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Aquat. Living Resour. 15 (2002) 87–94

Aquatic Living Resources

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Recruitment of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off central-south Chile in the 1990s and the impact of the 1997–1998 El Niño

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Received 23 March 2002; accepted 10 December 2002

Abstract

The recruitment of *Strangomera bentincki* (common sardine) and *Engraulis ringens* (anchovy) and the relationships with oceanographic conditions in the upwelling ecosystem of central-south Chile were investigated from 1990 to 1998, with emphasis on the 1997–1998 El Niño. Time series of recruitment, biomass, local sea surface temperature, and a coastal upwelling index were used to explore relationships during the spawning (July–August) and pre-recruitment (August–December) periods. The 1997–1998 El Niño caused physical changes in the small pelagic fish habitat off central-south Chile. Anomalous sea surface temperatures (SST) and upwelling indexes began to be detected from May 1997 and persisted into 1998. Recruitment of common sardine showed significantly negative relationship with SST anomalies during the pre-recruitment period, as well as with the upwelling index during the peak of spawning. However, the recruitment of anchovy did not seem to be affected by the environmental changes observed in the 1990s. Instead, the recruitment rate of anchovy showed negative relationship with the recruitment rate of common sardine. We conclude that the conditions of the 1997–1998 El Niño off central-south Chile affected the survival of common sardine offspring, and that the recruitment success of anchovy could be determined by less-abundant cohorts of common sardine through a biological mechanism of interaction.

Resumen

Reclutamiento de sardina común (*Strangomera bentincki*) y anchoveta (*Engraulis ringens*) frente a Chile centro-sur en los años 90, y el impacto de El Niño 1997–1998. Se analiza los cambios en el reclutamiento de *Strangomera bentincki* (sardina común) y *Engraulis ringens* (anchoveta) entre 1990 y 1998 en el ecosistema de surgencia de Chile centro-sur, y se analiza su relación con las fluctuaciones en las condiciones oceanográficas con énfasis en el evento El Niño 1997–1998. Se utilizó series de tiempo de reclutamiento, biomasa, temperatura superficial del mar (TSM) y de un índice de surgencia (IS) para explorar las relaciones reclutamiento-ambiente bajo la hipótesis que el reclutamiento es determinado durante el período de máxima actividad reproductiva (Julio–Agosto) ó durante la fase prerrecluta (Agosto–Diciembre). El Niño 1997–1998 causó cambios físicos en el hábitat de estos pelágicos pequeños que se caracterizaron por una disminución del IS y por TSM anómalamente cálidas entre mayo de 1997 y septiembre de 1998. El reclutamiento de sardina común mostró una relación significativa y negativa con las anomalías de TSM durante el período prerrecluta, como también con el IS promedio durante la máxima actividad reproductiva. Sin embargo, el reclutamiento de la anchoveta no fue afectado por los cambios en las condiciones ambientales observadas en los años 90. En cambio, la tasa de reclutamiento de esta especie presentó una relación negativa con la tasa de reclutamiento de sardina común. Nosotros concluimos que las condiciones de El Niño 1997–1998 frente a Chile centro-sur afectaron la abundancia de la cohorte de 1997 de sardina común, y que el éxito del reclutamiento de la anchoveta parece ser determinado por las cohortes menos abundantes de sardina común a través de un mecanismo biológico de interacción.

Keywords: Recruitment; Coastal upwelling; El Niño; Pelagic fisheries; Central-south Chile

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PII: S0990-7440(02)01158-0

1. Introduction

Common sardine, *Strangomera bentincki* (Norman, 1936), and anchovy, *Engraulis ringens* (Jenyns, 1842), are important small pelagic fish resources in the central-south area off Chile (34° S-40° S), where Talcahuano is the main port for landing (Cubillos et al., 1998). Common sardine is a Chilean endemic species distributed from northern Coquimbo (29° S) to Puerto Montt (42° S), while anchovy is distributed from northern Peru to southern Chile (Arrizaga, 1981; Serra, 1983). In central-south Chile, these small pelagics live within 50 nautical miles of the coast where biological productivity is generally high due to seasonal upwelling events, mainly from mid September to March (austral spring-summer) (Arcos and Navarro, 1986; Arcos, 1987; Cubillos et al., 2001).

