic fisheries in the Pacific Ocean is well established for sardine and anchovy (Kawasaki 1991, Lluch-Belda *et al.* 1989). The relationships of the Pacific stocks to sardine and anchovy off South Africa and Namibia appears to be inverse (i.e. 180° out of phase). MacCall (1996) has shown that interdecadal variability in the entire suite of coastal pelagic species appears to be similar in California and Japan, except that shifts in the California Current have been delayed by about 10 years relative to those in Japanese waters.

There may also be strong teleconnections with low-frequency changes in North Atlantic fish stocks. Alheit and Hagen (1997) described the episodic nature of the Bohuslän herring fishery, giving dates of the nine major events in the last thousand years. Figure 27 shows the dates of the Bohuslän herring fisheries in

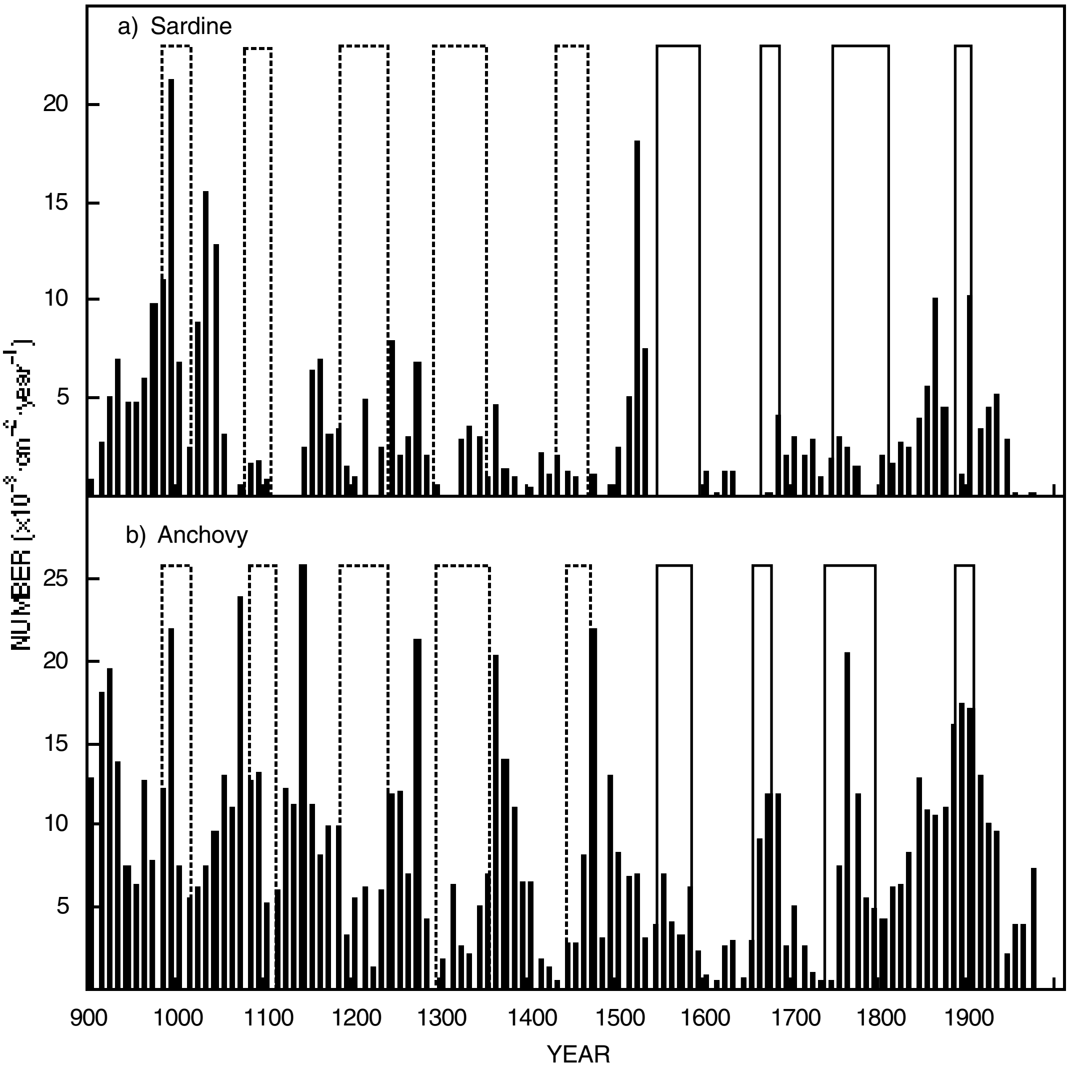

Fig. 27: Coincidence of Bohuslän herring episodes in Sweden (rectangles) with fluctuations in palaeo-sedimentary depositions of (a) sardine and (b) anchovy scales in the Santa Barbara Basin, California (bars). Dotted rectangles indicate less reliable dates for herring; dates in the earlier years are also less reliable for sardine and anchovy

Sweden superimposed on the palaeochronology of sardine and anchovy scales from the Santa Barbara Basin, California (Baumgartner *et al.* 1992). For the last 300 years, Bohuslän herring fisheries appear to coincide with low abundance of sardine and high abundance of anchovy off California. The match deteriorates for earlier centuries, but earlier dates from the sediments may be off by as much as 70 years (TB, pers. obs.).

The mechanisms driving these teleconnections are not clear, although some evidence is accumulating on interrelationships among patterns of atmospheric and oceanic circulation. Fluctuations in ENSO events are linked to fluctuations in the position and intensity of the atmospheric low pressure cell near the Aleutian Islands or "Aleutian Low". Parrish *et al.* (in prep.) have shown that latitudinal changes in the source of North Pacific water entrained into the California

Current and Alaska Gyre may be related to atmospheric circulation (especially the Aleutian Low), and may be a major factor influencing productivity in those coastal systems. Alheit and Hagen (1997) showed that the Bohuslän herring events are related to the North Atlantic Oscillation, which includes long-term fluctuations in the Icelandic Low. The Icelandic Low is linked to the Aleutian Low by the characteristic meanders of the circumpolar atmospheric circulation.

The known ocean-atmosphere interconnections are global in scale. The large physical dimensions of that system and the involvement of oceanic circulation and heat distribution supports mechanisms contributing to very low-frequency variability. However, the dominant frequencies of fish or ecosystem variability are even lower than is explained easily by known mechanisms: c. 60 years in the Pacific Ocean, and 100 or more years in the Atlantic Ocean, judging by the Bohuslän herring record. However, recent information for the South-East Atlantic suggests a shorter period.

HYPOTHESES REGARDING REGIME CHANGES

Two categories emerge of mechanisms that may initiate and sustain regimes of sardine and anchovy. There may be continuous modification of habitat, e.g. a trend to warming that permits an expansion in spawning range and enhanced egg production (Lluch-Belda *et al.* 1992a). Alternatively, there may be episodic environmental events that trigger changes in populations and ecosystems in well-separated areas. Formation of powerful year-classes could cause a population to expand quickly and, for short-lived species, a few poor year-classes could result in a rapid population decrease. Empirical evidence exists for both these forms of environmental influence at a global scale, and it is quite possible that several factors may operate at any one time.

Continuous modification of the environment

Two mechanisms that may sustain large shifts in abundance of sardine and anchovy populations over long periods are food and temperature.

FOOD

Off Japan during 1988 and 1989, the mean algal fraction of stomach contents of sardine was 0.65 and of anchovy 0.39. The modal prosome length of copepods eaten by sardine was 3 mm, and of copepods eaten by anchovy 6 mm (Li *et al.* 1992). Off Peru, during the period 1981–1982, sardine ate mainly small herbivorous copepods and tunicates, whereas anchovy fed on large copepods and euphausiids. Sardine were considered to be situated closer to the base of the trophic food-web than anchovy (Konchina 1991) and in offshore areas also ate some phytoplankton (KVS, pers. obs.). Off Namibia, King and Macleod (1976) considered sardine to be primarily phytophagous. Off South Africa, although sardine utilize phytoplankton to a greater extent than anchovy, both species are primarily carnivorous (Van der Lingen 1994, 1998). However, the two species are relatively distinct with respect to their utilization of zooplankton: sardine obtain most of their dietary input from small zooplankton that is captured by filter-feeding (Van der Lingen 1994, 1995), whereas anchovy obtain most of their food from large zooplankton, especially large copepods and euphausiids caught by particulate feeding (James 1987). These results are consistent in indicating that sardine feed on smaller organisms, and closer to the base of the food chain, than anchovy. Therefore, any change in the size structure of zooplankton, as reported, for example, by Verheye *et al.* (1998) for the southern Benguela system, may initiate regime changes.

There is also information that food may limit populations of sardine and anchovy, as follows.

South Africa — Since 1988, information has been collected from the western Agulhas Bank on food available for spawning anchovy (zooplankton biomass and production). In November 1988, food was insufficient for maintenance of anchovy at approximately 50% of stations examined (Hutchings and Boyd 1992). This may have contributed to a weak year-class that recruited in the austral winter of 1989 and led to the fluctuating decrease of anchovy (Appendix).

Japan — When populations are large, food may be limiting. Length at age of the Far Eastern sardine is substantially reduced when stock biomass is high. Figure 4 contrasts size of 3-year-old fish caught around Japan with the numbers of 1-year-old recruits in waters south-east of Hokkaido, the northernmost fishing ground for sardine on the Pacific coast of Japan. This is where sardine forage voraciously in summer-autumn before spawning in winter-spring along the southern coast of Japan. There is a close negative relationship between abundance of fish aged one and their growth.

