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Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report

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ABSTRACT

Regimes of high abundance of sardine (*Sardinops sagax* and *Sardina pilchardus*) have alternated with regimes of high abundance of anchovy (*Engraulis* spp.) in each of the five regions of the world where these taxa co-occur and have been extensively fished. When one taxon has been plentiful, the other has usually been at a reduced level of abundance, and vice versa. Changes in the four heavily fished regions that support *S. sagax*—the Japanese, Californian, Humboldt, and Benguela systems—from a regime dominated by one taxon to a high level of abundance of the other have occurred more or less simultaneously. In the Pacific Ocean, sardines have tended to increase during periods of increasing global air and sea temperatures and anchovies to decrease. The Japanese system is dominated by sardines to a greater extent than the other systems, and sardines off Japan appear to increase as the Kuroshio Current cools. At the eastern edge of the Pacific Ocean, sardines colonize cooler areas during periods of warming. The Benguela system is out of phase with the three Pacific systems. The four systems all appeared to be in a state of flux in the 1980s. Increased abundance of the

subdominant taxon is often one of the first signs of change. Sardines are relatively sedentary in refuge areas when scarce but change behavior to become highly migratory and colonize cooler areas when abundant. Anchovies, by contrast, expand around a fixed geographic center.

Key words: sardine, anchovy, global temperature change, abundance, regime changes, Kuroshio Current, California Current, Humboldt Current, Benguela Current

INTRODUCTION

Sardines are extensively fished in five of the world's coastal regions, off Japan and in the California, Humboldt, Benguela, and Canary current systems, but only slightly off Australasia. Sardines in five of these six regions are believed to be the same species—*Sardinops sagax* (Parrish et al., 1989). The sardine of the Canary Current system, including the Mediterranean and the North Sea, is a distinct genus—*Sardina pilchardus*. Anchovies (*Engraulis* spp.) have a wider distribution than sardines but co-occur with sardines in each of the six regions.

Populations of sardines and anchovies or both have undergone large changes in abundance in each of the five regions where they co-occur and have been extensively fished (Lluch-Belda et al. 1989). Often, anchovies were abundant when sardines were relatively scarce and vice versa (e.g., Daan, 1980; Silvert and Crawford, 1988). Sardines in the different regions of the Pacific Ocean and in the Canary Current tend to be abundant at almost the same time (Kawasaki, 1983, 1991b; Lluch-Belda et al., 1989). Catches of sardines in the Benguela Current are high when they are low elsewhere and vice versa (Crawford et al., 1991), thus being out of phase with the other locations. There is accumulating evidence that in all four regions where there are large fisheries for *S. sagax*, changes in the relative abundance of sardines and anchovies were initiated in the second half of the 1980s.

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From a 1988 workshop in La Paz, Baja California Sur, Mexico, these synchronous massive changes in abundance were described as a "regime problem" with global manifestations (Lluch-Belda et al., 1989). In November 1990 the authors again held a workshop in La Paz to discuss the large fluctuations that have taken place in the populations of sardines and anchovies. This paper documents the conclusions of that workshop, including the general characteristics of the regime cycle, as well as the recent variations in areas of major *S. sagax* fisheries.

