Regime shifts in the Humboldt Current ecosystem

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Abstract

Of the four major eastern boundary currents, the Humboldt Current (HC) stands out because it is extremely productive, dominated by anchovy dynamics and subject to frequent direct environmental perturbations of the El Niño Southern Oscillation (ENSO). The long-term dynamics of the HC ecosystem are controlled by shifts between alternating anchovy and sardine regimes that restructure the entire ecosystem from phytoplankton to the top predators. These regime shifts are caused by lasting periods of warm or cold temperature anomalies related to the approach or retreat of warm subtropical oceanic waters to the coast of Peru and Chile. Phases with mainly negative temperature anomalies parallel anchovy regimes (1950–1970; 1985 to the present) and the rather warm period from 1970 to 1985 was characterized by sardine dominance. The transition periods (turning points) from one regime to the other were 1968–1970 and 1984–1986. Like an El Nino, the warm periods drastically change trophic relationships in the entire HC ecosystem, exposing the Peruvian anchovy to a multitude of adverse conditions. Positive temperature anomalies off Peru drive the anchovy population close to the coast as the coastal upwelling cells usually offer the coolest environment, thereby substantially decreasing the extent of the areas of anchovy distribution and spawning. This enhances the effects of negative density-dependent processes such as egg and larval cannibalism and dramatically increases its catchability. Increased spatial overlap between anchovies and the warmer water preferring sardines intensifies anchovy egg mortality further as sardines feed heavily on anchovy eggs.

Food sources for juvenile and adult anchovies which prey on a mixed diet of phyto- and zooplankton are drastically reduced because of decreased plankton production due to restricted upwelling in warm years, as demonstrated by lower zooplankton and phytoplankton volumes and the diminution of the fraction of large copepods, their main food source.

Horse mackerel and mackerel, the main predators of anchovy, increase predation pressure on juvenile and adult anchovies due to extended invasion into the anchovy habitat in warmer years. In contrast to these periods of warm and cold temperature anomalies on the decadal scale, ENSO events do not play an important role for long-term anchovy dynamics, as the anchovy can recover even from strong ENSO events within 1–2 years. Consequently, the strong 1972–1973 ENSO event (in combination with overfishing) was not the cause of the famous crash of the Peruvian anchovy fishery in the 1970s.

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Contents

1. Introduction

Understanding the role of natural variability, occurring over a variety of time scales, is essential if we are to effectively manage marine living resources. One way to explore how ecosystems will react to global changes is to search for causal relationships of past patterns in natural variability. Evidence is accumulating that marine ecosystems undergo large-scale, decadal fluctuations which seem to be driven by climate forcing (Stenseth, Mysterud, Ottersen, Hurrell, Chan, & Lima, 2002) as is clearly demonstrated for the North Atlantic (e.g. Alheit & Hagen, 1997; Alheit & Hagen, 2002; Beaugrand, 2004; Beaugrand, Reid, Ibanez, Lindley, & Edwards, 2002; Fromentin & Planque, 1996), the North Pacific (e.g. Beamish, 1995; Hare & Mantua, 2000; Mantua, 2004; Wooster & Zhang, 2004) and eastern boundary systems (e.g. Alheit & Hagen, 2001; Chavez, Ryan, Lluch-Cota, & Niquen, 2003). Shifts in climate regimes can re-organize marine communities and trophodynamic relationships and induce changes in the mix of dominating species over decadal time scales. Long-term biological time series are important for retrospective analysis of decadal-scale climate impact on marine ecosystems and resulting ecosystem regime shifts. Fish populations usually provide longer records than other biological components of marine ecosystems because of their economic importance. The dynamics of exploited fish populations are affected by environmental variability as well as by human activities (fishing, habitat alteration) and retrospective studies will help to distinguish between the two effects. Although the potential impact of climate variability on marine ecosystems and their fisheries has been described in a number of cases, rigorous studies of these relationships were started only in the

1990s. This was certainly stimulated by the world-wide public awareness of global changes and the predicted greenhouse effect. The initiation of global international research programmes such as the World Climate Research Programme (WCRP) and the International Geosphere-Biosphere Programme (IGBP) vastly improved co-operation across disciplinary boundaries accumulating new knowledge on climate variability and ecosystem regime shifts, particularly on the decadal scale.

Small pelagic fish such as sardine, anchovy, herring and others represent about 20–25% of the total annual world fisheries catch (Hunter & Alheit, 1995). They are widespread, occur in all oceans and support important fisheries all over the world. They respond dramatically and quickly to changes in ocean climate. Most are highly mobile, have short, plankton-based food chains and some even feed directly on phytoplankton. They are short-lived (3–7 years), highly fecund and some can spawn all year round. These biological characteristics make them highly sensitive to environmental forcing and extremely variable in their abundance. Dramatic, sometimes hundredfold, changes in abundance over a few decades are characteristic for small pelagics, and well-known examples include the Japanese sardine, the Californian sardine, sardines and anchovies in the Humboldt Current (HC), sardines in the Benguela Current and herring in European waters (Alheit & Hagen, 1997; Schwartzlose et al., 1999). Their drastic stock fluctuations often resulted in catastrophic consequences for fishing communities, regions and even entire countries (Alheit & Hagen, 2002; Glantz & Thompson, 1981). Their dynamics thus have important economic as well as ecological consequences, as they are also important food sources for larger fish, seabirds and marine mammals. The collapse of small pelagic fish populations is often accompanied by sharp declines in marine bird (Crawford & Jahncke, 1999) and mammal populations (Trillmich & Ono, 1991) that depend on them for food. Major changes in abundance of small pelagic fishes are paralleled by marked changes in ecosystem structure, e.g., in abundance and species composition of zooplankton (Alheit & Bernal, 1993; Cury et al., 2000). Often they have been the first clear indicators for ecosystem regime shifts.

The HC ecosystem, as all eastern boundary currents, is dominated by anchovies and sardines. For a better understanding of its dynamics, the fisheries agencies of Chile and Peru, particularly the Instituto del Mar del Peru (IMARPE), started, as early as 1960, the collection of long-term time series of physical and biological variables. We will analyse these time series and present the evidence for past regime shifts in the HC ecosystem. During the Workshop on Regime Shifts in Villefranche-sur-Mer in April 2003, regime shifts were defined in a pragmatic way as ''changes in marine system function that are relatively abrupt, persistent, occurring at a large spatial scale, observed at different trophic levels and related to climate forcing'' (DeYoung, Harris, Alheit, Beaugrand, Mantua, & Shannon, 2004). We will investigate how far this concept applies to the HC ecosystem and try to answer the following questions: Are there different regimes in the HC ecosystem? Is the shift or transition from one to another regime abrupt or gradual? Is it possible to pinpoint decisive short periods when a new regime is initiated? How long do regimes last? Is the entire ecosystem affected by a regime change? What is the role of ENSO in regime changes?

2. Data

All catch data on anchovies and sardines until 1996 are from Schwartzlose et al. (1999). Data from 1997 and thereafter are from the official statistics of the Instituto del Mar del Peru (Lima, Peru) and the Instituto de Fomento Pesquero (Valparaiso, Chile). The data on anchovy catches off Talcahuano are from L. Cubillos (Instituto de Investigacion Pesquera, Talcahuano, Chile). Most figures present the catch data as percentages of the highest value, since trends of different fish stocks are best compared in this way. The Peruvian zooplankton data are from Carrasco and Lozano (1989). The samples were obtained by vertical hauls from 50 m depth using a Hensen net with 300-μm mesh size. Large coelenterates were removed prior to analysis. Sampling covered the entire Peruvian coastline and the offshore extension was 170 nm.

3. Dynamics of small pelagic fish populations

The commercial fisheries of the HC are dominated by five species: anchovy, sardine, horse mackerel, mackerel and hake (*Engraulis ringens*, *Sardinops sagax*, *Trachurus murphyi*, *Scomber japonicus* and *Merluccius gayi*). Over the last five decades, these fisheries have experienced dramatic changes in yields and species dominance (Alheit & Bernal, 1993; Schwartzlose et al., 1999). The most spectacular case, which is well documented in many fisheries textbooks, is the Peruvian anchovy fishery, once the largest fishery in the world with 13 million metric tonnes (MT) landed in 1970 (Tsukayama, 1983), which was 15% of the total world fisheries catch (Csirke, Guevara-Carrasco, Cardenas, Niquen, & Cipollini, 1996). According to Castillo and Mendo (1987), the real catch amounted to even 15 million MT, taking into consideration that underreporting of the real catches was frequent. The acquisition of reliable data on the total biomass of the four pelagic fish species for the entire period of their fisheries, which started in the early 1950s and 1960s, proved to be a problem. Catch data are available; however, they are often based on serious under-reports of the true catches (Castillo & Mendo, 1987; Menz & French, 1982). Although aware of the problem of under-reporting, we believe that the official statistics constitute the best data base available at present, and we assume that they reflect major trends in the fluctuations of fish stocks once the fisheries reached a certain level after their initiation. We are also aware of other factors which have a strong influence on trends in catch data, such as improved fishing methods, fishing bans, changes in mesh size and changes in vulnerability of fish caused by oceanographic factors.