Interannual climate variability and associated environmental changes can have appreciable effects on marine ecosystems and fisheries. Pelagic fish populations in coastal upwelling regions are especially sensitive to environmental variability (e.g. Sharp and Csirke, 1983; Pauly and Tsukayama, 1987; Shannon et al., 1988; Cury and Roy, 1989, 1991; Cury et al., 1995; Bakun, 1996; Binet, 1997; Cole and McGlade, 1998; Hutchings, 1998; Durand et al., 1998; Cole, 1999).

Interannual climate variability is particularly strong in the Southeastern Pacific Ocean due to the occurrence of El Niño-Southern Oscillation events (Barber and Chavez, 1986; Brainard and McLain, 1987). El Niño southern oscillation events propagate poleward along the coast of Ecuador and Peru, and impact the marine ecosystem with varying intensities. In 1997–1998, a strong El Niño event occured with important consequences for the pelagic fisheries along the South America coast (CPPS, 1999). However, it is not clear how El Niño events affect the upwelling ecosystem off central south Chile, and how the common sardine and anchovy populations are impacted by El Niño. Fonseca et al. (1986) found that a higher catch per unit effort (CPUE) of both species in a given year was related to warmer non-El Niño conditions during the spring of the previous year. However, a lower CPUE was observed when strong El Niño events occurred. Similarly, Yáñez et al. (1990, 1992) concluded that the relative abundance of common sardine and anchovy was inversely related to fishing effort, sea surface temperatures, and wind driven turbulence.

The studies of Fonseca et al. (1986) and Yáñez et al. (1990, 1992) suggest that recruitment of these small pelagics is negatively affected by environmental conditions imposed by a strong El Niño, but they used total catch per unit effort of both species. In this way, the impact of El Niño on each species have not been studied. In this paper, we investigate the recruitment fluctuations of common sardine and anchovy in the 1990s, including the 1997–1998 El Niño event, in relation to environmental conditions during the spawning or during the pre-recruitment period. We explored the hypothesis that recruitment is determined by environmental conditions occurring in the spawning season (July–August) or during the pre-recruitment period, which extends from August to December for both species (Cubillos et al., 1999, 2001). The environmental conditions in the spawning season are dominated by onshore transport (negative upwelling index) and low sea surface temperature, instead during the pre-recruitment period the wind pattern of the area changes from quasi-permanent north winds to intermittent south winds that produce moderate upwelling (Arcos and Navarro, 1986; Castro et al., 2000; Cubillos et al., 2001).

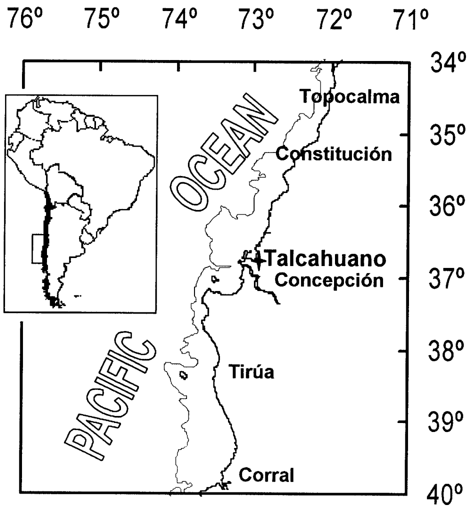

Fig. 1. Study area showing the 200-m isobath.

2. Materials and methods

2.1. Environmental variables

Environmental time series examined were sea surface temperature (SST) from the tidal station at Talcahuano (36° 41’ S, 73° 06’ W) and wind data from Carriel Sur (36° 46’ S, 73° 03’ W) meteorological station (Fig. 1). Hourly wind intensity and direction data were used to compute monthly average of a coastal upwelling index (CUI) for Talcahuano, according to the methodology of Bakun (1973) and Arcos and Navarro (1986). To compare the evolution of El Niño 1997–1998 in the Equatorial Pacific Ocean with local SST, we used Niño 3 and 4 SST anomalies which were obtained from NOAA (http://www.cpc.ncep.noaa.gov). Annual average anomalies were computed from monthly anomalies for the period 1982–1999.