THE REGIME CYCLES

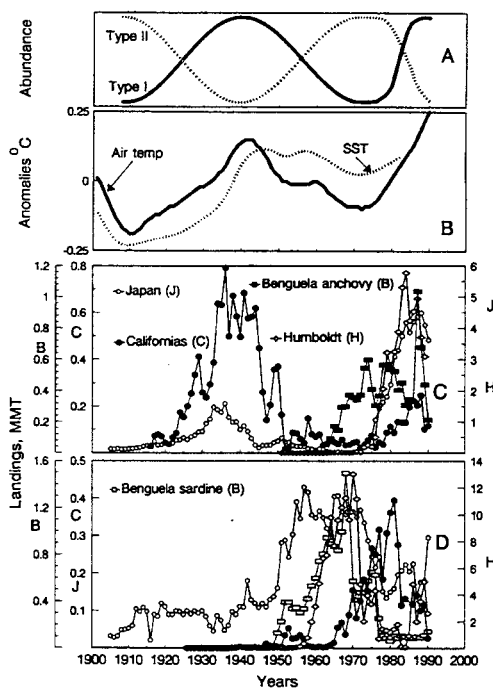
Based on the definition given by Lluch-Belda et al. (1989), the two phases (high and low) of the regimes of abundance of sardine and anchovy fishing were analyzed for each of the major areas using the existing historical data as well as personal experience. Catch data show that the sardine populations off Japan and California were in the high-abundance phase during the 1930s. These data also show the high-abundance phase during the 1980s off Japan, California, and Chile-Peru (Fig. 1C) as well as pilchard in the Canary Current. The low-abundance phase was present off Japan and California in the early 1900s, and from the 1960s to the early 1970s it was present off Japan, California, the Humboldt Current (Fig. 1C), and the Canary Current. The reverse was true for anchovies off Japan and California, in the Humboldt Current, and in the Benguela Current; sardines were abundant in 1960s and early 1970s but subsequently scarce, whereas anchovies showed the opposite trend (Fig. 1C, 1D).

The regime cycles are of two types. Type I includes sardines, while anchovies belong to type II. Each of the types has its particular ecological characteristics and strategies. Sardines in the Benguela Current belong to type I, notwithstanding that their cycle is out of phase with the other sardine populations. Except for the Benguela sardine the high-abundance phase of the type I is associated with global warm periods, while the contrary is true for the high-abundance phase of the type II. In other words, sardines tend to be abundant during high-temperature global regimes, while anchovies are abundant during low-temperature global regimes. This is illustrated in Fig. 1 for the full series available and in Fig. 2 for the expanded 1960–1990 period.

BIOLOGICAL CHARACTERISTICS OF THE TWO REGIME TYPES

There are significant differences between the two regime types. Sardines expand and contract their geo-

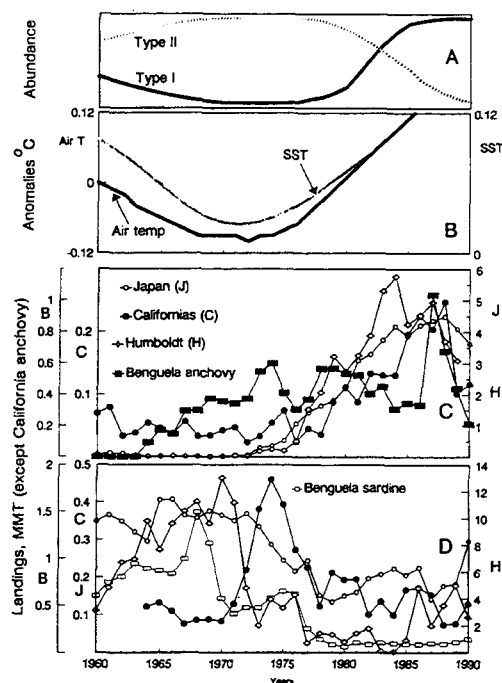
Figure 1. (A) Schematic cycles in regimes of abundance of sardine and anchovy. (B) Global air and sea surface temperatures anomalies as digitized from Jones (1991) and Reid (1987, 1991), detrended by means of q-spline procedure in a commercial statistical software package to remove the high-frequency variation. (C) Japanese (J), California–Baja California west coast–Gulf of California (C), and Humboldt (H) sardine landings and Benguela (B) anchovy landings. (D) Japanese (J), California (C), and Humboldt (H) anchovy landings and Benguela (B) sardine landings.



graphical range much more than anchovies do. Sardine populations expand rapidly poleward during warming periods, greatly shifting their main spawning and feeding areas. Anchovies seem to expand and contract around a fixed geographical center (Lluch-Belda et al., 1989).

