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Article

Eggs and larvae of anchoveta *Engraulis ringens* off northern Chile during the 1997-1998 El Niño event

Huevos y larvas de la anchoveta *Engraulis ringens* en el norte de Chile durante el evento El Niño 1997-1998

Pablo M. Rojas[1], Mauricio F. Landaeta[2] and Raúl Ulloa[3]

[1]División de Investigación en Acuicultura, Instituto de Fomento Pesquero (IFOP), Balmaceda 252, Casilla 665, Puerto Montt, Chile. pablo.rojas@ifop.cl
[2]Laboratorio de Ictioplancton (LABITI), Facultad de Ciencias del Mar y de Recursos Naturales, Universidad de Valparaíso, Casilla 5080, Viña del Mar, Chile
[3]Universidad Autónoma de Nayarit, Postgrado Ciencias Biológicas Agropecuarias y Pesqueras, Ciudad de la Cultura Amado Nervo, CP 63000, Tepic, Nayarit, México

Resumen.- Se analizó el impacto del fenómeno El Niño (1997-1998) sobre la dinámica espacial, así como sobre los cambios en los patrones de agregación de los huevos y larvas de anchoveta debido a la alteración de las anomalías térmicas. Se realizaron seis campañas bio-oceanográficas en el norte de Chile desde Arica (18°29'S, 70°19'W) a Antofagasta (23°38'S, 70°24'W) durante diferentes períodos (antes y durante) del evento El Niño 1997-1998. Se registraron cambios en la distribución vertical y patrones de agregación de las larvas de anchoveta, así como un aumento de la biomasa de zooplancton con la llegada de El Niño; además, las preferencias ecológicas de la anchoveta fueron alteradas por el desplazamiento gradual hacia el sur de las zonas de desove como resultado de la llegada de aguas cálidas subtropicales. Un aumento en la biomasa del zooplancton vinculada a un cambio en la composición de especies sugiere un impacto negativo en la alimentación de las larvas de anchoveta. Los resultados obtenidos indicarían que cambios bruscos en el ambiente tendrían consecuencias inmediatas en la distribución de los estados tempranos de la anchoveta, causando un potencial impacto en el reclutamiento de esta especie pelágica en el Sistema de Corrientes de Humboldt frente al norte de Chile.

Palabras clave: Sistema de la Corriente de Humboldt-Chile, larvas de peces, anomalías térmicas, surgencia costera, zooplancton

Abstract.- The impact of the El Niño event (1997-1998) on the spatial dynamics as well as on the changes in the aggregation patterns of anchoveta eggs and larvae due to the alteration in the thermal anomalies were analyzed. Six bio-oceanographic surveys were carried out in northern Chile from Arica (18°29'S, 70°19'W) to Antofagasta (23°38'S, 70°24'W) over different periods (before and during) of the 1997-1998 El Niño event. Changes in the vertical distribution and aggregation patterns of anchoveta in early life stages were registered as well as an increase in zooplankton biomass with the arrival of El Niño; moreover, the spatial distribution of anchoveta was altered due to the gradually poleward displacement of spawning areas as a result of the arrival of subtropical warm waters from the north. The increase in zooplankton biomass linked to a change in the species composition suggests a negative impact on the anchoveta larval feeding. Our results suggest that abrupt changes in the environment would have immediate consequences on the spatial distribution of anchoveta in early life stages, causing a potential impact on the recruitment of this small pelagic fish in the Humboldt Current System off northern Chile.

Key words: Chile-Humboldt Current System, fish larvae, thermal anomaly, coastal upwelling, zooplankton