2.2. Biomass and recruitment

Estimates for monthly biomass and yearly recruitment of common sardine and anchovy populations were carried by Cubillos et al. (2002). These estimates were computed by cohort analysis (Pope, 1972; MacCall, 1986) using an

Table 1
Recruitment (R, in number of individuals) and spawning stock biomass (S, in tons) of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) (after Cubillos et al., 2002)

	Common sardine		Anchovy	
Year	S (10^3 t)	R (10^9)	S (10^3 t)	R (10^9)
1990	395.0	90.5	–	15.3
1991	585.5	78.4	284.8	78.9
1992	326.4	44.4	311.5	56.9
1993	219.3	63.0	645.3	33.5
1994	157.0	43.3	624.6	25.8
1995	255.3	150.1	498.7	25.3
1996	550.7	67.5	284.7	110.9
1997	271.3	16.2	464.7	98.7
1998	162.9	90.0	781.0	64.3

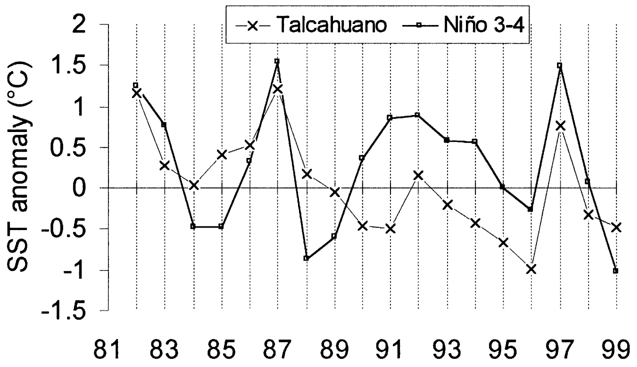

Fig. 2. Annual average anomalies of sea surface temperature (SST) in the Niño 3–4 region in the Equatorial Pacific, and the local SST anomalies in Talcahuano, Chile.

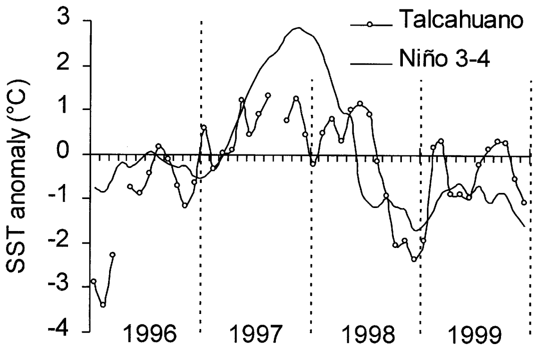

Fig. 3. Monthly anomalies of sea surface temperature (SST) in Talcahuano between 1996 and 1999, and the SST anomalies from the Equatorial Pacific Niño 3–4 regions

ADAPT approach (e.g. Gavaris, 1988) in which the unknown parameters were estimated by minimizing the squared differences between the observed and estimated catch per unit effort. Yearly pulse of recruitment dominates the population dynamics of both species (Cubillos et al., 2002). The recruitment of common sardine occurs in November each year, while the recruitment of anchovy tends to occur in January, approximately three to five months after the peak of spawning respectively. We used the total biomass in August as the spawner stock biomass for each species (Table 1).

Linear regression analyses were applied to analyze the incidence of environmental variables on recruitment, and also on the rate of recruitment (natural logarithm of recruitment per spawner biomass). Sea surface temperature and coastal upwelling index were used because these variables usually are correlated with processes that reflect the influence of the environment on the dynamics of small pelagic fish (e.g. Cury and Roy, 1989, Durand et al., 1998). Environmental variables were averaged for two periods: a) July–August, by considering winter environmental conditions during peak of spawning; and b) August–December, by considering the pre-recruitment period in which moderate upwelling can be found (see Arcos and Navarro, 1986; Strub et al., 1998; Cubillos et al., 2001).

3. Results

3.1. *El Niño events in central-southern Chile*

The occurrence of El Niño events in 1982–1983, 1987, 1992, and 1997–1998 were evident in the Equatorial Pacific, and also in coastal waters off central-south Chile (Fig. 2). As regards the 1997–1998 El Niño, positive anomalies were first detected in coastal SST in May 1997. They declined in January 1998 but warmer conditions persisted from February to July 1998 (Fig. 3).