Type I species, notably sardine, exhibit the phenotypic changes that correspond to the Kawasaki migratory phenotypic forms (Kawasaki, 1983). This biological variation, called phase variation, is similar to that long recognized in locusts, in which there are both solitary and gregarious phases. For example, the Far Eastern sardines, in the high-abundance phase, acquire smaller body sizes at the same ages and the capability of swimming longer distances as they occupy new,

Figure 2. Expanded plots from Fig. 1 during the period of 1960–1990, except that the California anchovy series is estimated biomasses instead of landings, since catches were initiated later.



broader, more productive areas. In the low-abundance phase, however, they are more or less restricted to limited areas, larger in body size at the same age, and non-migratory.

Type II species do not show these phenotypic shifts. Their populations seem to be distributed more evenly along their normal geographical range. When the type I species decline in numbers or are at low levels, the type II species have the ability to increase rapidly to very high numbers within their normal geographic range.

Genetic homogeneity might be expected in the type I species, owing to their being restricted to small refuge areas during their low-abundance phase where genetic interchange is higher. Since type II species do not contract or expand their geographic range significantly, they might be expected to have genetic heterogeneity. Hedgecock (1991) showed this to be the case for the California sardine and anchovy. Thus, both types of species are utilizing the high-productivity upwelling areas with quite different ecological genetic strategies.

RECENT CHANGES IN FOUR CURRENT SYSTEMS

The Japanese system

Twice this century, sardines have been abundant in waters around Japan. Large catches were made from the late 1920s to the mid-1940s. They were scarce through the 1950s and 1960s, but there was a spectacular increase in abundance starting in 1975 (Kondo, 1980). The highest ever annual catches were recorded in the late 1980s, when harvests were about 4.5 million tons (Fig. 1C). Landings of anchovy were low during the 1930s and 1940s, greatly increased in the 1950s and 1960s, and then decreased in the 1970s. However, during the 1980s, catches of anchovy increased to slightly above the level of the 1940s (Lluch-Belda et al., 1989), and in 1990 the increase in catch was from 182 thousand tons to 296 thousand tons (Fig. 1D).

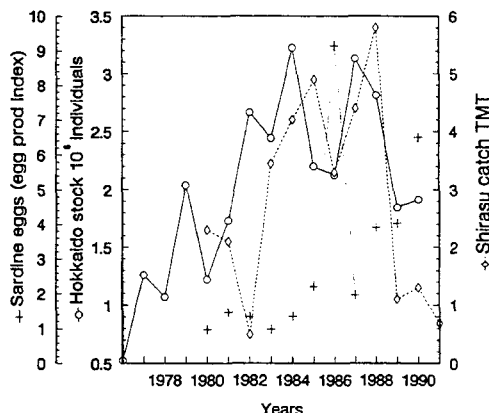
Although high catches of sardine were maintained until 1988, the abundance of sardine around Japan is believed to be decreasing. Available stock indices and catch rates have fallen in the northern fishing grounds off eastern Hokkaido (Fig. 2) (Wada and Kashiwai, 1991), a region where sardine is usually scarce during periods of low abundance (Lluch-Belda et al. 1989, Parrish et al. 1989). Further, there has been a recent increase in the growth rate of sardines. In the past there has been a density-dependent increase in growth rate at low stock sizes (Wada and Kashiwai, 1991). Another possible indication of a decreasing sardine biomass is the commercial catch of shirasu, larval sardine that is a highly prized delicacy in Japan. The catch fell markedly in 1989, continued to be low in 1990 without any decrease in fishing effort (Wada and Kashiwai, 1991), and fell further in 1991 (Fig. 3). The reduced shirasu catch occurred in spite of an abundant production of sardine eggs, as shown in Fig. 3 (Mori et al., 1988; Kikuchi and Konishi, 1990), indicating high mortality of ichthyoplankton.

By contrast, research boats have recently encountered exceptionally large shoals of anchovy, suggesting that the abundance of this species may be increasing. Anchovy catches began increasing in the 1980s (Fig. 1D).