Introduction

The coastal upwelling zone of the Humboldt Current System (HCS) in the eastern South Pacific is well known for its high primary productivity (up to 20 g C m^{-2} d^{-1}, Daneri *et al*. 2000, Montero *et al*. 2007), which sustains high zooplankton biomass and abundance of coastal and oceanic small pelagic fish such as anchoveta, sardine (Cushing 1990), horse mackerel (Alheit & Bernal 1993, Cubillos *et al*. 2008) and sculpin (Landaeta *et al*. 2010). High coastal productivity is sustained mainly by the fertilizing effect of the coastal upwelling driven by equatorward alongshore wind stress, producing important nutrient supply to the euphotic zone above the continental shelf. Also, the offshore propagation of mesoscale eddies and meandering currents contributes significantly to expanding the area of high chlorophyll concentration beyond the coastal upwelling centre (Correa-Ramirez *et al*. 2007). The HCS is subject to strong inter-annual variability due to the effects of the El Niño Southern Oscillation events (ENSO). Probably due to the catastrophic collapse of the Peruvian fisheries after the 1972-1973 El Niño event, much of the actual knowledge about the effects of the ENSO over the HCS region comes from studies on Peruvian ecosystems. Numerous reports have approached both the physical variability (Fahrbach *et al*. 1991) and the biological consequences of the El Niño event on the pelagic ecosystems (Barber & Chavez 1983, 1986, Thomas *et al*. 2001), benthic communities (Tarazona *et al*. 1988, Arntz & Tarazona 1990), and fisheries (Alamo & Bouchon 1987, Arntz & Tarazona 1990). For Chilean waters, the warm phase of ENSO events negatively affects the settlement of gastropods (Moreno *et al*. 1998), cohort somatic growth and survival rates of coastal fishes (Hernández-Miranda & Ojeda 2006), abundance and composition of pelagic copepods (Hidalgo & Escribano 2001) and larval fishes (Rodriguez-Graña & Castro 2003, Landaeta *et al*. 2009). However, during El Niño, the diversity of marine fishes increases (Kong *et al*. 1985) as well as the biomass of the calanoid copepod *Calanus chilensis* (Escribano & Hidalgo 2000). Some reports on the upwelling systems off northern Chile (18º-30ºS) have shown inter-annual fluctuation in the anchoveta catches (Blanco *et al*. 2001) along with changes in the composition and abundance of plankton communities (Iriarte *et al*. 2000, González *et al*. 2002).

The effect of each of the El Niño events on the pelagic ecosystems of the southeastern Pacific ocean has differed over time, this difference being strongly related to the intensity and duration of each event, the period of maximum intensity, the season and especially in regards to the composition of the fauna present in the ecosystem at the time of its occurrence (Zebiak 1999). During the El Niño of 1997-1998 the phytoplankton community off Antofagasta (23°38'S, 70°24'W) was mainly composed of small species, including diatoms and autotrophic flagellates. The zooplankton community off northern Chile during non-El Niño conditions was dominated mostly by large copepods and euphausiids endemic to the HCS (Hidalgo & Escribano 2001, Fernández *et al*. 2002). However, time-series data of zooplankton from the Antofagasta coast show a substitution toward small-sized species, although in general terms the total biomass close to the coast did not suffer a sudden collapse in comparison with previous years (Ulloa *et al*. 2001).

Regarding the commercially important pelagic species from northern Chile, the anchoveta *Engraulis ringens* is a fast growing species inhabiting coastal zones with high productivity rates (Bertrand *et al*. 2004a), whereas the sardine *Sardinops sagax* is associated to oceanic waters and frontal zones between these zones and the coastal waters (Castillo *et al*. 1996, Bertrand *et al*. 2004a). Anchoveta stocks in northern Chile are restricted to a temperature range fluctuating between 12º-18ºC during austral winter (unpublished data). Despite the importance of the information related to upwelling circulation in the Humboldt Current System (HCS) and its impact on the survival of eggs and fish larvae for the population dynamics of exploited fish, it is still insufficient and only limited to the anchoveta population (*Engraulis ringens*) from central-southern Chile (Castro *et al*. 2000, 2009, Hernández & Castro 2000, Bustos *et al*. 2008).

Low oxygen concentrations in subsurface waters of coastal upwelling zones might also affect zoo- and ichthyoplankton vertical distribution (Pavez *et al*. 2010). In the Humboldt Current System the layer of low dissolved oxygen concentration is rather shallow (Minimum Oxygen Layer, < 20 m) (Morales *et al*. 1996, Giesecke & González 2004). The limits of temperature and oxygen tolerance for anchoveta and sardine in this region have been reported to fluctuate between 14º-21°C and 16º-23°C, and between 1.8 ml L^{-1} and 2.0 ml L^{-1} respectively. These factors are often closely related (Morales *et al*. 1996). The above mentioned oxygen concentrations are found at 30 m depth and may be responsible for a restricted vertical distribution of the anchoveta.

Climatic changes at different time scales would be the responsible factors causing alterations to both the aggregation and spawning patterns of pelagic fish associated to coastal upwelling environments (Chavez *et al*. 2003, Bertrand *et al*. 2004a). In northern Chile, anchoveta showed similar responses to the effects of the El Niño event over the period 1957-2000, revealing a gradual decrease in abundance as the species approached the coast, with the sole exception of the 1992-1993 event where anchoveta abundance was not largely affected, despite the intensity of that event (Blanco *et al*. 2002).