In central-south Chile, the coastal upwelling index (CUI) tends to be positive from October to April when south and south-west winds prevail. On the contrary, downwelling tends to occur during May–September because northerly winds are dominant. Under El Niño conditions, northern and southern winds were generally weaker from April 1997 to April 1998 (Fig. 4a). This anomalous pattern is better observed in the anomalies for the period of favourable upwelling (October to April, Fig. 4b).

The average SST anomalies and CUI values during July–August (peak of spawning) and during August–December (pre-recruitment phase) are shown in Fig. 5. SST anomalies were negative from 1990–1996 and also in spring 1998. The only extreme positive anomaly in SST occurs in 1997. The CUI during July–August was negative, except in 1998 when it was slightly positive. During the pre-recruitment phase (August–December), the CUI was always positive.

3.2. *Biomass and recruitment*

The monthly estimates of the total biomass for common sardine and anchovy are shown in Fig. 6. There is a seasonal fluctuation in the biomass of the two species, with higher values during austral summer (January–February) and also a tendency for biomass of the two species to vary inversely.

The seasonal pattern of fluctuation in biomass is due to the yearly pulses of recruitment (Table 1). The strongest

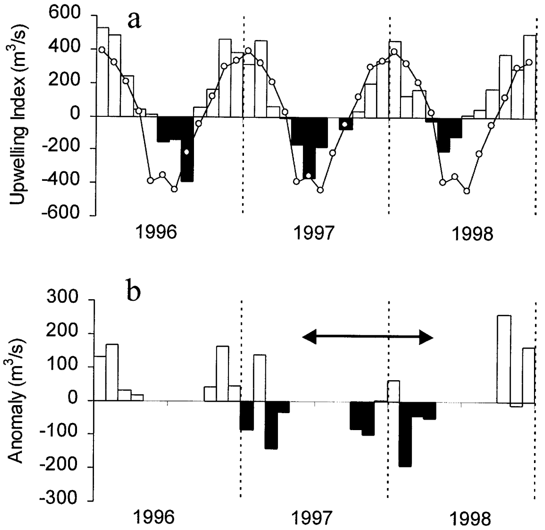

Fig. 4. Monthly values (bar) of the coastal upwelling index (CUI) and **a)** long-term seasonal signal (circles connected with a line, average of 1970-1999), and **b)** monthly anomalies for the period of active upwelling between October and April (b), at Talcahuano in the period 1996-1998 to illustrate the changes during El Niño of 1997–1998.

recruiting cohort of common sardine occurred in 1995, while the 1997 cohort recruitment was the lowest during the 1990s. In comparison, the anchovy cohorts of 1991, 1992, 1996 and 1997 were strong. The 1998 cohort was omitted in further analysis because the most recent year class tend to be uncertain in cohort analysis.

Anchovy recruitment tends to vary inversely with common sardine recruitment (Table 1). Hence, the biomass of the two species tends to have an inverse relationship (Fig. 6). Nevertheless, the relationship between recruitment of common sardine and anchovy was not significant, but the relationship between the rate of recruitment (ln(R/S)) for the two species was also inverse and significant (Fig. 7).

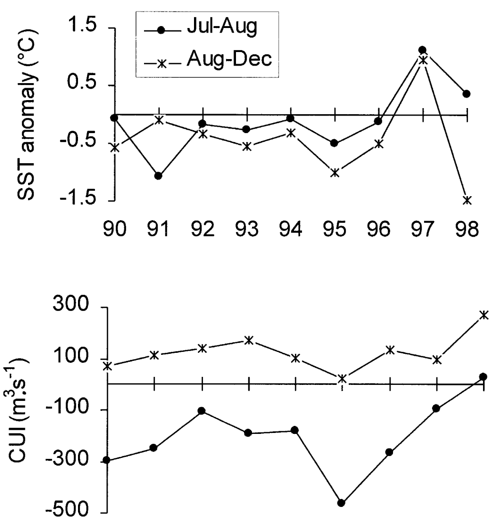

Fig. 5. Anomalies of sea surface temperature (SST) and coastal upwelling index (CUI) averaged for the peak of spawning (July-August) and for the pre-recruitment phase (August-December) of the small pelagic common sardine and anchovy off Talcahuano.