Off Japan, body condition of adult sardine has a striking effect on the quality and quantity of eggs produced. For females, positive correlations have been found between gonad index (GM/BL^3; GM = gonad mass, BL = body length) and condition factor (BM/BL^3;

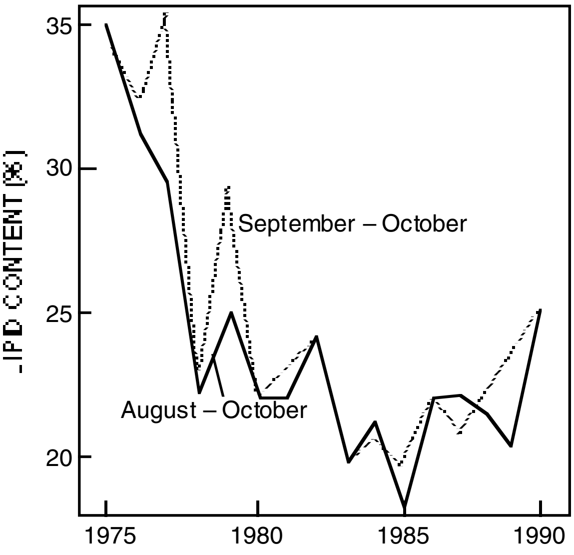

Fig. 28: Annual changes in average lipid content, expressed as its percentage contribution in the flesh of sardine >19.0 cm total length, in the months August–October and September–October in the waters south-east of Hokkaido, Japan, 1975–1990 (after Kawasaki and Omori 1995)

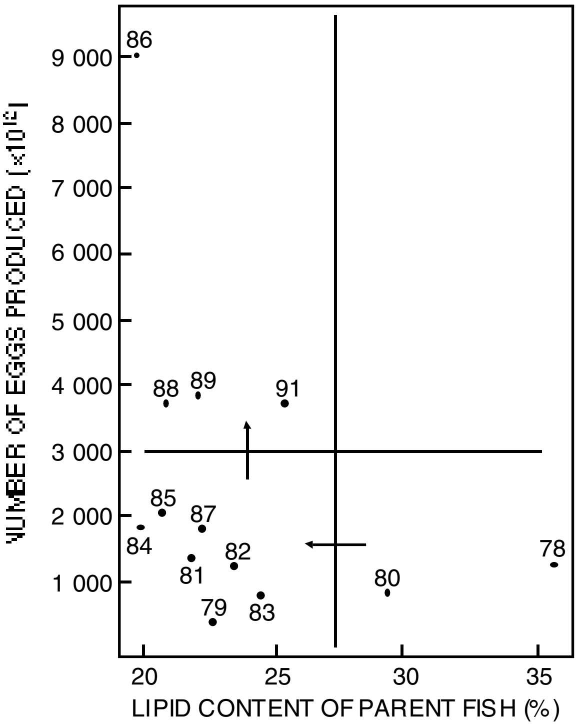

Fig. 29: Relationship between production of sardine eggs in waters off the Pacific coast of Japan and the lipid content in flesh of their parents in September–October of the preceding year, in waters south-east of Hokkaido. Year-classes are indicated. Arrows depict the probable hyperbolic relationship. Sources of data on egg production: 1978–1988 year-classes – Kuroda (1991); 1989–1991 year-classes – Long-term Forecasting on the Distribution and Abundance of the Important Fishery Resources and Related Oceanographic Conditions in the Sea of Chuo Blocs **93** (1994). After Kawasaki and Omori (1995)

BM = body mass), between yolk content (mm^3) of hydrated eggs and condition factor, and between ovary mass and lipid content in muscle (Morimoto 1996). The contents of lipid and eicosapentaenoic acid in ovaries were linked to their content in muscle, as well as to ovary mass (Morimoto 1996). These relationships indicate that adult body condition, and in particular the accumulation of lipid prior to spawning, will have a marked effect on the quality and quantity of eggs. This is likely to influence the survival of eggs and other early stages. However, until now, partly because of a lack of appropriate data, the relationship between the egg stage and year-class strength has been viewed mainly from a quantitative aspect, i.e. number of eggs produced (e.g. Ricker 1954, Watanabe 1983), and seldom from the qualitative aspect, i.e. egg quality.

Average lipid content in the flesh of sardine of total length >19.0 cm caught south-east of Hokkaido from August to October, just prior to spawning, was high from 1975 to 1977, but dropped in 1978 and reached a trough in 1985 (Fig. 28). In 1986, the lipid content started rising again. This shows that adult sardine were in good condition until 1977, but that condition thereafter deteriorated rapidly until 1985, when it improved again.

The relationship between the number of sardine eggs along the Pacific coast of Japan and the lipid content of the flesh of their parents in waters south-east of Hokkaido during September–October of the preceding year is shown in Figure 29. Arrows in the figure indicate the hyperbolic relationship between the two parameters. As there is a high correlation between the lipid content of the ovary and that of the muscle (Morimoto 1996), a similar hyperbolic relationship between the number of eggs produced and their lipid content can be postulated. It is noticeable that the 1978 and 1980 year-classes are located in the fourth quadrant, whereas the 1986 and 1988–91 year-classes are in the second quadrant. The 1979, 1981–85 and

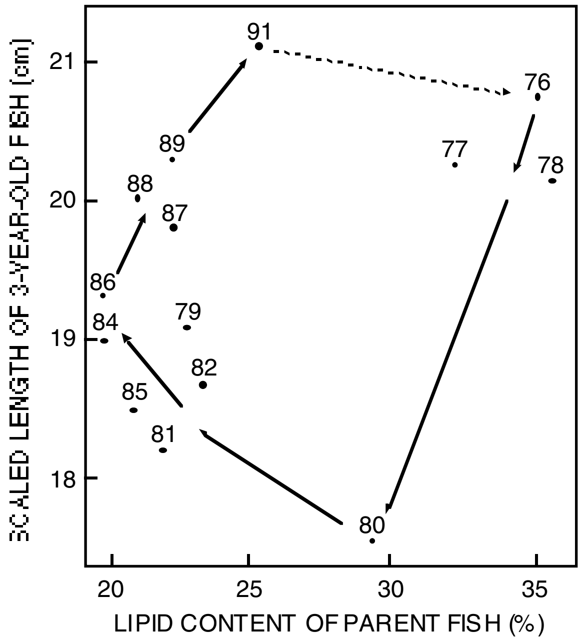

Fig. 30: Relationship between the scaled length of 3-year-old sardine in waters off north-eastern Japan in summer and the lipid content (as a percentage) in the flesh of parent fish >19.0 cm total length caught off south-eastern Hokkaido four years previously. Year-classes are indicated (after Kawasaki and Omori 1995)

1987 year-classes are in the third quadrant. As seen in Figure 3, the strong year-classes of 1978 and 1980 drove the proliferation of the sardine population there. They developed from high-quality eggs that were relatively few in number (Fig. 29). By contrast, the weak 1988–91 year-classes (Fig. 4) originated from abundant but low-quality eggs.

The relationship between the length of 3-year-old sardine sampled off north-eastern Japan in summer and the lipid content of their parents in autumn one year before their birth, i.e. four years previously, is shown in Figure 30. Parents of the 1976–78 year-classes had high-quality bodies, and large 3-year-old fish resulted. The 1980 year-class was produced from parents of moderately high quality and was abundant throughout its lifetime (Kawasaki 1993). Body size of this year-class was the smallest recorded. After this year-class, the lipid content of parent fish kept falling, but the body size of their offspring tended to rise until the 1986 year-class. Then, there was a recovery in the condition of parents, and the body size of their progeny continued to increase.

The overall process shows a clockwise rotation, indicated by arrows in Figure 30, representing a cycle of the population fluctuation of sardine. The cycle begins with the successful survival of a small number of eggs produced by high-quality parents, triggered by environmental (density-independent) processes (Kawasaki 1992). At large population sizes, sardine become an oceanic species off Japan. When they enter the oceanic phase, they expand their range and rapidly increase in number. The physical condition of adult fish deteriorates as a result of overcrowding, and the offspring produced become smaller in size. The cycle ends in a failure to survive, resulting from an enormous number of small fish produced by low-quality parents (density-dependent process; Kawasaki 1993). At low population levels, sardine off Japan are by nature a coastal species.

Kawasaki and Omori (1988) suggested that variations in solar radiation lead to variations in primary production. Because sardine utilize phytoplankton and small copepods to a greater extent than their competitors, their populations increase when phytoplankton stocks increase. This leads to less food for anchovy, which decreases (Kawasaki 1993). Kawasaki (1994) inferred that the synchronous increases of some sardine populations in the 1970s and 1980s were brought about by higher productivity throughout the world's temperate oceans, which stemmed from such variations as occur in thermohaline circulation on a 65- to 70-year cycle (Schlesinger and Ramankutty 1994). This results in a hypothetical pathway of the fluctuation cycle of a sardine population (Fig. 31, Kawasaki and Omori 1995).

TEMPERATURE

Lluch-Belda *et al.* (1991a) proposed that, off the Californias, the sardine population retreated southwards in cold years, but expanded both its spawning and feeding range to the north during warm periods. This resulted in increased egg production in warm years (Lluch-Belda *et al.* 1992a). Off the Californias, sardine spawn over a wider temperature range (13–25°C) than anchovy (11.5–16.5°C), and therefore are better able to take advantage of warm conditions (Lluch-Belda *et al.* 1991b). Sardine in the Humboldt system have also expanded in warm periods (Lluch-Belda *et al.* 1992b), although Serra *et al.* (1998) found no relationship between sardine recruitment and temperature.

Episodic environmental events

Support for episodic environmental events initiating regime changes comes from powerful year-classes

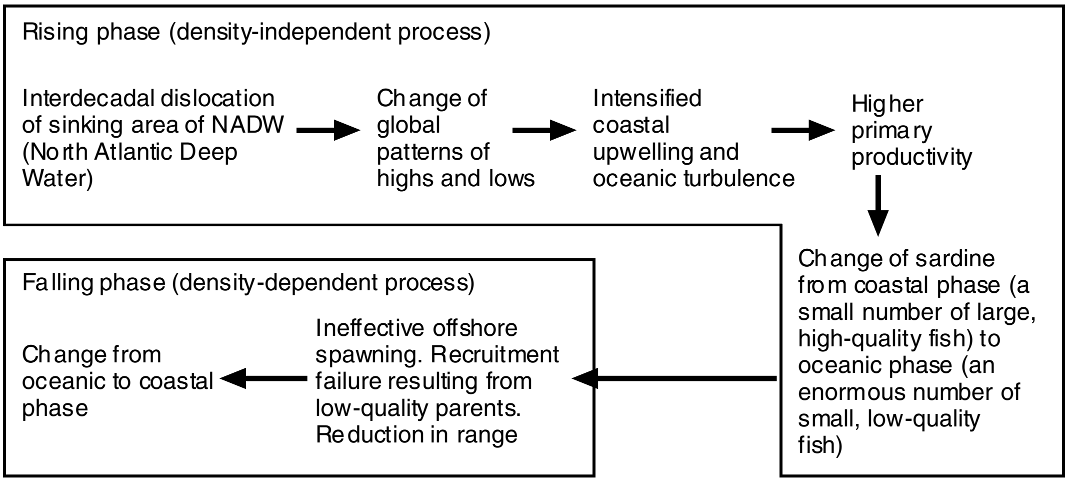

Fig. 31: Hypothetical linkages of processes involved in long-term fluctuations of the Japanese sardine (after Kawasaki and Omori 1995)

often playing a pivotal role in the recovery of a species, for example, sardine off Japan (Kondo 1980) and South Africa (Berruti and Colclough, 1987), and the fact that particular years have been identified as being either favourable or unfavourable in well-separated systems (see: Evidence for a worldwide cause of the major fluctuations of sardine and anchovy, section Empirical observations). Because of the high intrinsic reproductive rate (r) of sardine and anchovy, their populations can increase under favourable oceanographic conditions to very high levels within a few generations. However, an adverse environment may sometimes result in major mortality of eggs and larvae, and consequent recruitment failure subsequently. This is the origin of population collapse in many cases.

Serra *et al.* (1998) investigated formation of favourable sardine year-classes in the Humboldt system. Using an upwelling index as a measure of the environment, they found that an optimal environmental window existed for the formation of year-classes. This was the same for sardine at both high and low levels of biomass.