The California Current

Sardines were abundant in the northern portion of the California Current in the 1930s with catches exceeding 0.7 million metric tons (MMT) per year (Murphy, 1966), but the population declined by several orders of magnitude during the 1940s and 1950s and remained at very low levels until the late 1980s (Smith, 1990). From the mid-1970s, substantial catches of sardine were made in the Mexican fishery off central and

Figure 3. Sardine abundance indices off Japan.



southern Baja California but primarily in the Gulf of California (Fig. 4) (Lluch-Belda et al., 1989). Anchovy abundance increased markedly during the late 1960s to a peak in the mid-1970s and remained at high levels through the mid-1980s (personal communication). Anchovy catches peaked at over 0.3 MMT in 1981 but have declined to an average of about 0.1 MMT from 1983 through 1989 and fell to about 0.03 MMT in 1990 (Fig. 1D).

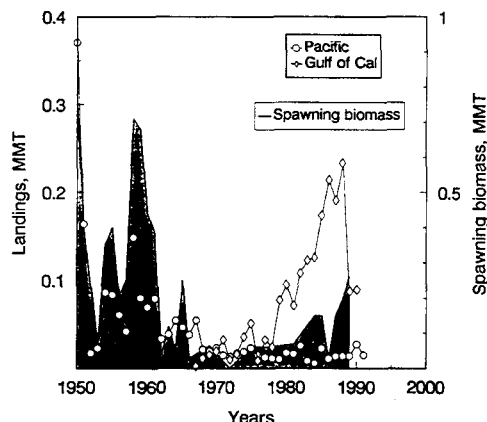
The sardine spawning biomass, which had been at extremely low levels for several decades, increased sharply during the 1980s (Fig. 4) (Smith, 1990). The estimate for the California sardine biomass for 1990 is between 100,000 and 600,000 tons (Barnes et al., 1991). This does not include the biomass off Baja California or the Gulf of California.

The Gulf of California may be a special location. The sardine fishery began in the late 1960s (Lluch-Belda et al., 1986). The catch increased over the years until 1988 and then dropped dramatically starting in 1989 (Fig. 4). The anchovy (*Engraulis mordax*) was first caught in the Gulf of California in 1986 (Hammann and Cisneros-Mata, 1989). Before that time, no eggs, larvae, or adults were ever recorded as having been in the Gulf. Anchovy currently dominates the fishery.

The Humboldt Current

Purse-seine fisheries off Peru and Chile developed after the sardine collapse in California in the late 1950s, with catches initially being dominated by anchovy. The anchovy fishery collapsed in the mid-1970s; landings plummeting from in excess of 13 MMT to less

Figure 4. Sardine spawning biomass off California and landings of the Pacific coast and Gulf of California.

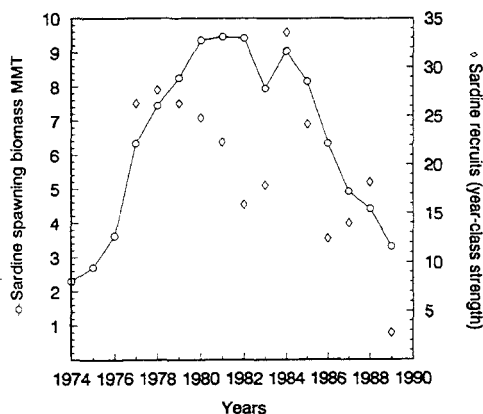


than 1 MMT in the space of a few years. Landings remained at low levels for a period of about 10 years, fluctuating between about 50 thousand and 4 million metric tons. Landings of sardine rose from about 20 thousand tons in the 1960s to more than 5 MMT in the mid-1980s. The catch has subsequently decreased, principally owing to the rather rapid decline of the Chilean catch.

Different stock units exist along the margin of the southeast Pacific (Serra, 1983; Parrish et al., 1989). The sardine and anchovy stocks off northern-central Peru and southern Peru-northern Chile are the largest and are those that sustain the main pelagic fisheries in the two countries (Serra, 1983; Zuta et al., 1983; Serra and Tsukayama, 1988). The fisheries in Peru and Chile are managed independently.