Seven discrete, commercially exploited anchovy and sardine populations inhabit the HC: three anchovy populations and four sardine populations (Table 1). Their combined area of distribution reaches from 1°S off southern Ecuador in the North to about 42°S off central Chile. Anchovies and sardines are found all over the HC (Fig. 1). Depending on the physical state of the system (regime), anchovies and, particularly, sardines extend or contract their area of distribution considerably (Alheit & Bernal, 1993). Sardines carry out extended migrations, particularly when environmental conditions are adverse. There were apparently periods when the two large sardine populations of the HC (northern and central Peru, southern Peru and northern Chile) mixed so much that they could not be separated. Consequently, their catch data have been combined in this paper. Records of the last 50 years clearly show that anchovy and sardines exhibit alternating fluctuations in abundance, in spite of several thousand miles distance between the most northern and the most southern stocks (Fig. 3).

3.1. Anchovy

Anchovy was the dominant species in the HC until about 1976 (Fig. 2). The stock in northern and central Peru which supported the famous Peruvian anchovy fishery in the 1960s and 1970s is by far the largest and most important stock. From 1960 until 1971, its mean biomass was between 10 and 16 million

Table 1
Commercially exploited clupeoid populations in Humboldt Current

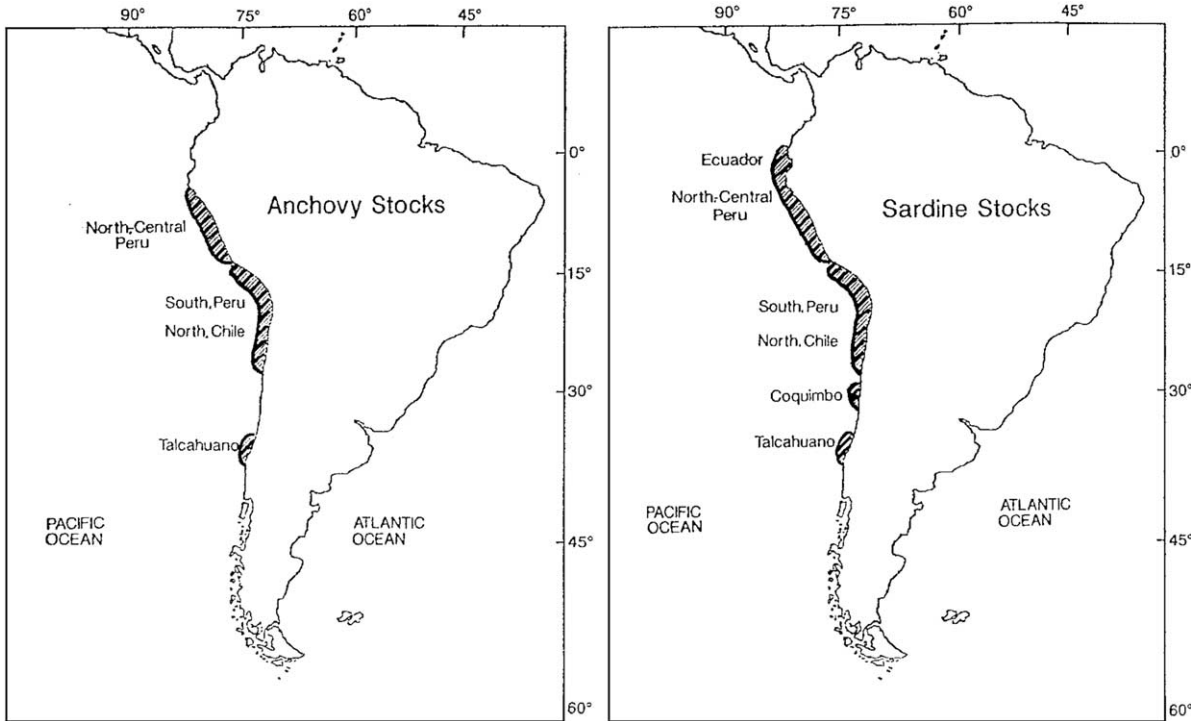| |
| --- |
| *Engraulis ringens* |
| Northern and central Peruvian anchovy |
| Southern Peruvian and northern Chilean anchovy |
| Talcahuano anchovy |
| |
| *Sardinops sagax* |
| Northern and central Peruvian sardine |
| Southern Peruvian and Northern Chilean sardine |
| Coquimbo sardine |
| Talcahuano sardine |

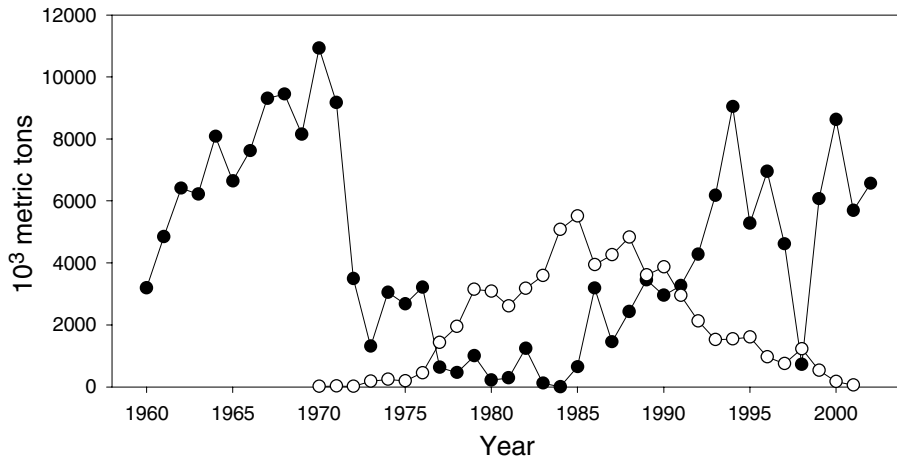Fig. 1. Schematic presentation of areas of distribution of anchovy and sardine stocks in HC ecosystem.

Fig. 2. Catches of anchovy and sardines in Humboldt Current. Full circles: northern and central Peruvian anchovy stock. Open circles: northern and central Peruvian sardine, and southern Peruvian and northern Chilean sardine (combined catches).

MT, according to the most recent estimates, peaking in 1970 and then decreasing dramatically to about 6 million MT in 1972 (Csirke et al., 1996). The 1960s, when the anchovy fishery was built up, may have been a period of exeptional and steadily high recruitment (Pauly & Palomares, 1989). The comparatively strong

ENSO of 1972 concentrated the anchovy near the coast where there were still some cold upwelling plumes; this made the anchovy extremely vulnerable to fishing. In 1972, for example, 4.4 million MT of anchovy were caught within 3 months in Peruvian waters (Tsukayama, 1983). Catches of the northern and central Peruvian anchovy stock peaked in 1970 with 10.9 million MT (Fig. 2), fell dramatically from 1970 to 1972, remained between 0.5 and 3 million MT until 1982 and decreased to an extremely low level during the early 1980s, particularly in response to the ENSO of 1982–1983. However, in 1984, the stocks recovered and catches rose to 3 million MT in 1986. Catches increased steadily thereafter to a peak of 9.8 MT in 1994, dropped to 1.0 million MT in 1998 because of another strong ENSO and have maintained at 6–9 million MT since. Comparing the annual catches of the three anchovy stocks in the HC, the almost simultaneous development from 1956 to 2001 is striking (Fig. 3).