Despite the confirmed ecological differences in the pelagic habitat between sardine and anchoveta associated with coastal upwelling zones off northern Chile, little is known about the effects on the distribution patterns of anchoveta eggs and larvae with the arrival of the El Niño 1997-1998 to the northern coast of Chile. The goal of this study is to analyze the consequences of the El Niño 1997-1998 on the Humboldt Current System off the northern coast of Chile at the epipelagic level, focusing mainly on the changes that occurred in the spatial distribution and aggregation patterns of the anchoveta eggs and larvae due to variations in thermal anomalies. Consequently we hypothesized that the spatial distribution of early life stages of anchoveta in coastal areas of northern Chile changed as El Niño 1997-98 event developed.

Materials and Methods

Oceanographic sampling

During 1996, 1997 and 1998, the Instituto de Fomento Pesquero (IFOP) carried out six oceanographic cruises off northern Chile between Arica (18º50'S) and Antofagasta (23º65´S). All surveys covered 34 stations along five transects, divided into offshore (beyond continental shelf, > 200 m depth) and nearshore (inside continental shelf with an extension of ~15 km wide) stations: Cruise 1 (September 3-9, 1996); Cruise 2 (May 25-31, 1997), Cruise 3 (August 15-22, 1997); Cruise 4 (December 12-19, 1997); Cruise 5 (February 28-March 7, 1998) and Cruise 6 (May 25-June 3, 1998) (Fig.1). According to the recorded values of sea-surface temperature (SST) and thermal anomaly changes, the cruises were grouped into two categories: Before El Niño (Cruises 1-2-3) and During El Niño (Cruises 4-5-6). At each station, data on the temperature (°C), salinity (PSU) and dissolved oxygen content (ml L^{-1}), were obtained from the surface to 600 m by means of a SENSORIAL CTD OCEAN model OS 200. Inter-annual variability in the monthly anomalies of SST was estimated by subtracting the average annual cycle in the period 1966-1999. Satellite NOAA images of SST were used in the analysis of the evolution of the El Niño event for the period 1995-1999. Off the northern Chilean coast (18º50'-23º65'S) monthly averages of SST were obtained and subsequently monthly anomalies were calculated using the climatologically distribution average of SST in the study area.

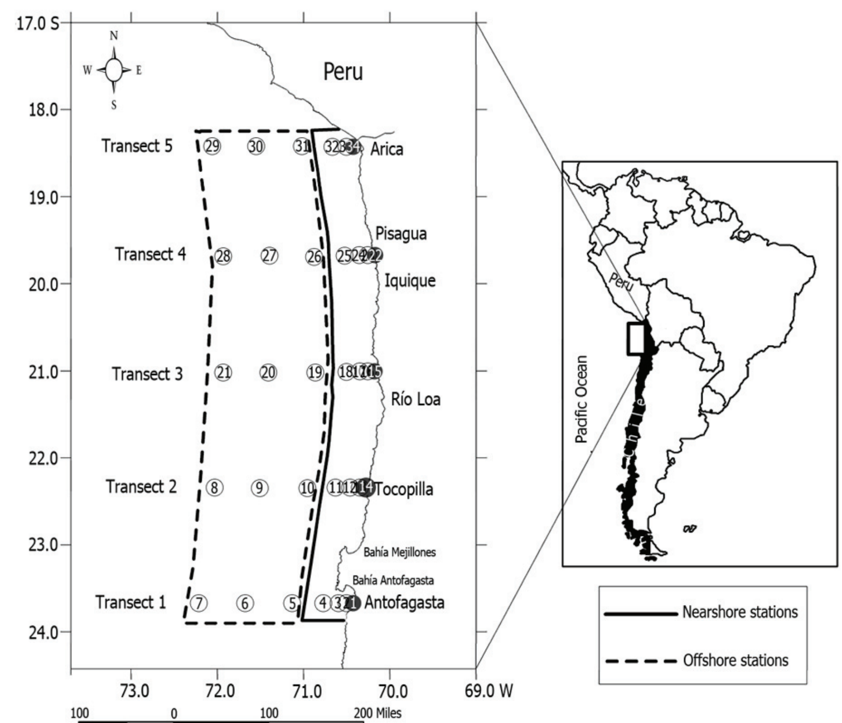

Figure 1. Geographic location of stations and transect off the northern coast of Chile. The continuous and discontinuous line shows the location of coastal and oceanic stations, respectively / Localización geográfica de las estaciones y transectos frente a las costas del norte de Chile. Las líneas continua y discontinua muestran la ubicación de las estaciones costeras y oceánicas, respectivamente