To explain alternation of dominance among species in ecosystems, several mechanisms have been suggested (Matsuda *et al.* 1992). These include:

(i) direct influence of environmental change on different species;
(ii) density-dependent change of intrinsic reproductive rate (r);
(iii) phase polymorphism of species;
(iv) competition between two species in a variable environment; and
(v) prey-predator system with one predator and two prey species, which have large fluctuations.

Because the species alternation occurs in near synchrony in different ecosystems, global-scale environmental change is likely to be the main factor causing fluctuations of sardine and anchovy. The question is what kind of environmental cue will induce species alternation by means of the hypotheses mentioned above?

Mortality

A large mortality of sardine around Australia during autumn 1995 drew attention to the fact that unusually high natural mortality may influence sizes of pelagic fish populations. A summary of the environmental and biological aspects of this event is reported here because of the unusual nature.

The first sardine deaths were in South Australia during March 1995 in the eastern region of the Great Australian Bight, southern Australia. Subsequently, dead sardine were found both east and west of this point-source, moving in a "bushfire-like" front at an average of 30 km·day^{-1}. By early May, the fronts had reached Albany in Western Australia and Bass Strait in Victoria. They continued moving up both coasts, reaching Carnarvon (Western Australia) and Noosa Heads (Queensland) by the end of June, so affecting sardine throughout their entire (6 700 km)

Australian distribution. In early June 1995, a similar pattern of deaths began in the north of New Zealand.

The pattern of deaths at all locations was similar, only adult sardine (>10 cm; 13 cm in Western Australia) being affected. No other species or even juvenile sardine were found dead. Moreover, neither predators nor scavengers died as a result of consuming the dead sardine. Fatalities lasted for only a few days at any one location, but the intensity did not appear to diminish with time or distance from the origin. Subsequently, no further deaths were observed. Affected sardine, aside from being dead, were in good condition, with many having advanced gonad stages. The dead fish usually had open mouths and gills that were pale in colour. Histopathology showed that the gills had epithelial hyperplasia (multiplication of the surface cells), synechiae of the secondary gill lamellae tips (they had stuck together), sloughing of epithelial cells and oedema. Therefore, the cause of death was asphyxiation. Identical patterns of damage were seen at all locations where the deaths occurred, indicating a common cause.

Possible causes of the gill damage include contact with toxic and non-toxic phytoplankton. Alternatively, this damage could have arisen from the pathogenic effect of some specific virus or bacterium to which only adult sardines were susceptible. Data collected in Western Australia clearly showed that sardine mortalities had no relationship with phytoplankton. Toxic phytoplankton were not involved in the deaths; few were seen in the phytoplankton samples and no toxic substances were found in any affected fish. There were no blooms of non-toxic phytoplankton anywhere along the coast during the periods of the mortalities. The composition of the phytoplankton present varied greatly among sites, independently of whether dead and dying sardine were in the region. Most sites where deaths were recorded had very low densities of phytoplankton. Furthermore, examination of the affected gills by scanning electron microscope showed no evidence that clogging or mechanical damage consistent with phytoplankton being responsible.

The stomach contents of the affected sardines varied greatly. In addition, many were empty. The slight difference in feeding capabilities between adult and juvenile sardine is insufficient to support the total lack of impact on juveniles. Similarly, the lack of an effect seen on the other coexistent, filter-feeding clupeids (anchovy and *Sardinella*) is a further rejection of the hypothesis that this phenomenon was somehow caused by phytoplankton blooms. Finally, the passage of the front of dying fish moved in the opposite direction to the prevailing currents and continued even after several severe storms. None of these observations are consistent with phytoplankton being involved.

The gill damage seen in the dead sardines collected in Western Australia was always associated with the presence of a Herpesvirus. This virus was not present in fish sampled ahead of the deaths, and was not found in samples of survivors after mortalities stopped. An amoeba was associated with gills of many dead fish, but this was usually in insufficient numbers to account for the damage seen and was not always present in fish with gill damage. Therefore, the virus was the only consistent factor in all of the kills around Australia and NZ. Furthermore, the rate of passage of the fronts was within the limits of daily movement rates of adult sardine.

The most likely hypothesis is that the virus was introduced recently into Australia. The association of the virus with the gill damage, the severity of the impact on the population and the "bushfire-like" passage of the front are all consistent with a novel pathogen infecting a naive population. Furthermore, once infection had passed an area, reinfection did not occur, suggesting that the surviving fish were resistant to infection.

In Western Australia, it is estimated that approximately 10–15% of the sardine biomass died, representing many thousands of tons.

CONSEQUENCES FOR ECOSYSTEM FUNCTIONING

The large changes in abundance of sardine and anchovy that have been observed may be expected to have major implications for ecosystem functioning. The sardine-anchovy systems have been termed "wasp-waist" ecosystems by Bakun (1996). This is because there is a high diversity of planktonic organisms on which sardine and anchovy prey, and these fish are in turn preyed upon by a large number of predators. However, transfer of energy from plankton to predators is mainly through just a few species of forage fish. When one forage fish dominates, most of the transfer of energy may be through just that one species – a wasp-waist in terms of species diversity. Changes in the relative abundance of forage fish species, especially shifts between sardine and anchovy regimes, may be expected to influence species at both lower (food) and higher (predator) trophic levels.

Impacts on lower and equivalent trophic levels

The collapse of an abundant forage fish must have an impact on other organisms in the system; more food should become available for other species. However, studies have shown that, if one planktivorous fish is reduced (e.g. by fishing), other species cannot be expected to benefit from food that would otherwise have been consumed to the same extent, i.e. it is unlikely that any one species would be able to take over fully the ecological niche of any other species (Jones and Henderson 1987). Nevertheless, it seems true that, in sardine-anchovy systems, the collapse of abundant species is generally followed by increases in other species that are at more or less the same trophic level (see: Sequence of events at times of major change; section, Species successions).

Impacts on seabirds

In the South-Eastern Atlantic, consequences of shifts between regimes of sardine and anchovy for African penguins have been explored (Crawford 1998). Between the 1950s and 1980s there were large decreases of penguins at most colonies between Lüderitz and Table Bay (Crawford *et al*. 1990b, 1995b). There, adult sardine were abundant in the 1950s. It is likely that the shift from sardine to anchovy during the 1960s and 1970s resulted in a substantial decrease in food in that region. Between the 1950s and 1970s, numbers of penguins increased south of South Africa, where the adult anchovy stock was located. Later, as the system reverted from one dominated by anchovy to one dominated by sardine, penguin colonies in the south decreased. Three new colonies were formed in the vicinity of Table Bay, and colonies between Table Bay and Lüderitz stabilized or increased. Overall, however, both the shift from sardine to anchovy and that from anchovy to sardine resulted in substantial decreases in numbers of African penguins.

There has been a similar long-term decrease in the population of Humboldt penguins *Spheniscus humboldti* off Peru and Chile, which is continuing (Luna-Jorquera 1998). As is the case with the African penguin, the Humboldt penguin appears unable to cope with the shifts in dominance between prey species in a system heavily exploited by man.

Off Namibia, the collapse of sardine was followed by severe decreases in numbers of Cape gannets. Conversely, off South Africa, there was an increased abundance of Cape gannets as sardine were replaced by anchovy (Crawford 1999). Off Namibia, gannets were unable to exploit effectively the mesopelagic horse mackerel and goby that replaced sardine, but off South Africa they were able to switch between sardine and anchovy as prey.

In the Gulf of California, there are large breeding colonies of birds that feed nearly entirely on sardine or anchovy. Of world populations, 99% of yellow-footed gulls *Larus livens*, 95% of Heerman's gulls *L. heermanni*, 95% of elegant terns *Sterna elegans*, 90% of Craveri's murrelets *Synthliboramphus craveri* and 90% of least petrels *Oceanodroma microsoma* breed in the Gulf of California. Therefore, any reduction in the fish population as a result of natural causes or fishery exploitation could affect numbers of these breeding birds. The reporting period, 1983–1992, showed that the birds had no difficulty changing their diet between anchovy and sardine (Velarde *et al*. 1994).

Clearly, if prey remains available within the foraging range/depth of seabirds, they are able to cope with regime changes, but, if not, there may be large decreases in numbers.

Distribution

That most of the catch of the Far Eastern sardine in the 1930s came from the Sea of Japan subpopulation and most of that in the 1980s from the Pacific subpopulation suggests a different geographic distribution of sardine during those two eras of abundance. Similarly, in the North-Eastern Pacific Ocean, the bulk of the catch in the 1930s and 1940s was from populations distributed along the western coast of North America, whereas from the 1970s to the 1990s, most of the catch was from the Gulf of California. Such an altered distribution of sardine can be expected to have a considerable impact on the ecosystem, both on food resources and on predators. Predators that are tied to land sites, such as seabirds and seals, will not easily be able to adapt to large changes in the distributions of forage species.

REGIME BEHAVIOUR IN OTHER SYSTEMS

Regime behaviour is evident in fluctuations of many North Atlantic fisheries. Alheit and Hagen (1997) reviewed patterns of historical changes in stocks of sardine *Sardina pilchardus* and herring *Clupea harengus* in northern Europe. During the last 1 000 years, there have been nine episodes of abundant Bohuslän herring occurring at relatively even intervals of about once every 100 years. In the last 400 years, the Biscay herring, French catches of English Channel herring and Devon and Cornwall herring have fluctuated in phase with the Bohuslän herring. In contrast, increased catches of Norwegian spring-spawning herring and of sardine in North Brittany and in Devon and Cornwall have occurred in the periods of scarcity of the Bohuslän herring and related stocks. Alheit and Hagen (1997) associated these fluctuations with low frequency fluctuations of the North Atlantic Oscillation Index.

Although Alheit and Hagen (1997) focused mainly on North Atlantic pelagic fish, there is also evidence that demersal fish, such as gadoids, can show low-frequency behaviours. For example, the "gadoid outburst" of the 1960s coincided with a decrease in herring stocks (Burd 1978), but it is unclear whether this was attributable to changes in climate or to changes in biological conditions associated with the decline in herring stocks.

Regime behaviour has been shown for many salmon stocks in the North Pacific (Francis and Hare 1994), and there is strong evidence that low-frequency fluctuations of Alaskan salmon populations are inversely related to fluctuations of California populations over interdecadal time-scales. Hollowed *et al.* (1987) examined recruitment variability in 59 stocks (28 species), including both pelagic fish and groundfish in the North-Eastern Pacific, and found strong patterns of covariability at all time-scales. Recruitment covariability at the lowest frequencies may have been a result of progressive exploitation (recruitment overfishing), but Hollowed *et al.* (1987) favoured the hypothesis that these long-term patterns were because of low-frequency climate variability.

There is limited evidence of regime behaviours in tropical waters, but most time-series of observations are still rather short. During the 1970s, the coastal waters of tropical West Africa experienced an exceptional abundance of triggerfish *Balistes* sp., a condition that lasted for several years (Caverivière 1991). Hobson and Chess (1996) report a perhaps similar episodic abundance of filefish *Pervagor spilosoma* in Hawaii. Extensive destruction of coral reefs by the crown-of-thorns starfish *Acanthaster planci* appears to be episodic, and may also be related to long-term climate variability (Birkeland and Lucas 1990, Moran 1986).