3.2. Sardine

Sardine spawning (Zuta, Tsukayama, & Villanueva, 1983) and catches (Serra, 1983) were insignificant during the 1950s and 1960s. From 1964 to 1971, the only distinct spawning areas were in northern Peru and in northern Chile (Bernal, Robles, & Rojas, 1983). After 1971, the sardine expanded to the northern and southern extremities of both refuge areas. Sardine spawning off Peru from 1966 to 1968 was poor and limited to the region between 6° and 10°S (Zuta et al., 1983). After 1969, an increase of spawning was observed. After the ENSO event of 1972–1973, sardine spawning increased strongly, and the spawning area expanded considerably, although the new spawning areas did not overlap with those previously occupied by the anchovy. From 1973 on, the area of distribution expanded and abundance of sardines increased notably in Ecuador, Peru and Chile (Zuzunaga, 1985). Between 1976 and 1980, spawning increased further (Zuta et al., 1983). From 1964 to 1973, no eggs or larvae were observed in Chile south of 25°S. However, a new spawning area off Talcahuano was established subsequently (Bernal et al., 1983; Serra, 1983). Sardine spawning increased and the geographic distribution of spawning expanded during warm years. This phenomenon appears to be related to the more frequent coastal advance of the subtropical surface waters (Santander & Flores, 1983; Tsukayama, 1983). Catches of sardines in the HC ecosystem increased after the ENSO event of 1972–1973 when anchovy biomass and landings dropped further (Fig. 2). Off Coquimbo, in 1973, sardine catches increased significantly and in 1974 the sardine became the dominant species. Sardines had never before been caught in the region off Coquimbo (Mendez, 1987). Significant increases in the catches of the other three sardine stocks were observed several years after the 1972–1973 ENSO: in 1976 of the stocks of northern and central Peru and of the stock of southern Peru and northern Chile and in 1978 of the stock off Talcahuano (Figs. 2 and 3). Catches of the two large stocks rose steadily until 1985.

Interestingly, during the ENSO in 1983, the landings from the stocks off southern Peru and northern Chile and off Coquimbo peaked, whereas the stock off northern and central Peru was at a low. This resulted from extensive southward migrations of the sardines apparently trying to escape the warm waters coming from the north, and from sardines concentrating close to the coast, thus becoming more vulnerable to fishing (Mendez, 1987; Tsukuyama & Santander, 1987). According to Mendez (1987), it was no longer possible in 1983 to separate the sardine stocks from northern and southern Peru. Also in 1983, during one of the strongest ENSO events of the 20th century, Chile landed the highest sardine catches ever recorded, whereas total catches of pelagic fish in Peru dropped considerably. Two years thereafter, in 1985, when the sardines had turned northwards again, Ecuador had a year of record sardine catches (Serra & Tsukayama, 1988). There is evidence that the sardines caught off northern Chile had migrated considerable distances southward from Peru. Their fat content was reduced by more than 40%, resulting in a low-quality, lower-priced fish meal (Romo, 1985). Off Ecuador and Chile, sardine catches decreased from 1985 on (Csirke et al., 1996). In contrast, Peruvian sardine catches reached their peak in 1988 and then started to decrease. However, because of the typical large migrations of sardines, it is difficult to decide, based on catch data
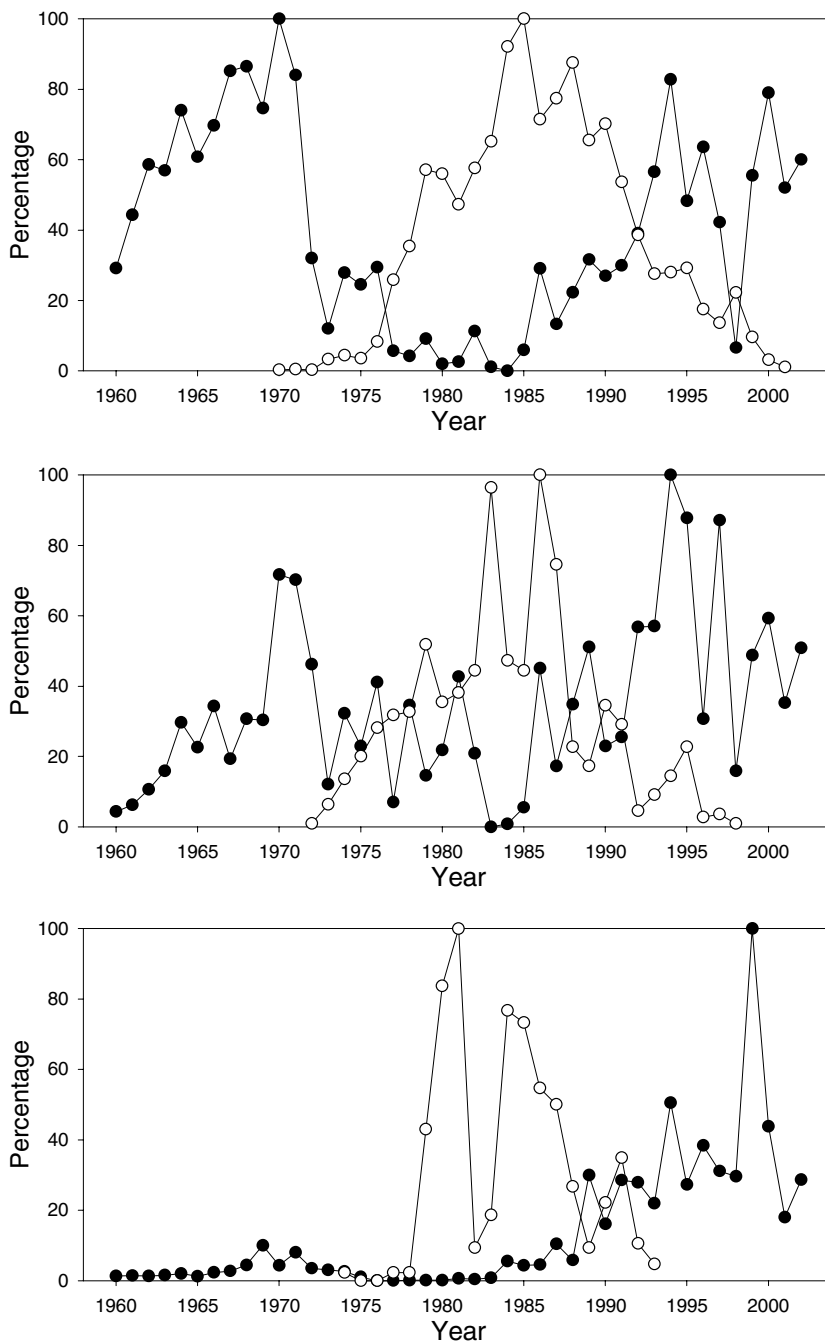
Fig. 3. Catches of anchovy and sardine stocks in Humboldt Current ecosystem expressed as percentages. The highest catch per stock corresponds to 100%. Upper graph: full circles – northern and central Peruvian anchovy (highest catch: 10.9 million MT in 1970); open circles – combined catches of northern and central Peruvian sardine and southern Peruvian and northern Chilean sardine (highest catch: 5.5 million MT in 1985) Central graph: full circles – southern Peruvian and northern Chilean anchovy (highest catch: 2.6 million MT in 1994); open circles – Coquimbo sardine (highest catch: 110 000 MT in 1986). Lower graph: full circles – Talcahuano anchovy (highest catch: 940 000 MT in 1999); open circles – Talcahuano sardine (highest catch: 86 000 MT in 1981).

alone, when the Humboldt sardine stocks really began their descending phase. Biomass data show that the 2-year-old recruits started a continuous down-turn after 1986 and the spawning biomass followed after 1987 (Csirke et al., 1996). Also, from the mid-1980s on, areas of distribution and concentration of sardines off Peru, started a slow decrease, whereas areas of distribution of anchovies increased at the same time (Csirke et al., 1996).

4. Evidence for regime shifts

All seven anchovy and sardine stocks show clear decadal variability in abundance and, in spite of the wide geographical distances between their habitats, they seem to swing in synchrony. When *E. ringens* supports high biomass, *S. sagax* exhibits low population levels and vice versa. Consequently, the HC ecosystem passes through alternating anchovy-dominated and sardine-dominated periods on the decadal scale. Critical periods of transition, turning points, were 1968–1970 when the famous Peruvian anchovy stock started to collapse, and 1985–88, when the HC system switched back from a sardine-dominated to an anchovy-dominated system. The fact that all seven clupeoid populations showed dramatic changes around these periods indicates the regime shift character of these processes. More and more additional biological evidence is being revealed which demonstrates a dramatic re-arrangement of the entire HC ecosystem during these transition periods.