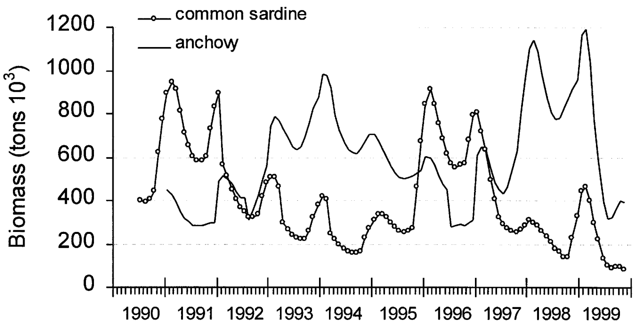

Fig. 6. Changes in biomass of common sardine and anchovy during the 1990s (after Cubillos et al., 2002).

3.3. *Recruitment and environmental variables*

The relationships between recruitment of the species and the environmental fluctuations were analyzed by considering the environmental conditions during the spawning period, and also during the pre-recruitment period. From the oceanographical point of view, these periods are different (Fig. 5). During the spawning period in July–August, the coastal upwelling index tends to be negative and SST tends to be colder. In turn, during August–December the coastal upwelling index is usually positive, indicating moderate upwelling activity.

Sardine recruitment was found to have a significant inverse relationship ($p<0.05$) with SST anomalies during the peak spawning season (July–August), but anchovy did not (Fig. 8). However, the relationship between the recruitment rate ln(R/S) and the SST anomalies in July–August were not significant for either species ($p>0.05$).

Similarly, a significant and inverse relationship ($p<0.05$) was found between the recruitment and recruitment rate of common sardine and the upwelling index averaged for July–August (Fig. 8b). In contrast, neither recruitment nor recruitment rate of anchovy were significantly explained by the upwelling index in July–August (Fig. 8b).

The recruitment and recruitment rate of sardine was significantly explained by the SST anomalies during the pre-recruitment phase (August–December, Fig. 9a). In contrast, although positive linear relationships were found for anchovy, these were not significant ($p>0.05$; Fig. 9a). The

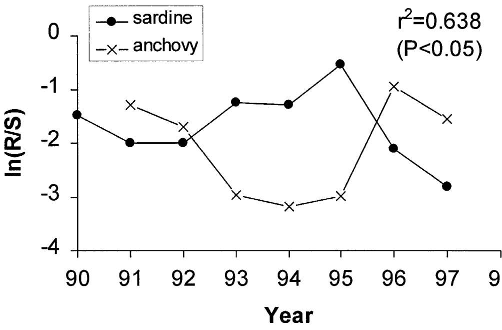

Fig. 7. Rate of recruitment of common sardine and anchovy during the 1990s.