Off Chile, there was a sustained decrease in the biomass of sardine aged three or older throughout the 1980s (Serra, 1991; personal communication). The biomass at the end of the decade was only about 40% of its level in 1980 (Fig. 5). Virtual population analysis suggests that weak year-classes were formed in 1982 and 1983, coinciding with the El Niño event of 1982–1983 (Fig. 5). These year-classes begin entering the exploitable population during 1986 and 1987 as fish aged three. Subsequent year-classes show a slight recovery but then a marked decrease in 1986, indicating that the resource is entering a phase of lower abundance. The start of the Chilean sardine decline has been blamed on overfishing (Serra, 1991; personal communication). However, the weak year-classes since 1986 began with entry to the spawning stock of

Figure 5. Sardine spawning biomass and recruits in the southern Humboldt Current.



the poor year-classes formed during the 1982–1983 El Niño.

Catches of anchovy off Chile and Peru have increased since the mid-1980s, and almost 5 MMT were landed in 1989 (Fig. 1D). After the 1982–1983 El Niño, intensive spawning of anchovy was recorded off northern Chile (personal communications). There was also a shift in the species composition of ichthyoplankton back to that typical of the late 1960s, when anchovy was dominant (Loeb and Rojas, 1988). Off northern Chile, virtual population analysis suggests that a powerful year-class of anchovy was formed in 1987, and this led to a biomass of spawners (fish aged one or older) in 1988 and 1989, more than double the level of 1984 (personal communication).

The Benguela Current

In the Benguela Current, sardine dominated purse-seine catches in the 1950s and 1960s, but it was replaced in the catches by anchovy in the 1970s (Crawford et al., 1987). Anchovy continued to dominate catches in the early 1980s, and a peak of nearly 1 MMT was landed in 1987. Thereafter, there was a rapid decrease in landings (Fig. 1C).

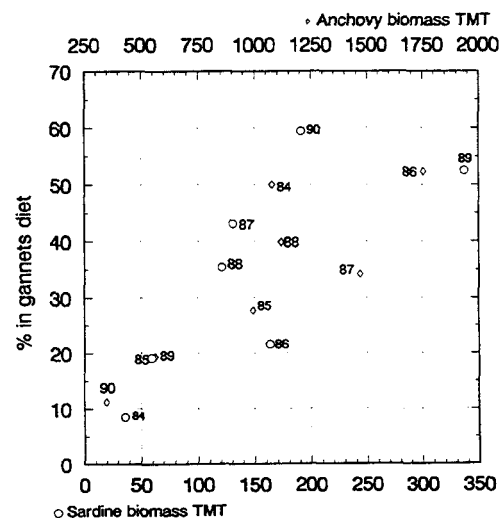
Stocks of sardine and anchovy off Namibia and South Africa are believed to be relatively discrete (Crawford et al., 1989) and are managed independently. Since the mid-1980s the biomass of anchovy spawners off South Africa has been measured by acoustic surveys (Hampton, 1987). Estimates of biomass were at first considerably higher than those calculated by virtual population analysis (e.g., Newman and

Crawford, 1980). The total allowable catch was approximately doubled in 1987 and 1988, and this was the main reason for the exceptionally high catches from the Benguela Current in these years.

Since the late 1970s the diet of Cape gannets (*Morus capensis*) has been monitored at two of its breeding localities off western South Africa on a monthly basis (Crawford and Shelton, 1981; Berruti, 1987). The annual contribution, by mass, of sardine and anchovy to the diet of Cape gannets reflects the changes in the biomass of the two prey species as measured by acoustic surveys (Fig. 6). In the 1980s there was a decrease in the contribution of anchovy to the diet of Cape gannets, with 1989 and 1990 being the lowest levels recorded to date and confirming low acoustic estimates of abundance of anchovy in these years. By contrast, the contribution of sardine to the diet of Cape gannets increased steadily after 1984, and in 1990 sardine contributed about 60% of the diet (Fig. 6).

It appears that sardine may currently be replacing anchovy as the dominant small planktivorous fish in the southern Benguela Current. Landings of anchovy by the Namibian purse-seine fishery have been low since 1984, except in 1987 when, as off South Africa, there was a large catch. Landings of sardine off Namibia increased through the decade by almost an order of magnitude. This suggests that there may also be a shift

Figure 6. The relationship between sardine and anchovy biomass and contribution by mass of these species to the diet of Cape gannets.



in dominance in the northern Benguela Current from anchovy to sardine.