4.1. Changes in the biota during 1968–1971

The HC ecosystem was affected in 1972–1973 by a very strong ENSO event, the first to attract the attention of the international scientific oceanographic community (Glantz & Thompson, 1981). However, the transition from an anchovy- to a sardine-dominated period started already as early as 1968, well in advance of the 1972–1973 ENSO event.

 (i) The biomass of the northern and central Peruvian anchovy stock fell from a peak of about 16 million MT in 1970 to about 6 million MT in 1972 (Csirke et al., 1996). Catches of Peruvian anchovy decreased dramatically from an all time high of 10.9 million MT in 1970 to 9.2 in 1971, 3.5 in 1972 and to 1.3 million MT in 1973 (Fig. 2). After 1968, the surplus production rate of anchovy, which is a more precise indicator of regime shifts than catches, turned negative (Jacobson et al., 2001).
 (ii) The anchovy recruitment collapse of 1971 began before the onset of the 1972–1973 ENSO (Csirke et al., 1996; Mendelsohn, 1989; Mendelsohn & Mendo, 1987; Pauly & Palomares, 1989).
(iii) Peruvian sardine spawning increased since 1969 (Zuta et al., 1983).
(iv) Relative abundance of sardine and horse mackerel increased in 1970 (Subsecretaria de Pesca, 1983).
 (v) Zooplankton volumes from Peruvian waters decreased drastically after 1968 and again after 1974 (Carrasco & Lozano, 1989) (Fig. 4).
(vi) Zooplankton biomass of northern Chile began decreasing in 1969 (Bernal et al., 1983).
(vii) Some of the strongest evidence for biological changes occurring in the HC prior to 1971 is presented by Loeb and Rojas (1988). They studied the interannual variation of ichthyoplankton composition and abundance relations off northern Chile from 1964 to 1983 and observed a marked shift in the relative abundance of larval fish of the non-fished mesopelagic species from 1969 to 1970. The abundance of mesopelagic species is not influenced directly by fishing activities and might, therefore, be a good indicator of environmental changes.

Interestingly, there was a secondary transition period in the HC from 1974 to 1976 when catches of all four sardine populations increased exponentially and the sardines expanded their spawning areas considerably (Fig. 3). At the same time, anchovy catches decreased further to low levels (Fig. 3) and zooplankton volumes off Peru took another downturn (Fig. 4).
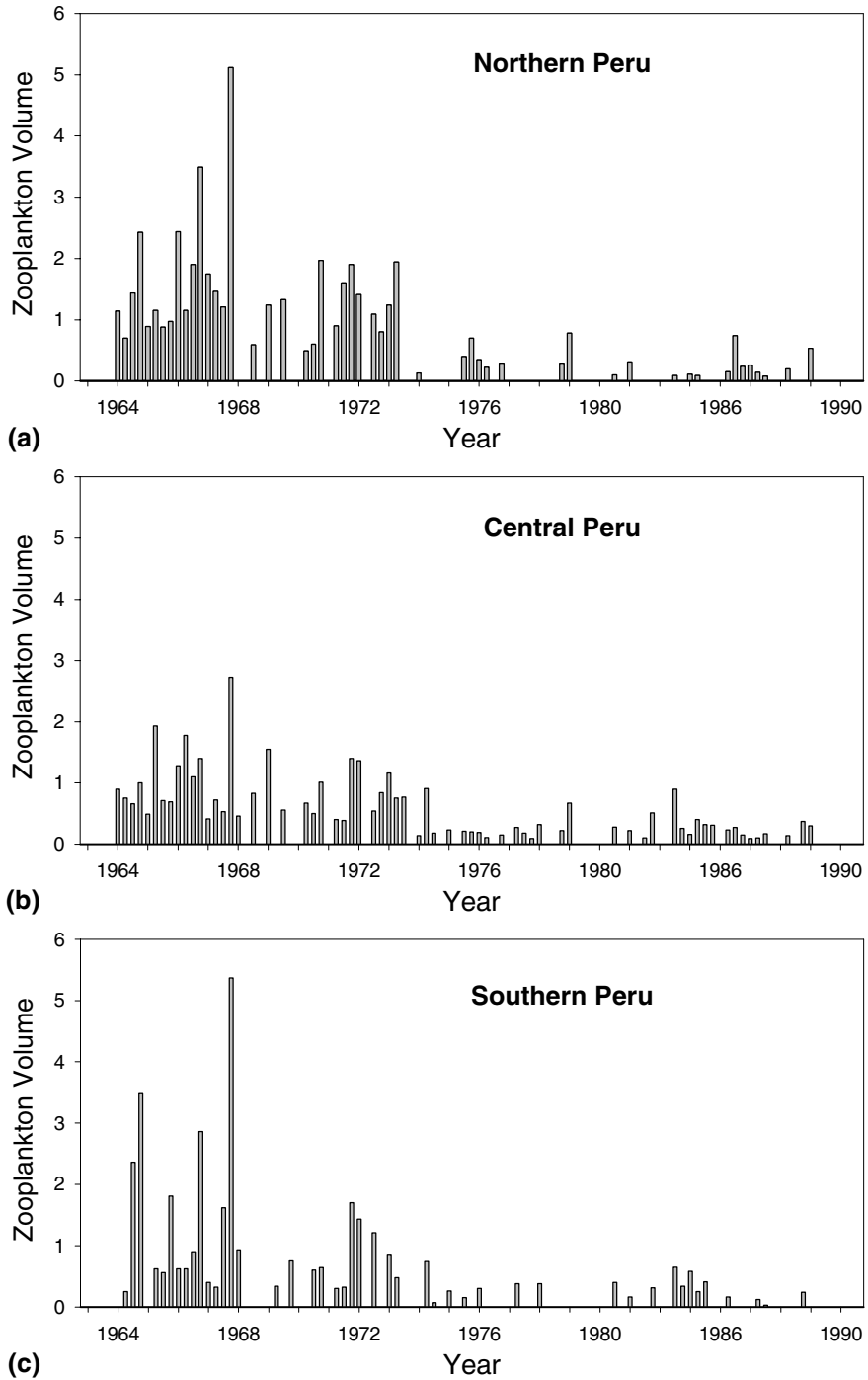
Fig. 4. Annual variation of zooplankton volumes off northern, central and southern Peru determined as ml/m^3. Data from Carrasco and Lozano (1989).
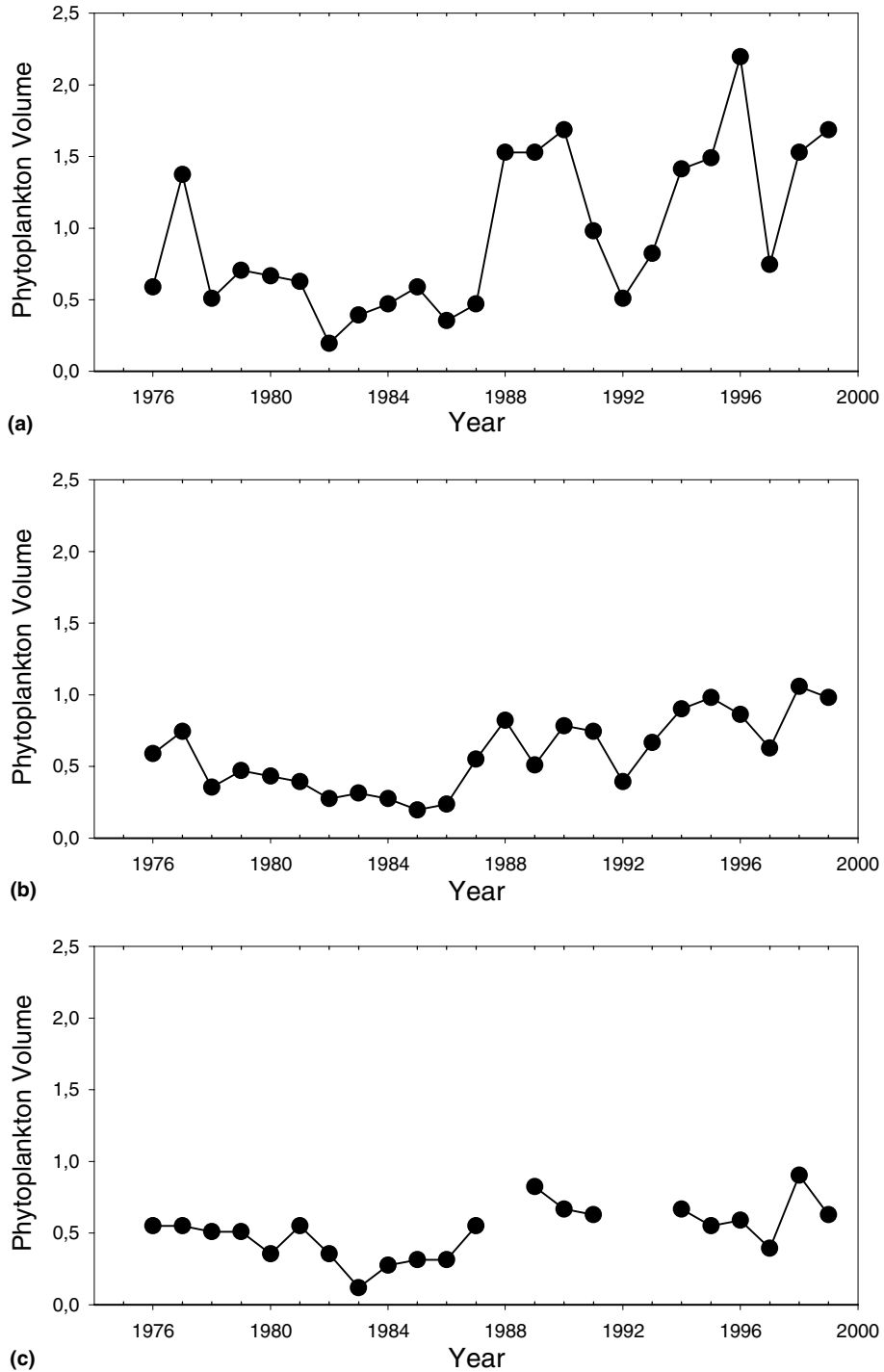
Fig. 5. Annual variation of phytoplankton volumes off Peru. Upper graph (a): from 0 to 30 nm off the coast; Central graph (b): from 30 to 60 nm off the coast; Lower graph (c): >60 nm off the coast. Modified after Sanchez (2000).