IMPLICATIONS FOR FISHERIES

Decade-scale regimes of high and low abundance appear characteristic of the four regions supporting the largest fisheries on sardine and anchovy. In the long-term, it is unrealistic to expect that fisheries on individual pelagic fish species can be sustained, and they should rather be geared to take advantage of periods of high abundance of these fish. For example, the South African fishery for horse mackerel in the 1950s was based on the powerful 1946, 1947 and 1948 year-classes (Geldenhuys 1973).

There is a practical lesson to be drawn from the confirmation of an episodic production of jack mackerel off California around 1950. MacCall and Stauffer (1983) were attempting to develop management advice for a proposed fishery on jack mackerel. They noted that many *Trachurus* fisheries around the world have experienced brief high harvests and sudden fishery collapses. Therefore, they tried to take a precautionary approach based on equilibrium or steady-state interpretations of the data (the regime problem had not yet been recognized). Accordingly, the length frequencies were interpreted as being representative of the sizes of fish normally to be found in the various sampling locations. They were puzzled that 30-cm fish were no longer found in southern California fisheries, and remarked on the peculiar absence of 35–45 cm fish. However, they mistakenly were concerned with where these "missing" fish might be, rather than realizing that these length data tracked a single pulse of jack mackerel production. The assumed abundance of 30–50 cm jack mackerel actually no longer existed anywhere in the system. Because of limited understanding of the nature of regimes in jack mackerel productivity, MacCall and Stauffer (1983) proposed harvest levels based on fish that may not have existed. Perhaps fortunately, the fishery never developed off California.

The most important point concerning management of fisheries for small pelagic fish species is to sustain the regimes of abundance for as long as possible. It should be borne in mind that fishing has potential to decrease the extent and duration of peaks in abundance, as well as to depress and prolong troughs. The worst-case scenario is for fishing to prevent recovery of a species, so converting a potential period of high abundance into continuation of a period of low abundance.

In this regard, Japan has had a bitter experience. The Hokkaido-Sakhalin subpopulation of Pacific herring, the largest subpopulation in the North-Western Pacific, collapsed in 1958. Thereafter, minimal catches were made along the coast of Hokkaido. However, in 1986, 3-year-old spawners of the Hokkaido-Sakhalin herring (the 1983 year-class) reappeared in quantity off the coast of Hokkaido adjoining the Sea of Japan and Okhotsk Sea. This herring was intensively exploited by offshore trawlers, 72 000 tons being caught in 1986 and 16 000 tons the following year. As a result, the 1983 year-class was virtually eliminated, and the hoped-for new regime of Pacific herring did not materialize.

Fishing may also have had an impact on the succession of pelagic fish species off Namibia (Crawford 1999). Off South Africa, anchovy became the dominant pelagic fish following the collapse of sardine in the 1960s. In Namibia, horse mackerel dominated after the collapse of sardine in the 1970s. A possible explanation for this is the disparate fishing policies that were pursued in the two countries. Once sardine had collapsed in South Africa, anchovy became an attractive alternative resource with which to perpetuate the fishery and attempts were made to manage it in a sustainable manner (Newman *et al*. 1979, Newman and Crawford 1980). When sardine collapsed off Namibia, the South African experience prompted belief that anchovy was a competitor of sardine and that this competition would be minimized by subjecting the anchovy to heavy fishing pressure (Butterworth 1983). Off South Africa, horse mackerel had been fished when sardine were abundant, and its dominant year-classes were depleted (Newman and Crawford 1980). Off Namibia, the fishery for horse mackerel was only commencing when the sardine collapsed (Crawford *et al*. 1987). In both instances, it was the fish species least intensively exploited that later dominated the forage-fish community.

The earlier decrease of sardine off southern Peru and northern Chile (the peak catch was in 1980) than off northern Peru (peak 1987 – Csirke *et al*. 1996) has been ascribed to heavy fishing of the former stock (GTE.IFOP-IMARPE 1998).

In some instances there have been large fluctuations in the biomass of a species that is decreasing (e.g. sardine off Namibia, anchovy off Peru and anchovy off South Africa). The sporadic appearance of relatively good year-classes has tended to mask the longer term downward trend. The relatively large catches that were permitted as a result of the good year-classes may have hastened collapses of these fish stocks.

GLOBAL CLIMATE

Database

In order to understand how future climate variations may influence marine ecosystems, it must first be understood how and why climate has varied in the past. Unfortunately, detailed records of regional and seasonal changes are limited to the period since about 1850. Prior to then, data are dependent upon proxy indicators of various kinds. Sources of proxy data include tree rings, ice and/or laminated sediment cores containing fish scales, banded corals and last but not least, historical documents. Such data are frequently limited to specific geographical regions and they often only provide information about a specific season when the influence of the climate was strongest.

Even after 1850, the coverage of available data can by no means be termed global. Instrumental measurements are affected by differences in instrumentation, methodology, times of observation and changes in the density and location of stations. Nevertheless, concerning air temperature, there is a clear warming trend in annual global land surface temperature of about 0.5°C over the past century. In order to estimate true global surface temperature fluctuations, marine temperature observations have recently been combined with the land data. The resulting trend of similar order cannot be considered linear; there are influences of decadal to multi-decade variability that appear to be a natural part of the global climate system (Jones *et al*. 1986). Satellites are currently providing the first datasets that are truly global in coverage.

Regional trends seem to differ widely and no region has been identified to be a reliable indicator of global trends. However, selected "regional groups" show similar climatic tendencies in areas separated by far distances (Glantz *et al*. 1991). Consequently, attention should focus on individual groups of areas and years when considering the decade-scale trends in large marine ecosystems. To identify climatic changes on this scale, there are two particular deficiencies in the historical record: oceanic datasets (deep-water formation, thermohaline overturning) and upper atmosphere datasets (stratospheric dust, jet streams).

Changes in climate involve changes in regional weather regimes, which may be manifest as shifts in the position of Asian monsoons, mid-latitude storm tracks and displacements of centres of action, such as the Icelandic Low, the Azores High and the Aleutian Low. For instance, the climate of Western Europe in winter depends on the number and location of atmospheric blocking events. A simple shift from two blocks to three blocks per season constitutes a major change in the regional climate.

Climatic tendencies in the teleconnected patterns

Two approaches to decadal Pacific climate variability have been described partially in the literature. The first is associated with an apparent "shift" in climate mean state or regime that occurred in the mid 1970s (Graham 1994, Miller *et al*. 1994). In the eastern North Pacific, there was anomalous horizontal advection of heat in the ocean, related to changes in atmospheric circulation. The origin of the shift seemed to be related to an abrupt increase in the sea surface temperature (SST) of about 0.5–1°C in the central and western equatorial Pacific, associated with decreasing cloud coverage and relaxed near-surface winds. However, the physical reason for that thermal anomaly is still unexplained in the literature.

The second approach calls for more gradual changes, more oscillatory in nature (Trenberth 1990, White and Cayan 1998). For example, anomalies of the SST in the North Pacific Ocean and those of sea-level air pressure vary in phase. SST anomalies can change, via modified heat fluxes, the transient activity in the atmosphere, which in turn changes the winds reinforcing the initial SST. Such simultaneous fluctuations in ocean and atmosphere indicate that their coupling is important for the decadal variability. Nevertheless, there seems to be considerable confusion in the literature as to whether there exists a discrete climatic shift or a kind of oscillatory phenomenon.

The period from the mid 1930s to the mid 1970s/1980s seems to offer some "keys" to the possible global driving forces that may be involved. This was a period of particularly abrupt decade-scale fall in a very "low-pass filtered" rendering of the Southern Oscillation Index (SOI). This standardized index yields a negative value for *El Niño* years and correlates with a deepened "Aleutian Low" pressure system, positive SST anomalies in the eastern Pacific, predominance of *El Niños* over *La Niñas*, etc. Both the *El Niño* and the Southern Oscillation form the complex global ENSO phenomenon. *El Niño* is the oceanic component with extremely anomalous warm water at the sea surface off Peru and Chile, whereas the Southern Oscillation is the atmospheric part in the coupled ocean-atmosphere system. The latter is usually described by anomalies in the sea level air pressure describing variations in the zonal Walker Cell over the tropical Pacific between Tahiti and Darwin. For example, the SOI suggests major ENSO events in the periods 1911–1912, 1918–1919, 1925–1926, 1940–1941, 1957–1958, 1972–1973, 1982–1983, 1992–1993 and 1997–1998.

There is some statistical evidence that a negative SOI correlates with a positive anomaly in the Aleutian Low Pressure Index (ALPI), and vice versa. For example, a deep Aleutian Low speeds up the onshore advection of warm water in the north and reduces coastal upwelling off California. Since *El Niño* is known to be the dominant mode of interannual-scale climatic variability throughout the world, the ENSO phenomenon seems an obvious candidate for implication in the global-scale "regime shifts", because of its pronounced extra-tropical consequences. ENSO-like changes are reported from areas around the whole globe. Their linkage is termed "teleconnection". It is believed that unstable air-sea interactions and the subsurface "thermal memory" of the ocean, which is caused by its large heat capacity, control such ENSO quasi-cycles.

Fluctuations in this subsurface memory can be described in terms of very low-frequency waves (east-propagating equatorial Kelvin waves, west-travelling Rossby waves, and poleward-propagating Kelvin-Rossby waves that are topographically trapped along the west coasts of continents). Therefore, a dependence of the typical oscillatory period on basin size is expected. The dominant ENSO period is about 4–6 years in the Pacific Ocean. Assuming that the nature of such air-sea interactions in the Atlantic is similar to that in the Pacific, this would imply a three-year oscillation for the Atlantic because its basin size is about half that of the Pacific. There is some observational evidence that this is indeed the case.

Differences between subsequent events of *El Niño* have tended to occur between epochs of high or low solar activity. When the solar activity is high, it seems to be that strong events recur at intervals of about 12–13 years, whereas a shorter interval of about 8–9 years probably dominates during periods of low solar activity. Nevertheless, in absence of a plausible physical relationship, the solar association should be considered with skepticism.

The Atlantic Ocean is the only ocean where the net meridional heat transport crosses the equator up to high latitudes. Oceanic currents effectively redistribute the stored heat content of tropical/subtropical latitudes up to higher latitudes to provide an essential part of energy for the wind systems of mid-latitudes via related heat fluxes from the ocean to the atmosphere. Here, the frequency of cyclones increases within the intensified belt of westerlies. The geostrophic component of the westerlies depends strictly on the meridional air pressure difference between subpolar and subtropical regions. Such gradients are well described by the pressure difference between Iceland and the Azores, which is characterized by a dipole-like pattern with north-south orientation. These differences indicate a whole range of different time-scales. Their temporal fluctuations are termed the North Atlantic Oscillation (NAO) in the literature (Van Loon and Rodgers 1978). Associated changes are not randomly distributed in time (i.e. not a white noise power spectrum) and several frequencies tend to dominate for one or several decades (a red power spectrum). Characteristic quasi-periods are found in the range of 70, 25–30 and 2–3 years.