Sampling and analysis of ichthyoplankton

Zooplankton was collected through stratified vertical samplings (0-20; 20-60 and 60-100 m depth). A WP-2 net was utilized, with an opening mouth of 57 cm diameter (0.25 m^2 mouth area), total length of 261 cm and 297 µm mesh size, equipped with a double opening-closing system, and a calibrated TSK flowmeter. A total of 204 samples were collected throughout the surveys, and preserved in 4% buffered formalin. In the laboratory, anchoveta eggs and larvae were removed for counting and identification, following Orellana & Balbontín (1983). Zooplankton biomass was measured through displaced volume of wet weight. The number of individuals collected in the different sampling strata was standardized to a number per unit of volume of filtered water (densities): 1,000 m^3 for fish larvae (densities) for comparisons in the vertical axis (mean depth). The integrated abundance of eggs and larvae in the water column (larvae 10 m^{-2}) was also estimated for each sampling station.

For the analysis and display of spatial information GIS, ArcView version 3.3 (ESRI 1996) was utilized. Data were analyzed using raster or grid models (Bosque-Sendra 1992). Files that contained the physical and biological attributes collected at each station were converted into SHAPE files. Coverage of points for each cruise was generated from these files. Furthermore, continuous surface grids were generated through the interpolation method, which were subsequently analyzed using the SURFACE module from ArcView. The grids were conducted at a distance of 10 km between points using a surface interpolation technique: IDW (Jongman *et al*. 1995), this method assumes that each point has a local influence that decreases with distance and does not require a semi-variogram. The IDW interpolation was used to generate grids of thermal anomaly, calculated on the basis of average monthly sea-surface temperature for the different cruises.

Data processing

Kruskal-Wallis test (1952) was applied to determine differences within eggs and larvae abundance and zooplankton biomass, using the location of the stations (coastal/oceanic) and periods (Before El Niño/During El Niño) as factors. To investigate the relationship between oceanographic variables and the anchoveta larvae and egg abundance as well as zooplankton biomass, Principal Component Analysis (PCA) was utilized (Jongmann *et al.* 1995), over log (x+1) transformed data to homogenize variances. This technique consists of identifying 'a minimum set of functional components' (oceanographic variables) to explain the distribution of dependent variables (larvae and eggs distribution). The Spearman correlation analysis (Hays 1981) was utilized to investigate changes in the relationships between biological (*i.e.*, anchoveta eggs-larvae and zooplankton abundance) and physical variables (*i.e.*, SST, thermal anomalies, salinity and oxygen) during different El Niño conditions. All statistical analyses were conducted using STATISTICA 7.0 software package.

Results

Physical environmental anomalies before El Niño

The spatial distribution of sea-surface temperature (SST; Fig.2) registered during September 1996 (austral spring) showed values fluctuating between 14.0-16.7°C, with cold zones corresponding to recently upwelled waters (Fig. 2a). For May 1997 (autumn), an increase in the surface temperature was observed with values from 18.0 to 22.4°C, although some isolated centres of cold water remained nearshore (Fig. 2b). In August 1997 (winter) the SST oscillated between 17.5-20.6ºC, with a strong presence of warm waters covering an area that includes Bahía Mejillones (Fig. 2c). The salinity registered in September 1996 showed values ranging between 34.4-34.9 psu, typical for Equatorial Subsurface Waters (ESSW). A small increase in salinity 34.7-35.3 psu was observed in May 1997 associated with revenue warm water from a subtropical origin (Fig. 3). The concentration of dissolved oxygen found during September 1996, May 1997 and August 1997 showed relatively stable levels ranging between 4.0-6.9 ml L^{-1} (Table 1).

Thermal anomalies

The warm SST anomalies reported in the Equatorial Pacific[1] clearly showed the El Niño events of 1982-83, 1987, 1991-1992 and 1997-98. While these events have been of different intensities, the local SST data shows an increase in anomaly values for coastal areas, mainly associated with upwelling zones (Fig. 4). According to information, the manifestation of the 1997-1998 El Niño event showed warm water anomalies in May 1997, reaching values of +1°C between August and December.