4.2. Changes in the biota during mid-1980s

In the 1980s, population trends reversed again. In August–September 1981, the spawning biomass of the northern and central Peruvian anchovy was estimated at 1.2 million MT applying the Daily Egg Production Method (Alheit, 1993; Santander, Alheit, & Smith, 1984). In 1982, recruitment from the 1981 year class was very poor and 1.2 million MT from the northern and central stock were caught (Schwartzlose et al., 1999). Consequently, the biomass of the once largest fish stock must have been very low before the onset of the 1982–1983 ENSO, very likely far below 1 million MT, as a result of excessive fishing pressure and poor recruitment (Alheit & Bernal, 1993). Tsukuyama and Santander (1987) report that, in 1983, Peruvian anchovy had the lowest biomass ever recorded which has been confirmed by more recent estimates (Csirke et al., 1996). After a long period with very low values, anchovy recruitment improved dramatically in 1984 which saw the best recruitment since 1970 (Csirke et al., 1996). Thus, this extremely low stock in the northern and central region off Peru virtually exploded to several million MT in 1984 (5 million MT) and 1985 (6 million MT) (Csirke et al., 1996), and 0.6 and 3 million MT were caught in 1985 and 1986, respectively (Schwartzlose et al., 1999). It is not known where this excellent recruitment originated from. Very few anchovies were caught during the 1982–1983 ENSO event. Arntz and Tarazona (1990) showed that some anchovies withdrew to deeper water (100 m) to survive the 1982–1983 ENSO. However, Barber, Chavez, and Kogelschatz (1985) reported that phytoplankton concentrations at these depths were too low to support large numbers of anchovies for any length of time. An alternative explanation might be that the recruitment of the northern and central stock off Peru came from the stock off southern Peru and northern Chile, where the effects of the 1982–1983 ENSO were less dramatic (Alheit & Bernal, 1993). Whatever caused this surprising recovery of the northern and central stock, it is obvious that the Peruvian anchovy can increase its population size rapidly and drastically when environmental conditions become favourable. After catches of all three anchovy stocks had declined to very low levels in 1983 and 1984 in response to a strong ENSO event during a sardine-dominated period, the two large stocks off Peru and northern Chile rose considerably again in 1986 and throughout the 1990s (Schwartzlose et al., 1999). Catches of the small anchovy stock off Talcahuano recovered already in 1984 (SUBPESCA, 2001). In contrast, in 1985, combined sardine catches off Peru and Chile reached their peak with 5.6 million MT and declined continuously thereafter up to the present (Schwartzlose et al., 1999). After extremely low values in the second half of the 1970s and, particularly, in the first half of the 1980s (Fig. 4), zooplankton volumes off Peru seem to have recovered towards the late 1980s, but, so far, have not reached the high values of the 1960s (Ayon & Guevara, 2003). A time series of phytoplankton volumes off Peru beginning in 1976 shows dramatic increases since 1986 in the areas between 30–60 and more than 60 miles offshore and since 1987 in the coastal region up to 30 nm offshore (Sanchez, 2000) (Fig. 5). Summing up, the HC ecosystem started to switch back in the mid-1980s from a sardine-dominated system as observed through the 1970s to an anchovy-dominated system which is still prevailing at the time of the writing of this paper (November 2003).

5. Trophodynamic relationships of anchovies

A better understanding of the trophodynamics of the anchovy, encompassing its main predators as well as its prey field, seems to be essential if we are to unravel relationships between climate variability and the HC ecosystem response. As regime shifts re-structure entire ecosystems, food chain processes and trophodynamics might be altered dramatically at the transition from one ecosystem state to another one. Altered trophodynamics, in turn, might even accelerate and aggravate regime shifts. Evidence for such changes in trophodynamics concurrent with regime shifts in the HC is accumulating.

5.1. Anchovies and sardines preying on meso-zooplankton and phytoplankton

Dynamics of Peruvian anchovy and meso-zooplankton seem to correspond rather well. Zooplankton volumes decreased drastically around 1968, prior to the drop of anchovy biomass and catches in 1970 (Fig. 6). Then in 1974, prior to the further down-turn of anchovy catches in 1976, zooplankton biomass decreased to very low levels and stayed low until the late 1980s (Ayon & Guevara, 2003). It is not clear when zooplankton biomass started a moderate recovery in the second half of the 1980s, as few plankton surveys were carried out during this period. However, it seems that anchovy recruitment, biomass and catches improved prior to the zooplankton biomass increase. In 1986, anchovy biomass was estimated to be around 5 million MT and catches had already risen to 3.5 million MT, but zooplankton biomass still remained rather low. Consequently, whereas it seems very likely that the decrease of the anchovy in the early 1970s was caused partially by a decrease of its food source, bottom-up control via the zooplankton, there is
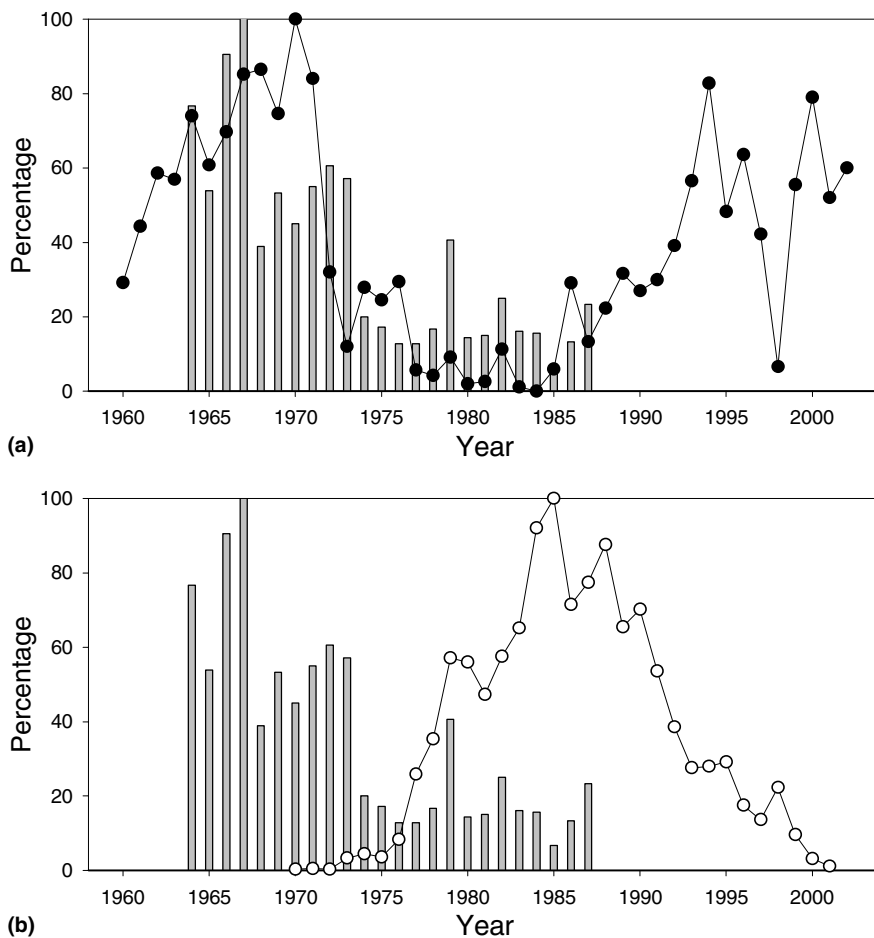