GLOBAL PHASE CHANGE

In each of the four systems where *S. sagax* is extensively fished, there is evidence for an increase in abundance of the low-abundance phase species since the mid-1980s. Catches of anchovy increased off Japan in the latter part of the decade, and research surveys also encountered increased quantities of anchovy. In the Humboldt Current, catches of anchovy increased in 1986 and have remained high since, although they show rather strong fluctuations. Off northern Chile a large anchovy year-class was formed in 1987, and it caused a large increase in spawner biomass in 1988 and 1989 (personal communication).

Off northern Baja California and southern California, where anchovy was the dominant species in the early 1980s (Lo and Methot, 1989; Smith, 1990), there is evidence that sardine increased toward the end of the decade. In the Benguela Current, where anchovies predominated in the 1970s and 1980, sardine has increased since 1984.

In most instances the high-abundance-phase species has decreased in abundance, but awareness of the decreases has arisen at various stages. The earliest suggestion that the abundance of sardine might be decreasing off Japan was a contraction in the eastward extent of the species range. In 1984, sardine was encountered across the northern Pacific to 174°W, but in 1985 and 1986 it was found only as far east as 174°E (Wada and Kashiwai, 1991). In the Gulf of California, sardine catches decreased substantially in 1989 and 1990. In the Humboldt Current, sardine catches decreased after 1985, but there was a clear trend to a reduced spawner biomass after 1982. Off California and northern Baja California, there was no indication of a decrease in anchovy, the dominant species, up until 1988. In the other region where anchovy dominated, the Benguela Current, the first indication of collapse was of an exceptionally poor year-class off South Africa in 1989. This was reflected in a sustained low contribution by anchovy to the diet of Cape gan-nets from mid-1989 onward.

Statistically significant relationships between historical records of catches off Japan, California, and South America suggest that changes in the Pacific Ocean occur simultaneously or with a short lag, depending on assumptions made concerning the age of recruitment of sardines to the fisheries (Crawford et al., 1991). Until the most recent changes, sardines in these three systems were in phase with one exception

(Kawasaki, 1983, 1991a; Kawasaki and Omori, 1988). Sardines off Japan, in the Humboldt Current, and in the Gulf of California attained high levels of abundance in the 1970s and 1980s, but sardines continued to be scarce off California and northern Baja California. At the time of the upswing in sardine abundance off Japan and in the Humboldt Current in the early 1970s, the biomass of sardine off California approached a zero level (Smith, 1990), but over the years the California sardine biomass has increased to between 100,000 and 600,000 tons (Barnes et al., 1991).

GEOGRAPHIC CHARACTERISTICS OF CHANGE

When sardine is replacing anchovy, as appears to have happened in the Benguela Current, the first signs of change may be an increased abundance of sardine. A reduced abundance of anchovy may be apparent only at a later stage.

When anchovy is replacing sardine, a contraction in the range of sardine, as off Japan and Chile, may be an early indication of change. Increased catches of anchovy were recorded off Japan, in the Gulf of California, and in the Humboldt Current from the mid-1980s, so in each instance considered, one of the first signs of change appears to have been an increased abundance of the subdominant species.

Altered behavior by *S. sagax* during periods of high and low abundance is of particular interest in that it is akin to the phase variation in such insects as locusts and armyworms (Dröschner, 1980). When at a low level of abundance, the species remains in coastal waters with a greatly reduced level of migration. At high abundance it becomes a widely migrating oceanic species, except when thermal barriers, for example, at the southern ends of Baja California west coast and the Gulf of California, restrict such behavior. We describe below the range expansions in each of the four systems we have considered.

Off Japan, at low abundance the sardine is restricted to the southern coasts of Honshu and Shikoku islands, with small pockets of spawning off these two islands. At high levels of abundance there is a large increase in range. Adult fish occur well into the oceanic Pacific, and they migrate northward along the eastern coast of Japan from July to October. This migration supports a large summer fishery off Hokkaido. Fish range even farther into the oceanic Pacific, where they were found east to 174°W in 1984 (Wada and Kashiwai, 1991). The species also colonizes the sea of Japan, where it is caught in coastal regions off western Japan and along the seaboard of the former Soviet Union and Korea

(Kawasaki and Omori, 1988). Spawning spreads to the north along the Pacific coast of Honshu and into the Japan Sea. When abundance is high, a large amount of spawning takes place off southern Kyushu Island.