[1]<http://www.cpc.ncep.noaa.gov>

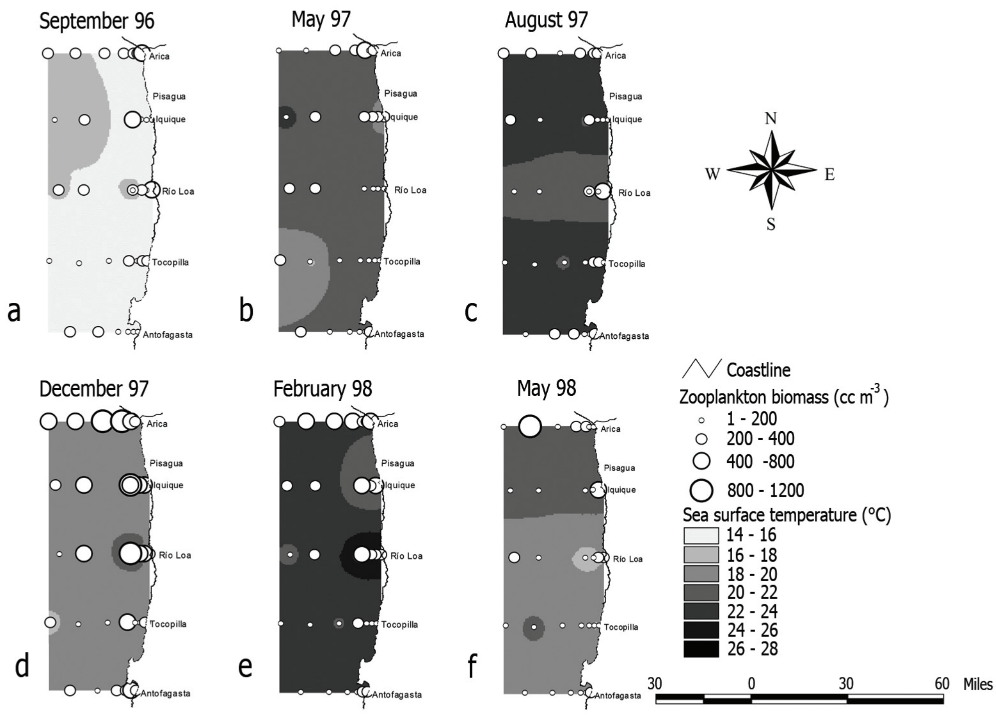

Figure 2. Spatial distribution of sea-surface temperature and distribution patterns of zooplankton for the different El Niño conditions / Distribución espacial de la temperatura superficial del mar y patrones de distribución del zooplancton para las diferentes condiciones El Niño

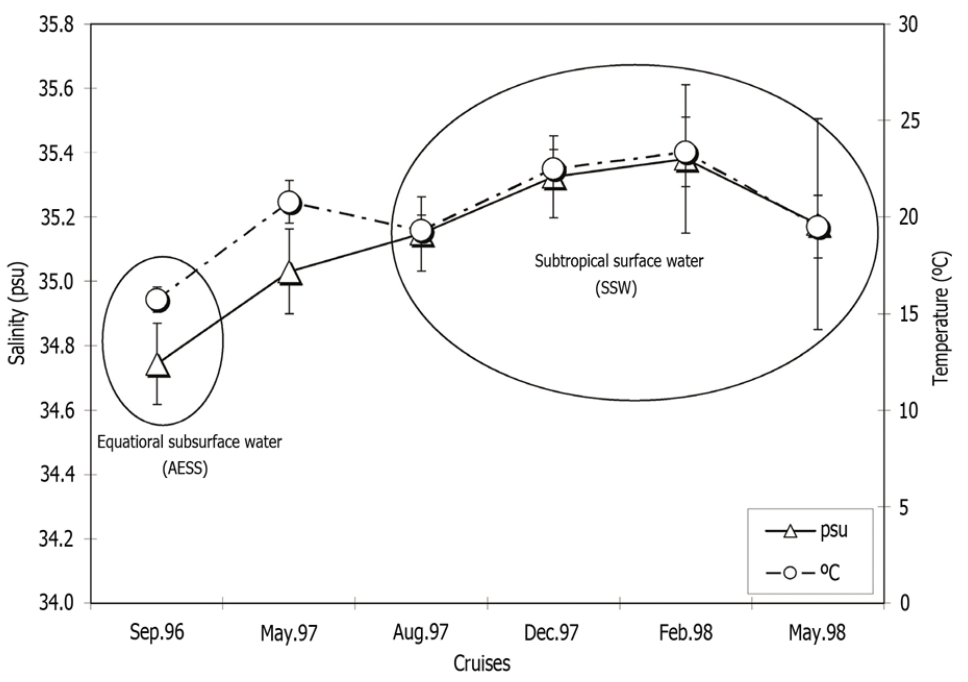

Figure 3. Relation between salinity and sea temperature for the different cruises, indicating the period where the study area is affected by Subtropical Surface Waters. Bars indicate values of standard deviation / Relación entre la salinidad y la temperatura del mar para las diferentes campañas, indicando los períodos donde el área de estudio es afectada por Aguas Superficiales Subtropical. Las barras indican los valores de desviación estándar