A positive NAO-index corresponds to intensified westerlies transporting relatively warm air masses to western Europe (mild European winters), whereas a negative NAO-index supports the inflow of cold Siberian air masses over north-eastern Europe, with a typical blocking situation over Scandinavia (severe European winters). The persistence of such a NAO-mode seems to be related to the persistence of anomalies in the SST and in the wind field through feedback mechanisms, which take place in the northern tropical/subtropical Atlantic Ocean (Hurrell 1996). However, other mechanisms must also be relevant because of such clear decade-scale signals. Suitable candidates are variations in subtropical and polar gyres, coverage of the sea-ice in polar regions and the deep-water formation and freshwater runoff of rivers.

At mid-latitudes, analysis of detrended SSTs confirms oscillations of about 30–70 years. In this context, the formation of North Atlantic Deep Water (NADW) can be expected to play a crucial role. In the late 1960s, a "freshwater anomaly" occurred in the Greenland-Iceland-Norway Sea region and travelled southwards with the East Greenland Current (Dickson *et al*. 1988). It passed the main region of deep-water formation (Greenland Sea) and reduced it temporarily. Its pathway turned north-eastwards in 1971–1972, after passing the Grand Banks. Numerical simulations confirm that the interdecadal climate variability in the North Atlantic is substantially influenced by the strength of the meridional thermohaline overturning cell. There is also some observational evidence that an increased injection of polar waters into the East Greenland Current is caused by a considerable intensification of northerly winds over the Greenland Sea and changes in the sea-ice conditions.

Long time-series also suggest that the atmosphere responds to anomalies in the SST (SSTA) as a result of variations in the subpolar gyre system in different ways. On interannual time-scales, the SSTAs are negatively correlated with the wind velocity south of about 50°N (SSTA >0 and NAO <0), whereas this correlation is positive on interdecadal time-scales (SSTA >0 and NAO >0). Therefore, interannual variability such as the NAO is mainly determined by air-sea flux variations, whereas the oceanic circulation dynamics seem to play an active role for interdecadal patterns. Therefore, climatic changes of the decade-scale stand for anomalies acting globally. For example, the "jump" of the early-mid 1970s is accompanied with a decreasing winter season SOI over the equatorial Pacific (*El Niño* tendency) and positive sea level anomalies along the coast off central Chile, an increasing winter season NAO-index over the central North Atlantic (intensification of westerlies), decreasing potential temperature of the Labrador Sea Water at the level of the potential vorticity minimum (intensified convection), increasing potential temperature at depths >2 000 m in the Greenland Sea (relaxed deep-water formation), but with a decreasing tendency for the Sahel precipitation index over sub-Saharan North Africa and a tendency for warmer water in the South Atlantic and Indian oceans. Because knowledge of mechanisms is incomplete, and global models are not yet sufficiently advanced to be expected to contain accurately all the processes that could connect these features, caution is needed. It is possible that some of the changes have been created by regional processes that have approximately coincided with other remote events. For example, the change in NAO is somewhat later than the change in many other phenomena around the globe, such as Sahelian rainfall.

Physical-biological linkages and methods

How are such globally occurring climate changes linked to "regime shifts" observed in sardine and anchovy populations? Changes of the gyre-scale circulation, which influence not only the oceanic warm-water sphere but also its cold-water sphere via anomalies in the deep-water formation, seem to be major factors in the decadal climate. Until now, three classes of physical processes tend to determine favourable reproductive habitat for many types of fish (Bakun 1996). These are:

(i) enrichment processes, namely
  - upwelling,
  - mixing,
  - cyclonic wind stress curl (Ekman divergence),
  - cyclonic eddy formation;

(ii) concentration processes, namely
  - convergent frontal formation,
  - anticyclonic wind stress curl (Ekman convergence),
  - lack of dispersion by turbulent mixing processes,
  - "encounter-rate" increases/decreases as a result of changes in the micro-scale turbulence;

(iii) retention processes:
  - lack of offshore transport in (1) Ekman field (near-surface and superficial layers), (2) geostrophic current (intermediate layers) and (3) offshore dispersion of eddy-like features (filaments) on the meso-scale,
  - availability of enclosed gyral circulations,
  - stability of current patterns to which life cycles are adapted.

Time-series of indices of variation of many of these processes can, in principle, be developed for use in retrospective analysis. Some may be directly related to wind and so may be formulated from COADS (Com-prehensive Ocean-Atmosphere Dataset) data (Roy and Mendelssohn 1998) or various meteorological fields. Ways to address others might be sought in satellite imagery or in hydrographic survey data and/or climatic atlases (e.g. Levitus). In addition, some new concepts and methods for retrospective analysis are now available. There is the concept of the "optimal environmental window", which directly relates regional wind conditions via production and turbulence to the survival of fish larvae (Cury and Roy 1989). Methods for the analysis of time-series involve power spectra

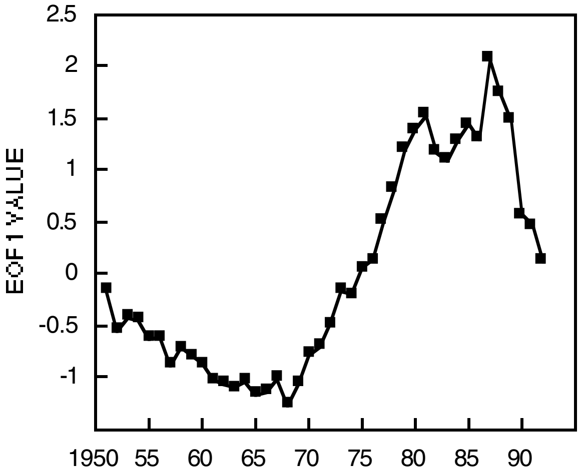

Fig. 32: Time-series (or "scores") of the first principal component (EOF1) of catches of sardine and anchovy in four regions – North-Western, North-Eastern and South-Eastern Pacific and South-Eastern Atlantic (see Table III), 1951–1992. Catches from the Gulf of California were excluded from the data for the North-Eastern Pacific. The EOF time-series is calculated by combining the eight original series of fish catches, with each series weighted by the Principal Component weights shown in Table III. All series were standardized prior to analysis, i.e. it is a correlation principal component analysis

to elucidate characteristic periods in the frequency domain and/or the use of empirical orthogonal functions (EOF), as well as principal oscillation patterns (POP) to help avoid the confounding of mechanisms that are acting on different time-scales. These may allow new inferences even from old data series that may have been previously addressed by conventional correlative methods. Finally, there is the realistic hope that unanswered questions can be addressed successfully by modelling approaches, as a result of rapidly increased computer power and a desire to address the modelling of the global environment. This is driven by a growing world population and global economy that, for success, will demand careful interaction with the environment through the next century.

Two cycles of decade-scale waves

Physical conditions influence marine ecosystems over a broad range of scales in time and space. Regional patterns occur in physical and chemical water characteristics, which alter the basic environmental conditions. Such "regime changes" reorganize marine ecosystems and synchronize variability in fish populations distributed around the world. The yearly identification of relative minimum/maximum values in landings suggests the existence of global "turning points", which switch the "regimes" from an increasing to a decreasing stage, or vice versa. For example, palaeosedimentary analysis of longer periods has indicated that there does seem to have been an alternation in dominance of either sardine or anchovy in the California system. The character of the series of landings seems less indicative of actual replacement of one component by the other, but rather a response of both to some common climatic forcing function. In any case, the idea that these variations may be somehow "linked" via a climatic forcing seems rather compelling.

Table III: First Principal Component (EOF1) of annual catches of sardine and anchovy in four selected regions of the world, 1951-1992. The values shown are the EOF-weights, which give the correlation between each individual time-series and the EOF1 time-series. The EOF1 time-series is shown in Figure 32. The EOF1 explains 61.1% of the total variance in the original eight series of fish catch. Catches from the Gulf of California were not included with the California catch

Region	Sardine	Anchovy
Japan	0.92	–0.88
California	0.75	0.78
Peru	0.90	–0.46
South-Western Africa	–0.82	0.67

Therefore, long-term fluctuations of pelagic fish production in this century probably can be conceived as a result of two climate-related "waves". Their first peak occurred in the late 1930s, influencing the years 1920–1950, while the second peak value started in the 1970s and apparently reached its maximum in the late 1980s and early 1990s. The latter cycle is illustrated in Figure 32, which shows the time-series of the first EOF of sardine and anchovy fish catch for four regions of the globe (Japan, California, South-West Africa and Peru/Chile – each region has a time-series of sardine and anchovy catch, making a total of eight time-series that were entered into a Correlation Principal Component Analysis). The statistical weights of the EOF (Table III) show generally out-of-phase behaviour for sardine and anchovy, whereas the marine ecosystem off South-Western Africa (Benguela Current) appears to be out of phase with that in Japan, California and Peru. The first EOF explains 61.1% of the total variance in the original eight indices. Inspection of Table III shows that the EOF combines the fish catch data in a way that is similar to other "regime indicator series" (Lluch-Cota *et al.* 1997).

Until now, only two cycles are well documented.

That means the available database is too sparse to prove statistically the apparent link between "regime shifts" in marine ecosystems and variations in the coupled ocean-atmosphere system on interdecadal time-scales. Generally, this situation will not be altered greatly by an increasing data coverage in space as a result of large international programmess like those of the World Climate Research Programme (WCRP), the World Ocean Circulation Experiment (WOCE), the Joint Global Ocean Flux Studies (JGOFS) and others such as the Global Ocean Ecosystem Dynamics (GLOBEC) and the Climate Variability and Prediction Research Programme (CLIVAR – component of WCRP) scheduled for or still running in the next decades. However, it is hoped that these programmes will ensure that, at the beginning of the next century, any "new climatic phase" will be better monitored as it affects not only oceanic but also terrestrial ecosystems worldwide. Furthermore, if actively persuaded, there are two specific ways in which the international programmes could improve knowledge of past events. First, palaeo-ecology holds the promise of improved understanding of decadal variability over the past few thousand years or so. Second, methods of assimilating sparse data using physical-based models are improving, and targeted studies making the best use of available data and rescuing data still held in manuscript form, may allow some of the major turning points in marine ecosystems this century to be studied in more detail.