Fig. 6. Annual variation of anchovy (northern and central Peruvian stock; full circles; upper graph) and sardine (northern and central Peruvian, and southern Peruvian and northern Chilean stock; open circles; lower graph) catches and zooplankton volumes (columns), all expressed as percentages. The highest catch or volume corresponds to 100%. Zooplankton volumes were calculated by summing all values from the different seasons and sub-regions in Peru (Carrasco & Lozano, 1989). The highest value was 21.64 ml/m³.

no clear indication whether the early phase of the anchovy recovery in 1984–1986 was based on a recovery of zooplankton. Sardine dynamics off Peru are opposite to those of anchovy and zooplankton volume development. Sardine catches increased considerably when zooplankton volumes were low from the mid-1970s to the mid-1980s and started to decrease again when the zooplankton presumably recovered moderately in the second half of the 1980s (Fig. 6). Understanding the trophic interactions between anchovies, sardines and zooplankton might be a key to understand their dynamics in the HC, however, information on food and feeding relationships of anchovies and sardines from eastern boundary currents is rare and contradictary. Only recently, van der Lingen (2002) studying feeding relationships of sardines in the southern Benguela current off South Africa clarified the feeding spectra of sardines and anchovies.

Anchovies and sardines alternate between two different modes of feeding: filtering for smaller and biting for larger particles (Louw, van der Lingen, & Gibbons, 1998). The two species are omnivorous preying both on phytoplankton as well as on zooplankton (Alamo & Bouchon, 1987; Espinoza & Blaskovic, 2000; van der Lingen, 2002), however, the extent to which they feed on either phyto- or zooplankton is a matter of controversy (van der Lingen, 2002). Their ability to build up large amounts of biomass has often been ascribed to their intensive feeding on phytoplankton (Walsh, 1981), but more recent studies in the southern Benguela current clearly demonstrated that both, anchovies (James, 1988) and sardines (van der Lingen, 2002), are primarily zooplanktivores that partition their food resources by size. Sardines feed on smaller particles, including phytoplankton, mainly by filter-feeding. In contrast, the main dietary components of the Benguela anchovy are larger prey items such as large calanoid copepods and euphausiids which are ingested by particulate-feeding (James, 1987; van der Lingen, 2002). Sardine and anchovy recruits caught in the same schools in the southern Benguela Current had fed on copepods of different sizes with sardines preferring significantly smaller crustaceans than anchovies (Louw et al., 1998). It is likely that phytoplankton is a more important food source for sardines than for anchovies (van der Lingen, 2002).

The intensive dietary studies on Benguela clupeoids by James (1988) and van der Lingen (2002) confirm the results of similar studies in other ecosystems. For Peruvian waters, Konchina (1991) showed that anchovies feed mainly on large copepods and euphausiids, whereas sardines prey preferentially upon small herbivorous copepods and tunicates. The size of food particles ingested by anchovy was 2.5 times larger than sardine prey and phytoplankton was more important in the diet of sardine than that of anchovy. Also, phytoplankton contributed more to the diet of sardine off Japan than to that of anchovy, and sardine consistently ingested smaller copepods than did anchovy (Li, Kawasaki, & Honda, 1992). Consequently, the differences in the diet between anchovies and sardines are globally consistent: sardines feed on smaller organisms closer to the base of the foodweb (van der Lingen, 2002). Models developed for (i) filter-feeding on phytoplankton, (ii) filter-feeding on micro-zooplankton and (iii) particulate-feeding on mesozooplankton showed that sardines can maintain themselves under all three scenarios whereby maximum growth is attained at high microzooplankton concentrations. In contrast to the broad-spectrum planktivorous sardine, the anchovy in the Benguela is a specialist planktivore that can survive only by particulate-feeding on mesozooplankton (Beckley & van der Lingen, 1999; James, Probyn, & Hutchings, 1989).

Zooplankton off Peru was collected using a net with 300-µm mesh size (Carrasco & Lozano, 1989). Such a net does not retain particles of the size preferred by sardines. van der Lingen (2002) demonstrated a close correspondence between the size frequency distributions of available (in plankton samples) and ingested prey, and between the composition of the ambient food environment and ingested prey. His findings show that the sardine diet is dominated numerically by small-sized prey, primarily dinoflagellates. The main items in the diet are cyclopoid and calanoid copepods and crustacean eggs. In spite of the numerical dominance of phytoplankton in the diet, the main dietary carbon contributions came from crustacean zooplankton and anchovy eggs. Similar results have been presented by Miller, Brodeur, and Emmett (2000) for the Californian sardine. Non-selective filter-feeding seems to be the main feeding mode of sardine on a global scale

(van der Lingen, 2002). When transferring these results to the HC, one has to bear in mind that the samples in van der Lingen's study were restricted in time (early southern hemispheric summer) and space (southern part of southern Benguela current and Agulhas Bank). It is therefore probable that sardines in other environments with a higher ambient concentration of dinoflagellates and diatoms, such as the upwelling regions of the HC, ingest a higher percentage of phytoplankton.

These studies on diets of anchovies and sardines in different eastern boundary currents elucidate the dynamics of anchovies, sardines and zooplankton in the HC under different regimes. The zooplankton as collected with a 300-μm Hensen net during the anchovy regime in the 1960s had relatively high volumes, presumably because of a relatively large fraction of large copepods, the primary food source for anchovies (Konchina, 1991; Li et al., 1992; van der Lingen, 2002). This high amount of large copepods was a prerequisite for maintaining a large anchovy population. When their main food source, the large copepods, started to decrease in the late 1960s, as is indicated by the decrease of zooplankton volumes (Fig. 4), the anchovy population also began to decrease dramatically. The further reduction of zooplankton volume was followed by a further decrease of the anchovy. The recovery of the anchovy populations in the second half of the 1980s might have been supported by the moderate recovery of large copepods. The sardines, in turn, were not affected by the reduced populations of large copepods in their feeding environment in the 1970s and the first half of the 1980s, as they are able to feed on much smaller particles than anchovies. Whether their primary food source of smaller particles such as small copepods increased during this period is not known as these organisms are not retained by a 300-μm plankton net. However, below we will present some indirect evidence for such a scenario.

5.2. Predation on anchovy eggs

Egg cannibalism in anchovies has been reported for the HC (Alheit, 1987; Santander, Alheit, MacCall, & Alamo, 1983), the California Current (Hunter & Kimbrell, 1980; MacCall, 1981), the Benguela Current (Valdés-Szeinfeld, 1991), Japanese waters (Hayasi, 1967) and the Patagonian shelf (de Ciechomski, 1967). Its contribution to daily egg mortality was estimated to be 22% in the HC (Alheit, 1987), 28% in the California Current (MacCall, 1981) and up to 80% in the Benguela Current (Valdés, Shelton, Armstrong, & Field, 1987). Egg cannibalism is a density-dependent process.

Not only anchovies, but also other fish species prey upon anchovy eggs, e.g., 40% of mackerel and horse mackerel stomachs were positive for anchovy eggs at a certain period in 1967 with a mean of 517 eggs per stomach (Muck & Sanchez, 1987). Anchovy eggs seem to be a primary food source for sardines. Sardines feeding on anchovy eggs have been reported from the HC (Alheit, 1987; Santander et al., 1983) and from the Benguela Current (Valdés-Szeinfeld, 1991; van der Lingen, 2002). About 86% of the Humboldt (Alheit, 1987) and 88% of Benguela sardines examined had anchovy eggs in their stomachs and predation of Benguela sardines on anchovy eggs could account for up to 56% of total anchovy egg mortality (Valdés-Szeinfeld, 1991). Anchovy eggs contributed about 15% of the dietary carbon of Benguela sardines, in some instances even >50% (van der Lingen, 2002).