Table 1. Summary of the oceanographic conditions for the different cruises (n=34). SD = standard deviation / Resumen de las condiciones oceanográficas en los diferentes cruceros (n=34). SD = desviación estándar

	Before El Niño			During El Niño		
Hydrographic condition	Sep.96	May.97	Aug.97	Dec.97	Feb.98	May.98
Temperature (°C)						
Range (min-max)	14.0-16.7	18.0-22.4	17.5-20.6	20.2-24.1	20.6-26.2	16.5-21.9
Mean	15.7	20.8	19.3	22.5	23.4	19.5
SD	0.6	1.1	0.8	1.0	1.8	1.6
Thermal anomalies (ºC)						
Range (min-max)	-1.7-0.5	0.03-5.0	1.5-4.5	0.05-4.9	0.3-4.7	-1.3-3.2
Mean	-0.8	2.1	3.1	2.9	2.4	0.8
SD	0.5	1.1	0.6	1.3	1.1	0.8
Salinity (PSU)						
Range (min-max)	34.4-34.9	34.7-35.3	34.8-35.3	35.1-35.5	35.0-35.8	34.7-35.7
Mean	34.7	35.0	35.1	35.3	35.4	35.2
SD	0.1	0.1	0.1	0.1	0.2	0.3
Oxygen (ml L^{-1})						
Range (min-max)	4.0-6.9	4.2-6.4	4.5-6.7	4.2-6.8	4.3-5.8	4.4-5.8
Mean	5.8	5.3	5.6	5.5	5.0	5.2
SD	0.6	0.4	0.5	0.4	0.3	0.2

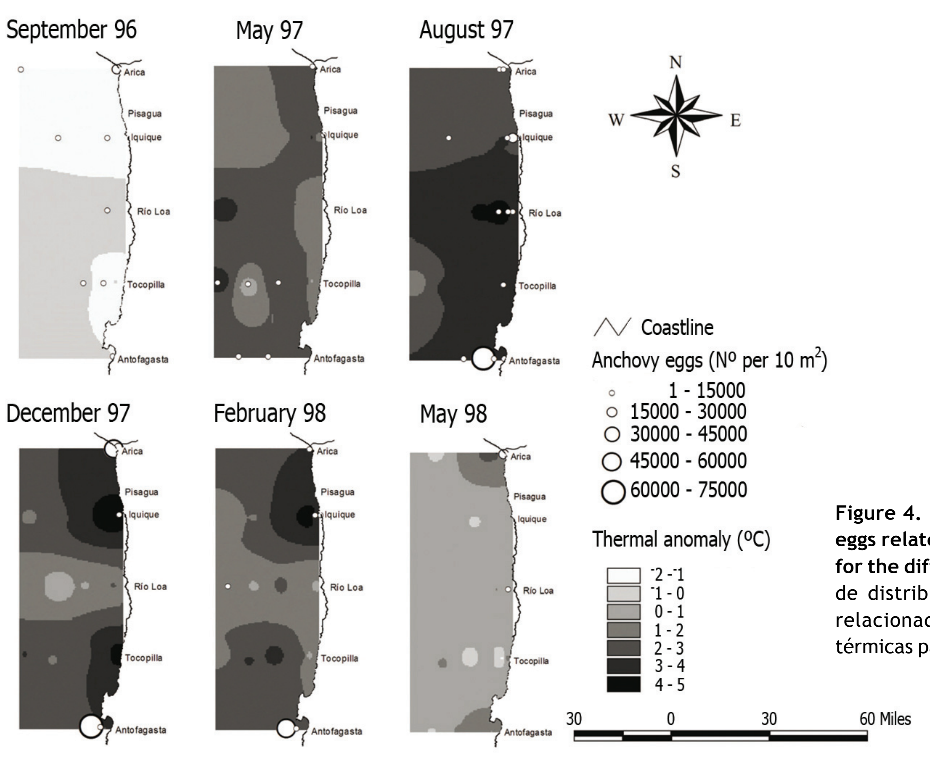

Figure 4. Distribution patterns of anchoveta eggs related to changes in thermal anomalies for the different El Niño conditions / Patrones de distribución de los huevos de anchoveta relacionados con cambios de las anomalías térmicas para las diferentes condiciones El Niño

Distribution and abundance of zooplankton biomass

Periods were characterized by differences in the distribution and abundance of zooplankton. In September 1996 the highest biomass concentrations were located at nearshore stations associated with cold waters. In May 1997 - August 1997, a clear decrease in zooplankton values associated with the presence of warm waters of subtropical origin were observed (Fig. 2).