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APPENDIX

Information collated pertinent to sardine and anchovy populations in the five regions of the world where *Sardinops* are found

Annual catch of sardine by Japan, Korea, former USSR and China in the North-Western Pacific, 1894–1996

Year	Catch (million tons)			
	Japan	Korea	USSR	China
1894	0.256			
1895	0.228			
1896	0.222			
1897	0.169			
1898	0.148			
1899	0.218			
1900	0.237			
1901	0.237			
1902	0.252			
1903	0.164			
1904	0.178			
1905	0.178			
1906	0.153			
1907	0.180			
1908	0.206			
1909	0.211			
1910	0.186			
1911	0.187			
1912	0.251			
1913	0.268			
1914	0.317			
1915	0.334			
1916	0.364			
1917	0.465			
1918	0.428			
1919	0.401			
1920	0.456			
1921	0.385			
1922	0.403			
1923	0.506			
1924	0.517			
1925	0.579	0.040		
1926	0.528	0.090		
1927	0.608	0.250		
1928	0.676	0.250		
1929	0.767	0.340		
1930	0.789	0.300	0.060	
1931	1.026	0.380	0.090	
1932	1.153	0.280	0.090	
1933	1.525	0.340	0.090	
1934	1.467	0.580	0.100	
1935	1.378	0.800	0.120	
1936	1.628	0.990	0.110	
1937	1.208	1.390	0.140	
1938	1.084	0.980	0.100	
1939	1.091	1.210	0.110	
1940	0.866	0.960	0.100	
1941	0.974	0.630	0.020	
1942	0.861	0.080		
1943	0.587			
1944	0.371			
1945	0.260			
1946	0.359			
1947	0.349			
1948	0.375			
1949	0.472			
1950	0.563			
1951	0.368			
1952	0.258			
1953	0.344			
1954	0.246			
1955	0.211			
1956	0.206			
1957	0.212			
1958	0.137			
1959	0.120			
1960	0.078			
1961	0.127			
1962	0.108			
1963	0.056			
1964	0.016			
1965	0.009			
1966	0.013			
1967	0.017			
1968	0.024			
1969	0.020			
1970	0.017			
1971	0.057			
1972	0.058			
1973	0.297	0.004		
1974	0.352			
1975	0.526	0.004		
1976	1.066	0.011		
1977	1.420	0.050		
1978	1.637	0.054	0.243	
1979	1.817	0.047	0.369	
1980	2.198	0.038	0.359	
1981	3.089	0.063	0.461	
1982	3.290	0.082	0.594	
1983	3.745	0.140	0.580	
1984	4.179	0.178	0.799	
1985	3.867	0.108	0.748	
1986	4.210	0.161	0.821	
1987	4.362	0.194	0.765	
1988	4.488	0.146	0.795	
1989	4.099	0.183	0.861	
1990	3.678	0.133	0.879	0.042
1991	3.010	0.045	0.656	0.063
1992	2.224	0.047	0.165	0.053
1993	1.714	0.031	0.004	0.047
1994	1.189	0.036	0.003	0.068
1995	0.661	0.014		0.058
1996	0.304			

Annual catch of anchovy by Japan, Korea, China and Taiwan in the North-Western Pacific, 1905–1996

Year	Catch (thousand tons)			
	Japan	Korea	China	Taiwan
1905	32			
1906	28			
1907	32			
1908	49			
1909	50			
1910	53			
1911	60			
1912	105			
1913	98			
1914	109			
1915	98			
1916	21			
1917	90			
1918	85			
1919	120			
1920	111			
1921	90			
1922	90			
1923	100			
1924	98			
1925	90			
1926	100			
1927	92			
1928	100			
1929	94			
1930	100			
1931	85			
1932	60			
1933	46			
1934	87			
1935	75			
1936	48			
1937	61			
1938	98			
1939	90			
1940	111			
1941	110			
1942	180			
1943	129			
1944	120			
1945	109			
1946	120			
1947	110			
1948	130			
1949	138			
1950	287	15		
1951	339	19		
1952	290	19		
1953	243	12		
1954	304	16		
1955	391	18		
1956	347	29		
1957	430	35		
1958	417	38		
1959	356	37		
1960	349	36		
1961	367	40		
1962	349	47		
1963	321	32		
1964	296	36		
1965	406	57		
1966	408	66		
1967	365	79		
1968	358	63		
1969	377	115		
1970	365	54		
1971	351	67		
1972	370	104		
1973	335	96		
1974	288	173		
1975	245	175		
1976	217	126		
1977	245	141		
1978	152	183		
1979	135	162		
1980	151	170		
1981	160	184		
1982	197	162		
1983	208	132		
1984	224	155		
1985	206	144		
1986	211	202		
1987	141	168		
1988	177	126		
1989	182	132		2
1990	311	168	54	3
1991	329	170	113	1
1992	301	168	193	1
1993	195	249	557	
1994	188	193	439	
1995	252	231	489	
1996	339			

Annual catch of sardine off California and for three regions of Baja California, 1889–1996. Some of the information for Baja California may be seasonal rather than annual data. Data for California are annual, published by California State Fish and Game

Year	Catch (tons)			
	California	Baja California Ensendada	Baja California Cedros	Baja California Magdelena
1889	498			
1890	596			
1891	425			
1892	342			
1893				
1894				
1895	327			
1896				
1897				
1898				
1899	1 072			
1900				
1901				
1902				
1903				
1904				
1905				
1906				
1907				
1908				
1909				
1910				
1911				
1912				
1913				
1914				
1915				
1916	24 970			
1917	65 903			
1918	71 816			
1919	63 771			
1920	38 865			
1921	34 003			
1922	59 980			
1923	77 004			
1924	158 172			
1925	138 971			
1926	182 044			
1927	231 911			
1928	303 836			
1929	373 240			
1930	235 992			
1931	216 088			
1932	267 601			
1933	351 443			
1934	578 715			
1935	573 277			
1936	717 740			
1937	452 043			
1938	608 195			
1939	528 669			
1940	447 445			
1941	617 098			
1942	519 775			
1943	525 270			
1944	556 939			
1945	339 427			
1946	224 838			
1947	118 020			
1948	171 510			
1949	307 428			
1950	320 251			
1951	131 203			
1952	13 490			
1953	17 050			
1954	73 381			
1955	71 352			
1956	42 899			
1957	29 202			
1958	114 559			
1959	53 243			
1960	44 241	18 882	1 017	
1961	42 446	10 551	10 719	
1962	17 044	10 391	4 229	
1963	11 045	11 679	7 339	
1964	18 679	18 045	8 441	
1965	20 830	10 533	11 714	
1966	18 027	11 135	8 396	
1967	25 149	14 695	12 962	
1968	9 451	0	9 395	
1969	8 519	0	8 471	
1970	7 813	0	7 612	
1971	8 810	0	8 675	
1972	11 259	0	6 472	4 618
1973	14 023	0	2 942	11 012
1974	19 222	0	3 080	16 136
1975	23 579	0	5 773	17 804
1976	15 913	0	4 964	10 942
1977	12 421	0	5 308	7 108
1978	9 505	0	6 208	3 293
1979	9 211	0	4 273	4 922
1980	25 518	0	4 854	20 630
1981	13 654	0	3 069	10 557
1982	16 292	0	6 801	9 362
1983	5 959	274	2 952	2 387
1984	4 811	0	2 127	2 453
1985	18 200	3 722	2 916	10 979
1986	20 480	243	4 751	14 341
1987	16 798	2 432	3 706	8 599
1988	19 096	2 035	1 257	12 080
1989	21 771	6 222	3 958	7 746
1990	33 936	11 375	2 816	16 975
1991	55 991	31 392	1 081	15 893
1992	58 612	34 648	992	5 026
1993	55 302	32 045	1 743	7 671
1994	69 770	20 877	1 686	33 787
1995	113 387	35 396	0	34 541
1996	98 988	39 065	0	25 795

Seasonal (June–May) catch of sardine in seven regions off the west coast of North America, by reduction ships fishing in the California Current, and overall, 1916/17–1967/68. These data were originally published as short tons in Glantz and Thompson (1981) and Radovich (1982) but are here given as metric tons. Some subsequent publications have used the original data as metric rather than short tons. The Baja California catch does not include catches made in the Gulf of California

Season	Catch (tons)								
	British Columbia	Washington	Oregon	San Francisco	Monterey	Southern California	Baja California	Reduction ships	California Current
1916/17					6 993	17 977			24 970
1917/18	73			63	21 596	44 171			65 903
1918/19	3 301			408	32 425	35 681			71 816
1919/20	2 975			907	39 037	20 852			63 771
1920/21	3 991			209	22 639	12 027			38 865
1921/22	898			73	14 775	18 258			34 003
1922/23	925			100	26 493	32 462			59 980
1923/24	880			172	41 649	34 303			77 004
1924/25	1 243			508	61 050	95 371			158 172
1925/26	14 467			508	62 592	61 404			138 971
1926/27	43 990			3 193	74 247	60 615			182 044
1927/28	62 066			15 138	88 904	65 803			231 911
1928/29	73 023			12 263	109 103	109 448			303 836
1929/30	78 310			19 918	145 165	129 846			373 240
1930/31	68 088			23 555	99 425	34 983		9 941	235 992
1931/32	66 755			19 598	62 654	38 928		28 153	216 088
1932/33	40 225			16 901	81 266	75 886		53 323	267 601
1933/34	3 673			32 957	138 299	115 001		61 513	351 443
1934/35	39 001			62 109	209 385	166 600		101 620	578 715
1935/36	41 105	9	23 791	69 065	167 314	135 189		136 803	573 277
1936/37	40 316	5 950	12 879	127 977	187 482	129 437		213 698	717 740
1937/38	43 609	15 510	15 102	121 282	95 177	100 069		61 295	452 043
1938/39	46 955	24 017	15 437	182 488	164 162	135 327		39 808	608 195
1939/40	5 007	16 108	20 253	192 695	206 682	87 924			528 669
1940/41	26 094	735	2 866	107 109	150 288	160 352			447 445
1941/42	54 465	15 510	14 376	169 236	227 010	136 501			617 098
1942/43	59 753	526	1 769	105 107	167 250	185 371			519 775
1943/44	80 487	9 469	1 651	114 746	193 750	125 167			525 270
1944/45	53 622	18	0	123 894	215 182	164 222			556 939
1945/46	31 110	2 095	82	76 281	131 986	157 873			399 427
1946/47	3 619	5 569	3 592	2 602	28 472	180 985			224 838
1947/48	444	1 234	6 286	85	15 990	93 981			118 020
1948/49		45	4 825	102	43 411	123 127			171 510
1949/50		23		15 820	119 514	172 071			307 428
1950/51		0		11 543	30 565	278 142			320 251
1951/52		1			14 419	102 604	14 179		131 203
1952/53					44	5 135	8 310		13 490
1953/54					53	4 022	12 976		17 050
1954/55					776	61 321	11 283		73 381
1955/56					470	67 066	3 816		71 352
1956/57					57	30 457	12 385		42 899
1957/58					15	20 185	9 001		29 202
1958/59					22 404	71 898	20 257		114 559
1959/60					14 611	19 180	19 452		53 243
1960/61					2 122	24 070	18 048		44 241
1961/62					2 024	21 130	19 292		42 446
1962/63					1 098	2 686	13 260		17 044
1963/64					921	1 748	16 674		19 343
1964/65					279	5 256	24 598		30 133
1965/66					137	515	20 178		20 830
1966/67					21	291	17 715		18 027
1967/68						64	25 085		25 149