5.3. Predation on anchovy juveniles and adults by mackerel and horse mackerel

Horse mackerel and mackerel are opportunistic predators, feeding exclusively on anchovy when these are abundant and vulnerable and switching to a diet dominated by zooplankton (mainly copepods and euphausiids) when anchovy is less abundant and/or vulnerable (Muck & Sanchez, 1987). The extent of their predation depends on the overlap of the areas of distribution of the three species that, in turn, is regulated by temperature. Both predators prefer higher ambient temperatures (horse mackerel 17–24 °C; mackerel 16–25 °C) than anchovy (15–20 °C) and are usually farther offshore than the anchovy (Muck & Sanchez, 1987). Consequently, overlap and predation increase when SSTs increase during El Nino, when the biomass

of both predators in the area of distribution of anchovy also increases (Muck & Sanchez, 1987). When SSTs decrease, horse mackerel and mackerel seem to withdraw from the anchovy main distribution area. Muck and Sanchez (1987) assume that the massive increase of anchovy biomass in 1984–1985 was due to horse mackerel and mackerel leaving the anchovy area because of a cold La Nina phase. They estimated that the anchovy consumption exerted by horse mackerel and mackerel was well above the corresponding estimates of other predators such as bonito, seals and birds. Horse mackerel was by far the most important predator of anchovy in the 1970s (Pauly & Palomares, 1989).

6. Impact of physical forcing on food chain processes

The regime shift from an anchovy-dominated system to a sardine-dominated system in the early 1970s and the return in the second half of the 1980s seem to be related to the approach and retreat of warm oceanic water masses from the tropics and subtropics towards the coasts of Peru and Chile (Santander & Flores, 1983; Tsukayama, 1983). The "warm water phase" of the HC ecosystem from 1968 to 1985 seems to have set in motion a number of key food chain processes which have initiated the decrease of the anchovy populations. The effects of such a "warm water phase" might be viewed as those of a long-lasting, very moderate ENSO. It seems to have similar influences on the anchovy populations as an ENSO event, e.g.:

(i) During warm periods, the area of distribution of anchovy is reduced, which leads to higher densities and increased food competition (Tsukayama & Alvarez, 1981). The reaction of anchovy to the intrusion of warm ENSO waters is to move close to the coast where cold water pockets may remain for some time (Muck & Sanchez, 1987; Yanez, Barbieri, Silva, Nieto, & Espíndola, 2001). Valdivia (1978) reports that during the 1972 ENSO, anchovies were so highly concentrated on the coast and, hence, so vulnerable to the fishery, that 170,000 MT were caught on a single day. It seems likely that a "warm water phase" has similar average effects on the anchovy to an ENSO event. The schools will concentrate nearer to the coast and egg cannibalism and catchability will increase. At the same time, sardine will move closer to the coast, similar to its ENSO behaviour (Yanez et al., 2001). Consequently, predation pressure on anchovy eggs and, maybe, larvae will increase.

(ii) Also, during warm periods, as in spring and summer or during ENSO, two important anchovy predators, horse mackerel and mackerel, migrate deeper into the anchovy area (Muck & Sanchez, 1987) increasing predation pressure on anchovy eggs, juveniles and adults. During ENSO years, the biomass of mackerel and horse mackerel in the anchovy habitat more than doubled and it increased 3.5-fold at the peak of the 1972 and 1976 ENSO. The timing and the dependence of these migrations on coastal SST are proven through ichthyoplankton surveys, fishery catch data and the temperature preferences of both species (Muck & Sanchez, 1987). Coastal SST seems to be an adequate parameter for quantification of the distributional overlap between anchovy and its two predators. Hence, it could be considered as a measure of predation on anchovy.

(iii) When zooplankton biomass values of a normal year (1981) off Peru were compared with those of an ENSO year (1983), it was found that they had markedly decreased. This decrease was mainly due to the copepods which had decreased to about one sixth of their normal abundance (Carrasco & Santander, 1987). During the development of the 1997/1998 ENSO, González (2000) observed a shift in the size spectrum of crustacean zooplankton towards small-sized copepods from pre-ENSO to fully developed ENSO conditions. Abundances of small cyclopoid copepods (*Oncaea* spp. and *Oithona* spp.) increased from 3-fold to 1 order of magnitude (*Oithona*) as the ENSO event developed from January 1997 to January 1998. It is assumed that the decrease of zooplankton volumes and biomass off Peru and northern Chile between 1968 and 1974 was due to a similar shift in size distribution of copepods creating a feeding environment more favourable for sardines than anchovies.

7. Regime shift scenario

Based on our present knowledge, the following chain of events leading to the regime shifts observed from the 1960s to the present is suggested:

Phase 1. Around 1968–1971, warm oceanic subtropical water masses move nearer to the Peruvian and Chilean coasts (Santander & Flores, 1983; Zuta et al., 1983). This pushes the anchovy closer to the coast, increasing density-dependent egg cannibalism (Alheit, 1987; Santander et al., 1983) and augmenting its catchability (Csirke, 1989). At the same time, a larger proportion of horse mackerel and mackerel intrude into the anchovy area of distribution because of elevated SSTs and enhance predation pressure on anchovy eggs as well as on adults and juveniles (Muck & Sanchez, 1987). The warm water masses change the composition of the coastal plankton communities as evidenced by a drastic change in the larval fish community (Loeb & Rojas, 1988) and the reduction of zooplankton volumes off northern Chile (Loeb & Rojas, 1988) and Peru (Carrasco & Lozano, 1989). This reduction of zooplankton volumes probably indicates that the abundance of the primary food source of the mainly particulate-feeding anchovies, the large calanoid copepods (Beckley & van der Lingen, 1999; Konchina, 1991; van der Lingen, 2002), has decreased in the now warmer coastal waters, just as it happens during ENSO periods (González, 2000). All these processes lead to a decrease of anchovy biomass (Pauly & Palomares, 1989; Tsukayama, 1983; Zuta et al., 1983) and catches, a down-turn in the surplus production rate (Jacobson et al., 2001) and a recruitment collapse in 1971 (Mendelsohn, 1989; Mendelsohn & Mendo, 1987; Pauly & Palomares, 1989). Already in a state of collapse due to this interplay of adverse physical and biological processes, the anchovy populations were exposed to continuous heavy fishing pressure during this entire period. Then, in 1972, they were hit by a massive ENSO event, aggravating their situation. However, interestingly, they managed to recover rather quickly from this ENSO as demonstrated by their increased biomass (Pauly & Palomares, 1989) and catches (Fig. 3) from 1974 to 1976. The sardine did not play any major role in the coastal system of Peru during the whole period, particularly up to the 1972–1973 ENSO. Its spawning had increased since 1969 (Zuta et al., 1983) and, also, its relative abundance had increased since 1970 (Subsecretaria de Pesca, 1983). Catches increased after the ENSO event in 1972–1973, but on a rather low level. It is not clear which environmental processes improved conditions for sardines.

Phase 2. A climate event in the North Pacific, initiated by a geographic shift and an extension of the Aleutian Low, caused a warming trend in many Pacific ecosystems in winter 1976/1977 (Mantua, 2004), which is now called the North Pacific regime shift (Hare & Mantua, 2000). At the same time, may be in relation to North Pacific climate processes, SSTs in the coastal waters of the HC system increased further. This probably strengthened all the processes described above: zooplankton volumes and anchovy biomass collapsed further to very low values (Figs. 3 and 4). In contrast, sardine stocks, as indicated by catches, increased exponentially from 1976 to 1980. This caused increased predation pressure on anchovy spawn as sardines feed to a large extent on anchovy eggs (Alheit, 1987; van der Lingen, 2002), so compensating for reduced density-dependent anchovy egg cannibalism. However, the explosion of the Humboldt sardine catches cannot be a consequence of the climatic changes in the North Pacific. The jump in sardine catches was from 1976 to 1977. As sardines are 2–3 years old when they show up in the commercial catches, excellent sardine recruitment must have happened before 1976. Also, zooplankton volumes were reduced before 1975. Consequently, it is not known whether the climate event of 1976 in the North Pacific triggered any additional processes with an adverse effect for HC anchovy. However, it aggravated already on-going food chain processes that were detrimental for anchovies.