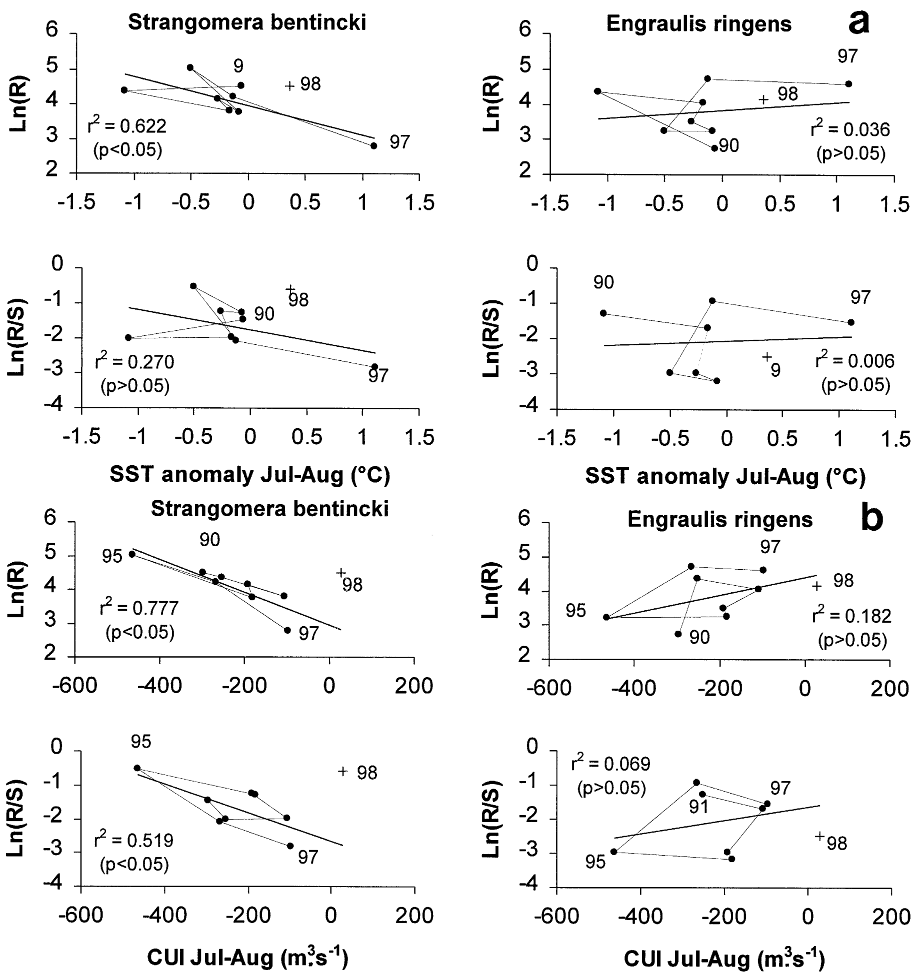

Fig. 8. Relationships, during the peak of spawning (July-August), 1990-1997, between recruitment of common sardine (left) and anchovy (right) and **a)** the anomalies of sea surface temperature (SST), **b)** the coastal upwelling index (CUI).

coastal upwelling index during the pre-recruitment did not have a significant relationship with either species (Fig. 9b).

It should be noted that the 1998 data-point was not included in the regression analyses, however this data-point does lie close to that predicted by SST anomalies during the pre-recruitment period for sardine (Fig. 9). Inclusion of the 1998 data-point did not stop the relationships being significant (p<0.05), but this was not the case for the sardine spawning period regressions (see Fig. 8).

4. Discussion

In the central-south area off Chile, El Niño events of 1982–1983, 1987, 1992, and 1997–1998 were reflected in the local coastal sea surface temperatures (SST). Under non-El Niño conditions, this area is dominated by the presence of cold waters (SST<14 °C) within the first 50 nautical miles from the coast (Strub et al., 1998). Farther offshore, there are subtropical surface waters with SST higher than 15 °C. When a strong El Niño occurs, warmer sea surface temperatures penetrate onshore and to the south (Fonseca, 1985), while the upwelling induced by southerly winds become weaker. In 1997 the average annual SST anomaly was about +1 °C above the mean, and downwelling and upwelling were less intense, particularly from June 1997 to June 1998 (Fig. 3).

The 1997 common sardine cohort recruitment was the lowest in the 1990s (Table 1), probably a direct consequence of the 1997–1998 El Niño event. On mechanisms whereby El Niño impact sardine recruitment involves larval and juvenile feeding preferences, in terms of prey type and prey size. Prior to and during the El Niño 1997–1998 event, the microbial food web in oceanic and coastal zones off northern Chile was very active, and pico and nanoplankton size fractions dominated the total primary production (González et al., 1998, 2000). In this way, a shift in the size-spectrum of trophodynamic scenarios between El Niño and non-El Niño conditions could explain effects on offspring survival of common sardine in central-south Chile. In California, for example, Fiedler et al. (1986) found that growth of juvenile and adults of northern anchovy (*Engraulis mordax*) was significantly slowed during 1983, probably due to reduced availability of zooplankton prey. The authors