Annual catch of anchovy off Washington, California and Baja California, 1889–1996.The Baja California catch does not include catches made in the Gulf of California

Year	Catch (tons)		
	Washington	California	Baja California
1889		56	
1890		61	
1891		66	
1892		68	
1893			
1894		209	
1895			
1896			
1897			
1898			
1899		7	
1900			
1901			
1902			
1903			
1904			
1905			
1906			
1907			
1908			
1909			
1910			
1911			
1912			
1913			
1914			
1915			
1916		241	
1917		240	
1918		394	
1919		730	
1920		258	
1921		883	
1922		296	
1923		139	
1924		157	
1925		42	
1926		27	
1927		167	
1928		162	
1929		274	
1930		145	
1931		154	
1932		150	
1933		159	
1934		129	
1935		90	
1936		98	
1937		113	
1938		368	
1939	3	1 077	
1940		3 159	
1941		2 053	
1942		847	
1943	2	787	
1944		1 946	
1945		808	
1946	17	978	
1947	40	9 510	
1948	405	5 823	
1949	406	2 067	
1950		2 439	
1951		3 477	
1952		27 891	
1953		42 918	
1954		21 205	
1955	1	22 347	
1956		28 460	
1957		20 274	
1958		5 801	
1959		3 587	
1960		2 529	
1961		3 856	
1962		2 051	
1963		3 229	669
1964		7 087	944
1965	1	12 038	4 599
1966		44 383	9 171
1967	48	54 957	13 243
1968	154	29 959	20 104
1969	161	71 671	14 267
1970	199	124 419	3 871
1971	81	65 013	27 977
1972	124	101 848	20 079
1973	158	147 634	32 623
1974	249	122 747	14 840
1975	284	213 956	39 807
1976	187	201 166	55 162
1977	143	253 828	76 061
1978		147 639	142 214
1979		246 355	135 032
1980		290 245	192 474
1981	1	316 405	242 906
1982	5	221 005	258 745
1983	3	92 172	174 636
1984	10	106 201	87 429
1985	12	120 804	102 933
1986	22	93 801	117 192
1987	77	114 501	93 547
1988	40	81 484	124 482
1989	61	83 471	79 495
1990	50	3 206	81 810
1991	54	4 238	98
1992	41	1 165	831
1993	44	1 998	2 324
1994	69	3 749	284
1995		1 881	875
1996		4 424	2 831

Estimates of biomass of sardine, anchovy and chub mackerel (fish aged one and older) off California and northern Baja California, 1929–1996

Year	Biomass (thousand tons)		
	Sardine	Anchovy	Chub mackerel
1929			149
1930			153
1931			198
1932	3 821		277
1933	3 619		308
1934	4 016		289
1935	3 348		234
1936	2 179		158
1937	2 063		106
1938	2 249		96
1939	2 054		91
1940	1 997		64
1941	2 727		56
1942	2 255		55
1943	1 799		79
1944	1 430		78
1945	771		55
1946	634		44
1947	649		26
1948	980		13
1949	987		33
1950	729		41
1951	280		33
1952	194		15
1953	270		5
1954	245		17
1955	173		37
1956	141		43
1957	197		35
1958	226		17
1959	132		15
1960	88		29
1961	54		37
1962	29		60
1963	20	637	76
1964	11	379	51
1965	4	261	20
1966	4	275	9
1967	4	214	2
1968	3	187	2
1969	3	331	2
1970	3	221	2
1971	<3	360	2
1972	<3	391	2
1973	<3	1 598	2
1974	<3	1 246	2
1975	<3	1 326	4
1976	<3	902	5
1977	<3	521	75
1978	3	395	106
1979	4	673	307
1980	4	513	371
1981	5	356	572
1982	5	714	872
1983	5	397	830
1984	15	822	740
1985	18	723	534
1986	27	412	549
1987	46	241	533
1988	61	441	512
1989	78	245	339
1990	89	153	330
1991	182	172	233
1992	187	145	109
1993	208	156	90
1994	360	392	71
1995	357		28
1996	462		56

Seasonal (June–May) catch of sardine and anchovy in the Gulf of California, 1969/70–1996/97

Season	Catch (tons)	
	Sardine	Anchovy
69/70	11 287	–
70/71	19 558	–
71/72	32 617	–
72/73	9 924	–
73/74	16 180	–
74/75	36 648	–
75/76	51 263	–
76/77	8 802	–
77/78	32 600	–
78/79	24 627	–
79/80	77 566	–
80/81	93 989	–
81/82	71 425	–
82/83	111 526	–
83/84	146 467	–
84/85	160 391	–
85/86	240 226	2 081
86/87	272 574	39
87/88	261 363	777
88/89	294 095	7 706
89/90	109 942	18 493
90/91	113 631	12 768
91/92	6 858	5 167
92/93	7 549	1 606
93/94	127 486	–
94/95	170 473	1 039
95/96	200 870	4 217
96/97	202 970	0

Annual catch of sardine off northern and central Peru, southern Peru, northern Chile, Coquimbo and Talcahuano, for Peru overall, for Chile overall and for Peru and Chile combined, 1970–1996

Year	Catch (tons)							
	Northern and Central Peru	Southern Peru	Peru (total)	Northern Chile	Coquimbo	Talcahuano	Chile (total)	Peru and Chile
1970	449		449	13 886			13 886	14 335
1971	6 051		6 051	23 180	31		23 211	29 262
1972	6 338		6 338	10 830	1 422		12 252	18 590
1973	132 252		132 252	50 797	6 572		57 369	189 621
1974	72 183	421	72 604	169 459	15 179	1 670	186 308	258 912
1975	61 684	1 167	62 851	133 967	22 471	–	156 438	219 289
1976	172 894	1 807	174 701	280 283	31 268	–	311 551	486 252
1977	815 897	55 006	870 903	557 662	34 845	1 623	594 130	1 465 033
1978	1 173 966	83 982	1 257 948	692 389	36 303	1 570	730 262	1 988 210
1979	1 525 040	201 991	1 727 031	1 420 086	56 561	37 068	1 513 715	3 240 746
1980	1 022 030	458 366	1 480 396	1 606 049	38 987	72 327	1 717 363	3 197 759
1981	870 839	312 108	1 182 947	1 425 499	42 250	86 226	1 553 975	2 736 922
1982	1 389 274	120 503	1 509 777	1 663 257	49 211	7 697	1 720 165	3 229 942
1983	990 197	181 994	1 172 191	2 420 732	105 677	16 260	2 542 669	3 714 860
1984	2 501 560	286 938	2 788 498	2 286 083	52 456	66 381	2 404 920	5 193 418
1985	2 514 244	387 522	2 901 766	2 607 114	49 315	62 788	2 719 217	5 620 983
1986	1 661 590	63 009	1 724 599	2 216 728	110 003	47 092	2 373 823	4 098 422
1987	2 387 502	91 663	2 479 165	1 782 418	81 638	42 620	1 906 676	4 385 841
1988	3 404 896	65 934	3 470 830	1 356 751	25 019	22 970	1 404 740	4 875 570
1989	2 156 532	46 127	2 202 659	1 405 140	18 893	8 152	1 432 185	3 634 844
1990	3 134 141	34 652	3 168 793	700 386	38 253	18 905	757 544	3 926 337
1991	2 335 712	79 452	2 415 164	583 299	31 844	30 225	645 368	3 060 532
1992	1 314 683	179 878	1 494 561	634 296	5 364	9 260	648 920	2 143 481
1993	1 178 738	27 644	1 206 382	315 218	9 920	3 626	328 764	1 535 146
1994	1 469 772	323	1 470 095	11 725	5 431	–	17 156	1 487 251
1995	1 574 728	255	1 574 983	65 492	6 480	281	72 253	1 647 236
1996	940 560	378	940 938	46 131	1 042	380	47 553	988 491

Annual catch of anchovy off northern and central Peru, southern Peru, for Peru overall, for Chile overall and for Peru and Chile combined, 1951–1996

Year	Catch (tons)				
	Northern and Central Peru	Southern Peru	Peru (total)	Chile (total)	Peru and Chile
1951					12 000
1952					16 000
1953					37 000
1954					43 000
1955					65 689
1956					132 378
1957					347 405
1958					777 134
1959					1 982 580
1960	3 196 372	113 785	3 310 157	168 818	3 478 975
1961	4 846 829	164 101	5 010 930	235 780	5 246 710
1962	6 410 436	281 085	6 691 521	384 457	7 075 978
1963	6 215 293	419 544	6 634 837	474 515	7 109 352
1964	8 088 295	785 072	8 873 367	910 504	9 783 871
1965	6 645 222	597 172	7 242 394	408 479	7 650 873
1966	7 623 459	906 362	8 529 821	1 015 156	9 544 977
1967	9 314 686	509 938	9 824 624	688 571	10 513 195
1968	9 450 926	811 735	10 262 661	945 645	11 208 306
1969	8 157 982	802 656	8 960 638	637 830	9 598 468
1970	10 929 649	1 347 373	12 277 022	588 527	12 865 549
1971	9 179 443	1 097 390	10 276 833	836 362	11 113 195
1972	3 492 886	954 479	4 447 365	309 222	4 756 587
1973	1 312 861	200 115	1 512 976	146 540	1 659 516
1974	3 053 318	530 158	3 583 476	348 329	3 931 805
1975	2 672 706	406 104	3 078 810	206 460	3 285 270
1976	3 210 634	652 416	3 863 050	433 293	4 296 343
1977	625 911	166 195	792 106	19 881	811 987
1978	464 110	722 931	1 187 041	191 886	1 378 927
1979	1 000 362	362 401	1 362 763	24 030	1 386 793
1980	223 099	497 025	720 124	78 556	798 680
1981	287 777	937 391	1 225 168	196 527	1 421 695
1982	1 240 410	480 027	1 720 437	75 538	1 795 975
1983	118 051	366	118 417	0	118 417
1984	2 403	22 415	24 818	230	25 048
1985	648 161	146 447	794 608	51 877	846 485
1986	3 185 991	312 194	3 498 185	941 378	4 439 563
1987	1 455 237	246 469	1 701 706	305 300	2 007 006
1988	2 434 105	285 636	2 719 741	688 183	3 407 924
1989	3 451 982	462 729	3 914 711	1 168 205	5 082 916
1990	2 952 965	179 939	3 132 904	575 080	3 707 984
1991	3 267 117	419 619	3 686 736	521 334	4 208 070
1992	4 276 687	843 652	5 120 339	918 280	6 038 619
1993	6 179 606	631 429	6 811 035	1 079 775	7 890 810
1994	9 047 114	781 322	9 828 436	2 134 430	11 962 866
1995	5 276 505	971 498	6 248 003	1 604 650	7 852 653
1996	6 952 926	183 930	7 136 856	988 674	8 125 530

Annual catch of sardine off New South Wales, Victoria, South Australia, Western Australia and in total for Australia, 1975–1996