An important signal regarding anchoveta egg abundance (29,539 eggs per 10 m^2) for the nearshore stations off Arica was detected in September 1996 (Fig. 4). The distribution and abundance of anchoveta larvae in September 1996 was relatively homogenous in most stations. However, two centres of higher larval abundance were found in the stations nearshore to Arica and Rio Loa (19,916 and 14,958 ind. per 10 m^2, respectively). In May 1997, all the stations registered a low abundance of anchoveta eggs and larvae, particularly for nearshore areas (Figs. 4 and 5). The August 1997 cruise showed a general low abundance of anchoveta eggs and larvae. However, two zones which showed a large abundance of anchoveta eggs (71,908 eggs per 10 m^2) and larvae (17,614 ind. per 10 m^2) were found in the nearshore stations of Antofagasta (Fig. 6). In general, the larvae show a low-abundance (> 250 per 1,000 m^3) in most stations. An increase in fish larvae abundance from South to North was found in the study area, mainly associated with surface layers in those nearshore stations.

Physical environmental anomalies during El Niño

The SST in December 1997 (austral summer) demonstrated the arrival of El Niño to the northern coast of Chile with values of 20.2-24.1°C, with the intrusion of warm waters extending to Antofagasta (Fig. 2d). During February 1998 (summer) SST oscillated between 20.6-26.2°C, indicating that the El Niño condition was maintained in the area (Fig. 2e). The SST values for May 1998 (autumn) fluctuated between 16.5-21.9°C. Figure 2f shows the presence of sea water < 22ºC in the studied area, and a near area with cold (16-18ºC) waters. In December 1997 the salinity showed values that fluctuated between 34.8-35.8 psu typical for Subtropical Surface Waters (SSW). No significant differences were detected in the salinity values before and during El Niño (Fig. 3). During December 1997, February 1998 and May 1998, a decrease in the maximum oxygen values was also observed (Table 1).

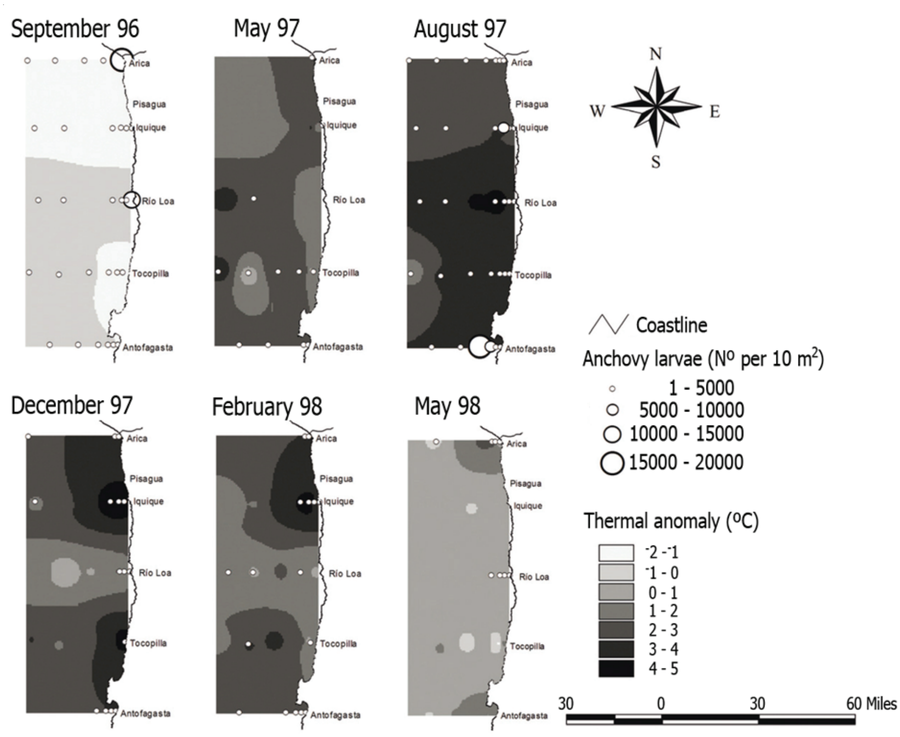

Figure 5. Distribution patterns of anchoveta larvae related to changes in thermal anomalies for the different El Niño conditions / Patrones de distribución de larvas de anchoveta relacionados con cambios de las anomalías térmicas para las diferentes condiciones El Niño