Off California and northern Baja California, during periods of low abundance the sardine was still plentiful off central and southern Baja California. It retreated to its area of refuge (Lluch et al., 1991). Off California, from the early 1970s, when the sardine biomass was at a near-zero level, through 1990, it has expanded to between 100,000 and 600,000 tons (Barnes et al., 1991). At this time we cannot tell what is happening to the population biomass. The California sardine catch is not an index of abundance because of the state's imposed catch limits, and the cruises for estimating the biomass are not extensive. The catch in 1990 of pure loads of sardines was lower by about 12 percent from the year before off northern California (California Department of Fish and Game, 1991), perhaps a sign of reduced migration from the south.

In the Humboldt Current, sardines, when at a low level of abundance, spawn off northern Peru and off northern Chile. The main center of fishing is off northern Chile, and sardines are distributed from northern Peru to about 30°S. When sardines are abundant, spawning spreads along central Peru and also occurs at about 30°S and 36°S. The distribution extends north to Ecuador and south to about 40°S. Fishing takes place off southern Ecuador, northern and southern Peru, and northern Chile and at various localities off central Chile. The Chilean fishery is based on fish aged about three or older (Serra, 1983). It is not known whether the large southward extension in distribution is mainly attributable to these older fish, analogous to the northward migration of older sardine to British Columbia in the California Current (Murphy 1966), or whether a substantial number of juveniles also occur in the south. A limited number of juveniles have been caught in the south by research surveys. It is clear that the sardine fishery at Talcahuano (36°40'S) was declining while catches at Arica (18°30'S) were still at a high level. This is similar to the collapse of the Californian fishery for sardine from north to south in the 1940s and 1950s. The reduced catch started in British Columbia (50°N) and progressed southward to southern California (30°N) (Murphy, 1966; Radovich, 1982).

In the Benguela Current, at low levels of abundance, spawning by sardines is largely confined to northern Namibia (Le Clus, 1990) and to the western Agulhas Bank off South Africa (Crawford, 1991). Sardines are distributed off northern Namibia and southern South Africa but are scarce in intermediate areas

(Crawford, 1991). At high levels of abundance, spawning extends up western South Africa to Cape Columbine (Crawford, 1991), and sardines are often plentiful in the relatively cool water of the central Benguela system. For about a decade the sardines supported a fishery at Luderitz, the coldest portion of the Benguela Current with sea surface temperatures of 13°–14°C (Parrish et al., 1989). This fishery collapsed ahead of the fishery at Walvis Bay, similar to the early collapses of the cold-water fisheries off British Columbia.

There are several differences between the Japanese region and the other regions where types I and II prevail. The anchovy biomass has not reached anywhere near that of the sardine off Japan, unlike the other systems. Another difference is that the Kuroshio Current was cool during the 1980s at the peak of the sardine biomass and during the global warming phase. These differences may be a significant key to understanding the general phenomenon of regime shift. If regime shifts are associated with the strength of the major ocean gyres, a reduction in gyral flow would cause the eastern boundary currents to warm up (owing to less subpolar input) and cause the western boundary currents to cool off (owing to less tropical input). The lack of a large anchovy biomass off Japan may be due to the fact that cooling here produces more sardines, whereas cooling produces more anchovies in the eastern boundary currents.

Collapses of sardines in the Pacific Ocean have occurred at the same time that there has been a shift from warmer to cooler global temperature regimes; the reverse (the increased abundance of these populations) has been parallel to the shift of cool to warm global temperature regimes. Global temperatures, of both air and sea, appear to coincide with the regime events taking place in the sardine and anchovy populations, but the cause in each region may be a manifestation of some other event associated with the global temperature changes. As yet, we have not been able to determine what triggers the changes in each location.

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