Year	Catch (tons)				
	New South Wales	Victoria	South Australia	Western Australia	Total Australia
1975	130			460	590
1976	216			482	698
1977	236			519	755
1978	268			964	1 232
1979	160			633	793
1980	109			761	870
1981	68			1 491	1 559
1982	84			1 649	1 733
1983	141	3 500		2 073	5 714
1984	150	4 000		2 953	7 103
1985	128	1 000		4 734	5 862
1986	117	800		5 545	6 462
1987	141	700		8 077	8 918
1988	67	800		8 909	9 776
1989	110	500		7 238	7 848
1990	124	900		9 231	10 255
1991	117	1 200		8 644	9 961
1992	130	3 230		7 135	10 495
1993	154	2 882	750	8 118	11 904
1994	347	2 535	1 500	8 961	13 343
1995	256	2 346	3 000	10 278	15 880
1996	343	773	3 500	11 723	16 339

Estimates of the spawner biomass of sardine off Albany, Western Australia from a simulation model (Model) and the Daily Egg Production Method (DEPM), 1987–1997

Year	Spawner biomass (tons)	
	Model	DEPM
1987	19 500	
1988	15 000	
1989	14 000	
1990	15 000	
1991	12 000	
1992	13 800	17 000
1993	31 000	24 000
1994	24 300	31 300
1995	15 360	17 600
1996	8 000	
1997	6 000	10 000

A recruitment index for sardine in the Albany region, Western Australia, the sea level at Freemantle and the relative strength of the Leeuwin Current, 1981–1995

Year	Recruitment Index	Sea level index	Relative strength of the Leeuwin Current (residual)
1981	1.000	72.33	−0.10
1982	0.700	67.08	−5.35
1983	1.100	73.08	0.65
1984	1.200	76.58	4.15
1985	0.816	73.75	1.32
1986	1.324	69.41	−3.02
1987	1.411	65.50	−6.93
1988	0.493	77.08	4.65
1989	1.137	78.08	5.65
1990	3.356	69.96	−2.47
1991	0.411	69.45	−2.98
1992	0.037	69.90	−2.53
1993	0.016	64.68	−7.75
1994	0.540	68.32	−4.11
1995	1.000	74.93	2.50

Annual catch of sardine and anchovy off South Africa and off Namibia, 1950–1997. Values for the period 1950–1984 are from Crawford *et al.* (1987) and for Namibia include catches of sardine made off Angola

Year	Catch (tons)			
	South Africa		Namibia	
	Sardine	Anchovy	Sardine	Anchovy
1950	85 300		46 700	
1951	101 900		127 200	
1952	170 000		225 800	
1953	132 500		262 200	
1954	88 300		250 600	
1955	121 900		227 100	
1956	76 600		308 200	
1957	109 500		374 000	
1958	194 500	200	268 800	
1959	260 200	1 400	278 900	
1960	318 000		293 100	
1961	402 200		350 100	
1962	410 200		411 400	
1963	390 100	300	607 700	
1964	256 100	92 400	717 600	600
1965	204 500	171 000	780 200	1 000
1966	118 000	143 900	775 600	3 300
1967	69 700	270 600	969 600	24 300
1968	107 800	138 100	1 400 100	161 200
1969	56 100	149 200	1 178 400	226 100
1970	61 800	169 300	564 600	188 900
1971	87 600	157 300	327 500	184 700
1972	104 200	235 600	446 900	149 500
1973	69 000	250 900	469 200	361 100
1974	16 000	349 800	730 400	249 100
1975	89 200	223 600	564 800	191 100
1976	176 400	218 300	460 600	89 300
1977	57 800	235 500	276 000	132 900
1978	97 000	209 500	51 000	363 600
1979	52 900	291 400	39 100	288 100
1980	50 400	315 500	11 800	209 800
1981	46 200	292 000	52 400	216 500
1982	33 500	306 900	53 300	86 500
1983	60 500	240 200	48 500	187 400
1984	27 200	272 500	73 300	16 900
1985	33 000	272 600	57 600	50 700
1986	35 500	299 600	52 900	16 000
1987	34 300	596 000	66 000	376 000
1988	32 900	596 900	62 400	117 000
1989	34 500	294 100	77 600	78 800
1990	54 900	149 900	89 000	50 500
1991	101 500	150 700	68 000	18 000
1992	104 500	349 400	82 000	38 000
1993	50 700	235 600	114 800	63 100
1994	92 600	155 600	116 500	25 100
1995	112 800	170 200	92 500	47 400
1996	105 200	40 700	2 400	1 500
1997	117 000	60 100	32 000	2 500

Estimates of the spawner biomass of sardine off South Africa (Armstrong *et al.* 1983) and Namibia (Thomas 1986) using virtual population analysis, 1950–1985

Year	Spawner biomass (million tons)	
	South Africa	Namibia
1950	0.298	
1951	0.330	
1952	0.345	6.331
1953	0.298	5.598
1954	0.265	4.917
1955	0.234	4.665
1956	0.183	4.777
1957	0.197	5.008
1958	0.291	5.346
1959	0.444	5.853
1960	0.594	6.653
1961	0.626	7.662
1962	0.523	8.762
1963	0.375	10.306
1964	0.348	11.139
1965	0.227	10.149
1966	0.110	8.165
1967	0.062	6.100
1968	0.071	4.215
1969	0.063	2.420
1970	0.080	1.465
1971	0.074	1.399
1972	0.079	1.767
1973	0.053	2.164
1974	0.059	2.167
1975	0.097	1.605
1976	0.120	0.842
1977	0.033	0.320
1978	0.065	0.103
1979	0.045	0.049
1980	0.042	0.054
1981		0.153
1982		0.161
1983		0.134
1984		0.150
1985		0.170

Estimates of the spawner biomass of sardine and anchovy and of the biomass of recruiting young-of-the-year anchovy off South Africa (updated from Hampton 1992, 1996 and Barange *et al.* 1999) and of numbers of recruiting young-of-the-year sardine (updated from Hampton 1992 and Barange *et al.* 1999), and contribution of sardine and anchovy to the diet of Cape gannets off western South Africa (updated from Crawford and Dyer 1995), 1978–1997

Year	Spawner biomass (million tons)		Sardine recruitment ($\times 10^9$)	Anchovy recruitment (million tons)	Contribution to diet (% by mass)	
	Sardine	Anchovy			Sardine	Anchovy
1978					9.85	50.96
1979					5.90	51.36
1980					4.50	50.88
1981					4.30	56.40
1982					1.90	63.55
1983					5.80	44.14
1984	0.032	1.067			7.70	49.38
1985	0.054	0.975	0.310	5.44	18.00	26.72
1986	0.160	1.747	0.466	6.79	20.80	50.04
1987	0.129	1.456	0.575	11.83	36.15	37.60
1988	0.113	1.104	0.508		34.00	41.10
1989	0.286	0.536	0.132	6.84	49.25	17.55
1990	0.263	0.469	0.150	3.30	59.50	9.70
1991	0.441	1.682	0.377	4.34	34.55	34.90
1992	0.327	1.501	0.388	16.09	26.10	42.50
1993	0.464	0.800	0.163	29.98	48.10	23.65
1994	0.597	0.476	0.110	7.20	56.00	8.35
1995	0.620	0.432	0.398	48.65	55.85	20.40
1996	0.505	0.143	0.068	9.97	56.50	5.85
1997	0.769	0.841	0.497	68.82	49.35	16.20

Harvest of seabird guano at islands and platforms off Namibia and islands off South Africa, 1892–1995

Year	Harvest (tons)		
	Namibian islands	Namibian platforms	South African islands
1892		–	1 633
1893		–	1 089
1894		–	2 592
1895		–	2 903
1896	2 714	–	454
1897	2 740	–	2 987
1898	2 762	–	2 217
1899	2 006	–	2 544
1900	2 112	–	1 490
1901	1 584	–	932
1902	2 218	–	2 138
1903	2 363	–	2 063
1904	2 260	–	2 007
1905	3 167	–	2 417
1906	2 654	–	2 087
1907	2 549	–	2 204
1908	3 819	–	2 902
1909	4 374	–	1 762
1910	3 444	–	2 287
1911	2 589	–	1 627
1912	3 776	–	2 005
1913	3 737	–	2 454
1914	4 383	–	2 994
1915	3 757	–	2 794
1916	3 404	–	2 857
1917	4 163	–	2 157
1918	4 599	–	2 668
1919	4 650	–	3 303
1920	5 841	–	3 635
1921	4 742	–	2 969
1922	5 407	–	3 079
1923	5 950	–	3 118
1924	6 041	–	1 668
1925	4 893	–	2 224
1926	5 074	–	4 286
1927	5 423	–	3 729
1928	5 588	–	3 641
1929	5 251	–	2 315
1930	4 417	–	1 255
1931	4 517	8	2 660
1932	4 847	24	1 072
1933	3 151	43	1 952
1934	3 333	71	1 441
1935	4 396	82	2 119
1936	3 282	143	2 554
1937	3 461	332	2 176
1938	2 699	1 669	1 598
1939	3 108	1 720	2 995
1940	4 196	1 765	2 962
1941	3 638	2 554	2 930
1942	3 538	2 320	1 591
1943	2 952	2 706	2 391
1944	3 941	1,555	2 608
1945	4 246	911	2 875
1946	2 983	1,665	2 086
1947	3 725	2,223	2 027
1948	3 225	1,039	1 599
1949	2 515	910	1 737
1950	2 971	577	1 673
1951	2 970	1 014	2 063
1952	3 384	1 432	1 722
1953	3 300	1 353	1 850
1954	3 473	1 451	1 799
1955	2 823	1 552	1 620
1956	2 159	1 247	1 918
1957	3 119	1 222	1 662
1958	2 844	1 699	1 821
1959	3 520	1 631	1 814
1960	1 911	1 421	1 783
1961	3 147	1 557	2 303
1962	3 153	1 723	1 675
1963	1 333	2 159	1 249
1964	3 147	1 418	1 121
1965	2 387	1 965	1 004
1966	2 413	2 073	915
1967	2 163	2 359	918
1968	2 255	1 797	998
1969	2 617	1 586	1 223
1970	1 173	2 218	1 198
1971	1 203	1 545	791
1972	1 536	2 423	807
1973	1 917	3 611	1 360
1974	1 430	1 119	868
1975	786	2 778	655
1976	786	2 983	465
1977	1 976	1 845	688
1978	2 948	3 365	764
1979	3 132	796	335
1980	2 847	3 293	437
1981	1 855	3 494	394
1982	2 111	3 171	330
1983	3 131	3 899	2 598
1984	2 129	4 827	379
1985	2 480	3 945	454
1986	1 348	1 582	87
1987	1 784	4 299	1 035
1988	0	2 708	88
1989	2 050	2 309	87
1990	0	3 418	78
1991	0	3 266	80
1992	0	1 854	2
1993	0	4 203	0
1994	0	2 323	281
1995	0	1 104	0