Phase 3. In the mid-1980s, the warming phase came to an end and the warm waters started their retreat from the coast (Yanez et al., 2001). Phytoplankton biomass started to increase moderately in 1984 and 1985 and, then, considerably from 1986 and 1987 on (Sanchez, 2000). Unfortunately, only a few zooplankton surveys were carried out in Peruvian waters in the second half of the 1980s. It seems that zooplankton volumes began to recover moderately in the second half of the 1980s (Ayon & Guevara, 2003). Following

the ENSO in 1982–1983, the Peruvian anchovy had excellent recruitment in 1984 and 1985 and the population rose from an extremely low biomass, probably well below 1 million MT, to catches of 3 million MT in 1986. Catches of Chilean anchovies also increased dramatically. At the same time, after 1984, sardine recruitment began to decrease in Chile (Yanez et al., 2001) and, after 1986, in Peru (Csirke et al., 1996) and sardine catches started to decrease off Peru and Chile after 1985 (Schwartzlose et al., 1999).

8. Conclusions

The data presented and analysed answer the questions posed in Section 1. Are there different regimes in the HC ecosystem? Clearly, alternating anchovy- and sardine regimes have been observed in the HC ecosystem. Three of them have been described in this analysis. There is evidence for a fourth regime in the 1930s and 1940s, a sardine-dominated one, based on accumulation rates of fish scales in sediment cores (Schwartzlose et al., 1999). Is the shift or transition from one to another regime abrupt or gradual? The turn-over from anchovies to sardines in the late 1960s and the early 1970s lasted several years. The ecosystem started to change around 1968–1969 at the peak of anchovy dominance with the approach of warm subtropical oceanic waters to the HC coast, the decline of zooplankton volumes, the re-arrangement of the larval fish community, the increase of sardine spawning and the down-turn of the anchovy surplus production rate. This was followed in 1970–1971 by the decline in anchovy recruitment and the collapse in anchovy biomass and catches. Finally, between 1974 and 1976 zooplankton volumes decreased to new minima, anchovy catches declined further and catches of all four sardine populations increased exponentially. Whereas the reaction of single populations or ecosystem components was abrupt, e.g., drastic changes happened from one year to the other, the period of re-arrangement of the entire ecosystem from the physical trigger to sardine dominance took several years. A similar transition period of several years was observed for the return to an anchovy-dominated system in the second half of the 1980s.

Is it possible to pinpoint decisive short periods when a new regime is initiated? It was from 1968 to 1970 when the advance of warm water masses triggered the drastic changes described above leading to a sardine regime and from 1984 to 1986 when the warm period ended, resulting in the return to another anchovy regime. Interestingly, both transition periods coincide with the peak in biomass and catches of anchovies (1968–1970) and sardines (1984–1986). How long do regimes last? It is rather difficult to determine the exact duration of a regime because different components of the ecosystem are involved and the alternation between dominant species shows considerable overlaps. For example, from 1986 to 1995, catches of both, anchovies and sardines, were very well above 1 million MT, respectively. The most precise measurement of a regime is probably the duration of the physical forcing signal, in the HC case the period from the start of the advance (1968–1970) to the beginning of the retreat (1984–1986) of the warm water masses. This period lasted 16 years and should be called the "sardine regime". However, after 1986, sardine biomass and catches were still high, but decreased considerably (Fig. 3). Anchovy biomass and catches were also relatively high after 1986, but, in contrast to sardine, they increased continuously.

Is the entire ecosystem affected by a regime change? Apparently, a regime change in the HC is triggered by the advance and retreat of warm subtropical oceanic water masses towards the Peruvian and Chilean coasts. The underlying, probably basin-scale, physical processes are not clear; however, they seem to lead to persistent "warm" and "cold" phases in the coastal waters of the HC (Yanez et al., 2001). These warming and cooling trends set in motion a number of changes in trophic relationships. Some of these changes seem to work their way up in food chains, as changes in phytoplankton, zooplankton and fish populations have been observed in consecutive years, indicating bottom-up control as described by Cury et al. (2000) for some upwelling systems. Other changes seem to occur simultaneously and independently at different trophic levels, being induced by fish migrations resulting in intensification or reduction of predation pressure on different components of the ecosystem, as is typical for top-down control. In any case, the entire ecosystem

seems to be re-arranged, from phytoplankton to top predators (e.g., horse mackerel, mackerel). Summing up all these observations, it becomes clear that the definition of regime shifts by DeYoung et al. (2004) can be applied to the decadal-scale dynamics of the HC ecosystem as recorded over the last 50 years.

What is the role of ENSO in regime changes? ENSO is the strongest climate signal of global impact that affects marine ecosystems, fish stocks and fisheries and that occurs with a frequency of 3–7 years. However, clearly, long-term dynamics of the anchovy and sardine populations in the HC are controlled at the decadal time scale. Single ENSO events can dramatically affect these populations, but, although ENSO is commonly thought of having long-lasting detrimental effects on the anchovy, it turns out that ENSO causes short-term perturbations in the dynamics of anchovy from which it seems to recover rather quickly within one or two years during the following La Nina phases. The data-rich time series collected by IMARPE span the last 40 years. During this period, the HC system was affected by three very strong ENSO events: 1972–1973, 1982–1983 and 1997–1998. Interestingly, they occurred each time at different phases in the long-term anchovy/sardine cycle. In 1972–1973, the anchovy was hit by a strong ENSO when in its descending phase, just after the HC ecosystem had started to change from an anchovy- to a sardine-dominated system. Biomass and catches were reduced by ENSO, but recovered thereafter again before continuing their decline caused by the changing regime conditions. In 1982–1983, at the peak of the sardine biomass and catches, just before the regime changed back to anchovies, another very strong ENSO affected the anchovy population that was already at an extremely low level. Surprisingly, one year later in 1984, the anchovy began a very successful recovery that continues up to now (November 2003). In 1997–1998, the anchovy was struck again by a very strong ENSO when probably at the peak of the present anchovy regime. Catches recovered very quickly and reached pre-ENSO levels. Independently of the timing of ENSO, the anchovy recovered after each event. Single ENSO events do not seem to affect the duration of an anchovy or sardine regime nor the shift from one to the other. Moreover, strong ENSO events occur during anchovy (cold) as well as during sardine (warm) regimes.

Hence, whereas a strong ENSO is only a short-term perturbation for the HC anchovy, its long-term dynamics are controlled by climate variability on the decadal scale leading to alternating anchovy and sardine periods induced by regime shifts which re-structure the entire ecosystem. Single ENSO events do not seem to affect the long-term dynamics of the anchovy. The famous spectacular crash of the Peruvian anchovy fishery has often been ascribed to a combined negative impact of overfishing and the 1972–1973 ENSO and still serves as a text book example. Csirke (1989) reported that fisheries scientists and administrators tended to agree that the anchovy collapse was caused by a combination of both fishery-related factors and El Nino-related adverse environmental conditions. However, as shown above, in 1968, the HC ecosystem was already on its way to a new regime, a sardine-dominated system, and the Peruvian anchovy stock had entered its environmentally induced descending phase before the onset of the 1972/1973 ENSO (Alheit & Bernal, 1993). Thus, the 1972–1973 ENSO event was not a cause of the collapse of the anchovy fishery. But it cannot be denied that the anchovy crash was very likely accelerated and aggravated by the extremely high fishing mortality in the late 1960s and early 1970s. Whereas single ENSO events do not seem to play a major role in regime changes or long-term population dynamics of anchovies, it is not clear whether the frequency and strength of ENSO events change with the persistent warming and cooling phases of HC waters which seem to govern regime changes.

The realization that long-term dynamics of exploited anchovy and sardine populations are controlled by large-scale physical processes does not lead to the conclusion that fisheries management is of no importance, as, in addition to the impact of natural variability, the dynamics of exploited fish populations are heavily influenced by fishing mortality. In contrast, the new evidence gives us a valuable tool for a better future fisheries management. For example, fishing activities could be adapted to whether fish populations are on the ascending or the descending slope in the course of their decadal-scale population variability. The problem, of course, is to find out which regime and which phase of the regime are prevailing. This is the task of research projects such as the "Small Pelagic Fishes and Climate Change" (SPACC) project (Hunter &

Alheit, 1995) of the IGBP Global Change Core Programme "Global Ocean Ecosystem Dynamics" (GLOBEC) programme (IGBP, 1997).

Acknowledgements

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