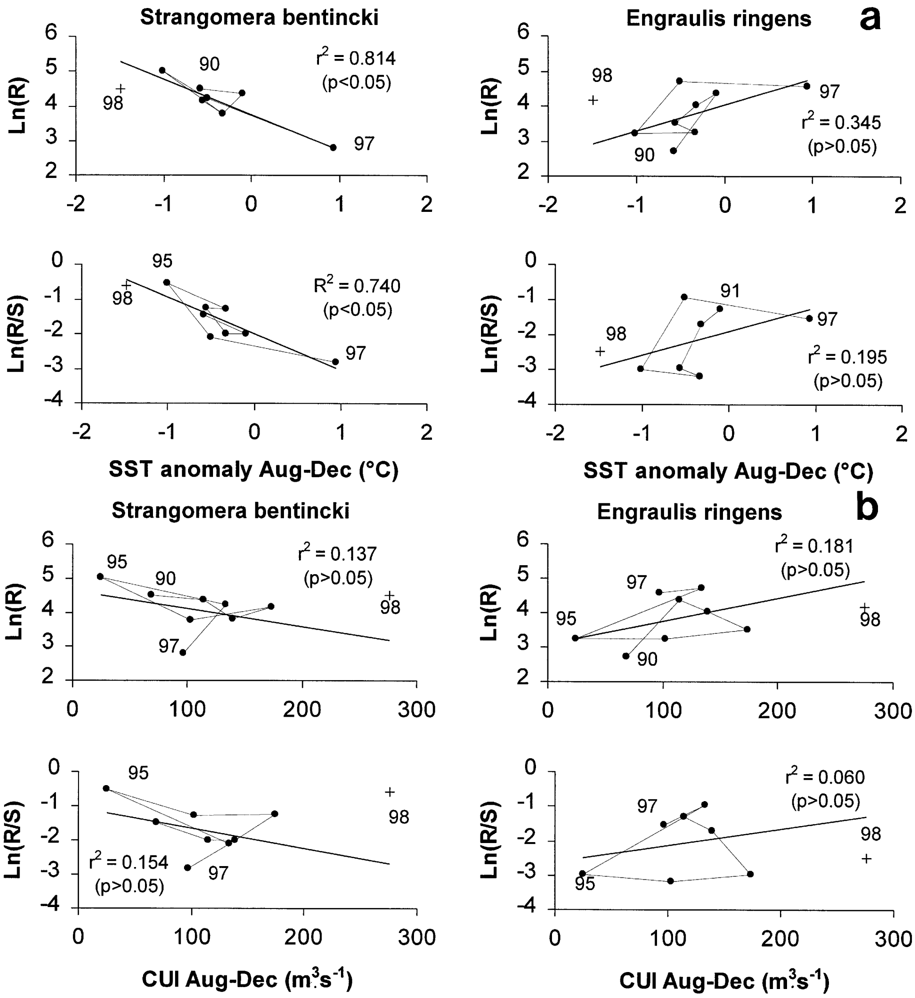

Fig. 9. Relationships, during the pre-recruitment period (August-December), 1990-1997, between recruitment of common sardine (left) and anchovy (right) and **a)** anomalies of sea surface temperature (SST), **b)** the coastal upwelling index (CUI). The upwelling index is positive and represents upwelling or offshore transport.

discussed that the reduced growth rates of 1982 year-class fish adults, and juvenile fish during summer 1983 and summer 1984, were likely caused by El Niño's impact on the availability of appropriate zooplankton community during the 1982–1983 El Niño event.

In central-south Chile, recruitment of common sardine was inversely related to SST anomalies and the coastal upwelling index in July–August (Fig. 8). In comparison, the relationships between recruitment of anchovy and SST and the upwelling index examined were not significant. The relationships were dominated by the warmer conditions associated to the 1997–1998 El Niño in central-south Chile. If this extreme anomaly is dropped from the regression, some relationships could not be significant because the variation in SST is small under non-El Niño conditions in central-south Chile.

Linear regression was used to explore probable relationships between recruitment and environmental variables. These relationships could also be studied by using non-linear analyses on a longer time series (e.g. Cury and Roy, 1989), by using other statistical techniques like Generalized Additive Models (Daskalov, 1999). Therefore the linear relationships found here should not be used for forecasting until verified whit more data, and perhaps more sophisticated analyses. It should be also noted that the proportion of published environment-recruitment correlations that have been verified upon re-test is usually low (Myers, 1998).

Despite the relationships between oceanographic conditions and anchovy recruitment not being significant (perhaps due to insufficiently long time series), the recruitment rate of anchovy was significantly negatively related to the recruitment rate of common sardine (Fig. 7). In this way, a biological mechanism of interaction between the two species appears to be operating.

A long-term worldwide alternation in abundance between sardine (*Sardinops sagax*) and anchovy (*Engraulis* spp) has been observed in five regions where the genera co-occur (Schwartzlose et al., 1999). Between 1990 and 1997, common sardine and anchovy recruitment were related in different ways to inshore SST conditions in central-south Chile (Figs. 8 and 9), and neither stock appears to conform to the same trend that has been observed for anchovy and sardine (*Sardinops sagax*) in Perú, northern Chile, California, and the eastern North Atlantic: namely, that sardine stocks tend to flourish under warmer conditions, and that anchovy populations flourish during cooler conditions (Sharp and McLain, 1993; Cushing, 1996; Cole and McGlade, 1998). However, the alternation between sardine and anchovy in those systems is occurring over a long period and therefore it should not be considered with the short-term changes observed (may be biennual) between common sardine and anchovy during the 1990s in central-south Chile.

In central-south Chile both species inhabit an area where biological productivity of coastal waters is high (Daneri et al., 2000), and food unlikely to be a limiting factor under normal conditions. However, under El Niño conditions, food availability/size spectra could be important (Gonzalez et al., 2000). In this way, extreme positive SST anomalies could be reflecting changes in food availabilty/size spectra during the pre-recruitment period, and this could explain the significant relationship between sardine recruitment and recruitment rate and the SST anomalies during the pre-recruitment phase (Fig. 9).

Cubillos et al. (2001) suggested that the reproductive strategy of the two species is to spawn at the end of winter when environmental conditions are better for retention of eggs and larvae onshore, according to the triad hypothesis of Bakun (1996). The spawning of common sardine is very much restricted to the end of winter (peak in August, Cubillos et al., 1999), just when a regime of northern winds and downwelling changes to a regime of southern winds, which produce moderate upwelling events (Cubillos et al., 2001). In contrast, spawning of anchovy extends to September–October in some years, after the peak of common sardine spawning (Cubillos et al., 1999). The environmental cues or the biological mechanism causing anchovy and common sardine to be out of phase with one another (on the short term) are likely to be operating during the larvae and early juveniles stages. If a small year class of common sardine is produced, the offspring survival of anchovy might be favored through an opportunistic competitive advantage of anchovy, and vice versa.

The mechanisms controlling the recruitment success are complex, and they cannot be revealed from correlation/regression studies. However, because common sardine and anchovy are similar in size, and they tend to form mixed schools, and because the growth and reproductive strategies are similar (Cubillos et al., 2001), the biological mechanism of interaction between common sardine and anchovy could be related to the early school dynamics (Fréon and Misund, 1999). Fish of a species that are driven to join schools of another more abundant species must effectively subordinate its specific needs and preferences to the 'corporate volition' of the school that is largely driven by a different set of needs and preferences (Bakun and Cury, 1999). In this way, the inverse relationship between the recruitment rate, and the short-term alternation between the biomass of common sardine and anchovy in central-south Chile could be explained by the 'school trap' mechanism suggested by Bakun and Cury (1999). In this context, a small year-class of one species could be adversely affected by a dominant year-class of the other species.

Accordingly, such a change can be initiated by an ecosystem event such as El Niño. A shift in the size-spectrum of trophodynamic scenarios during El Niño could negatively affect the offspring survival of common sardine during the pre-recruitment phase. Also, a strong El Niño event could impact recruitment of common sardine by an alteration in retention-concentration processes related to downwelling during the winter peak of spawning (July–August). Consequently, a less abundant cohort of common sardine could positively affect the recruitment success of anchovy due to anchovy being the early dominant in the mixed schools. Overall, we postulate that the conditions of the 1997–1998 El Niño in the central-area off Chile affected the survival of common sardine offspring and that this small cohort was important for the recruitment success of the 1997 cohort of anchovy through a biological mechanism of interaction such as the "school trap" of Bakun and Cury (1999).

Acknowledgements

LC is grateful to Philippe Cury and Andy Bakun for comments about the 'school trap' hypothesis. Also, we are grateful to J. Alheit (Germany), G. Daskalov (Institute of Fisheries, Bulgaria), and an anonymous referee for comments and suggestions on an early draft of this paper.

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