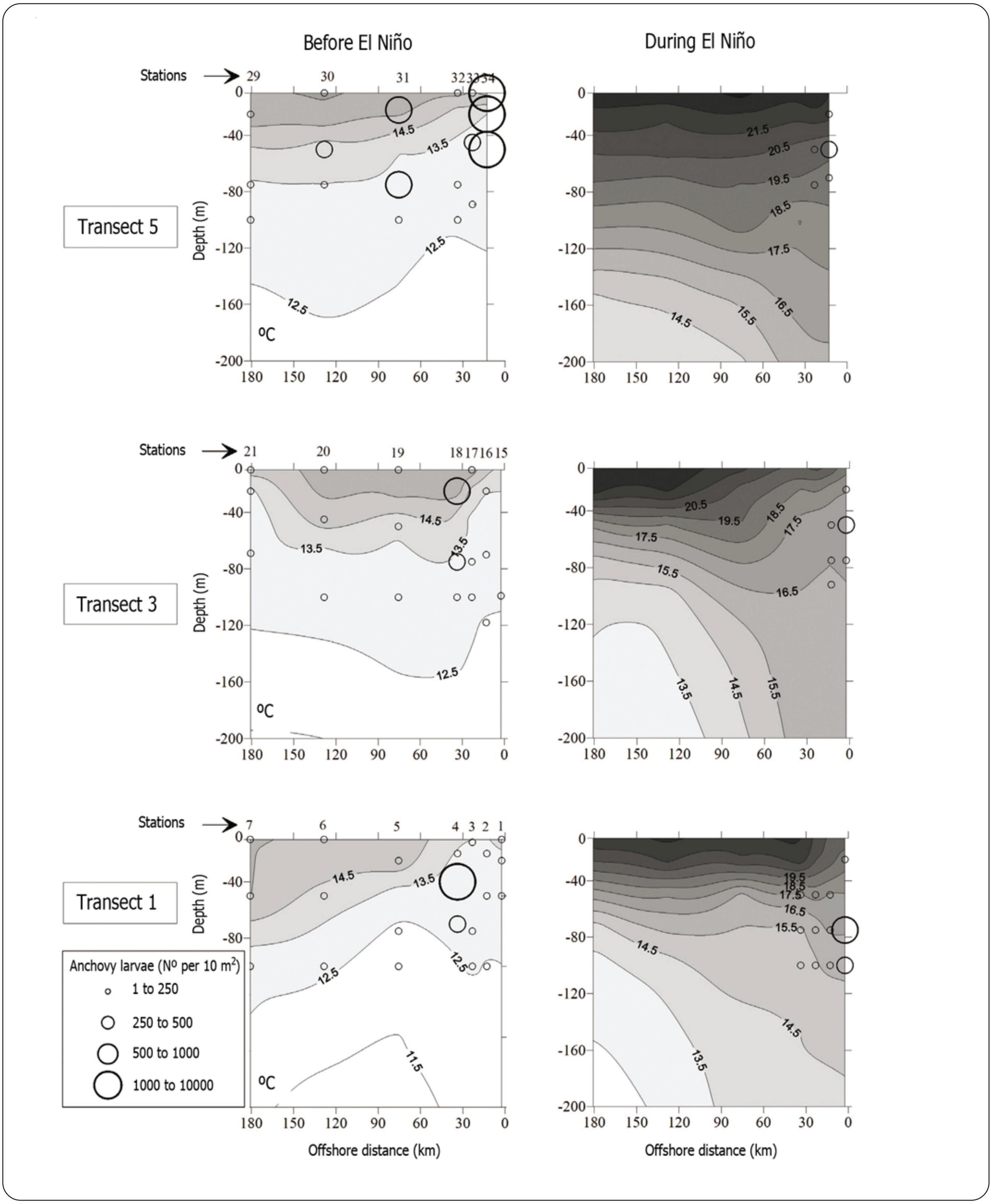

Figure 6. Vertical distribution of anchoveta larvae at three transects for different El Niño conditions / Distribución vertical de larvas de anchoveta en tres transectas para las diferentes condiciones El Niño

Thermal anomalies

In December 1997 and February 1998 the study area showed high thermal anomaly values mainly in coastal stations associated with cold upwelling waters, whereas during the May 1998 cruise a decrease in the thermal anomaly values was registered, which indicates that the phenomenon began to move away (Fig. 4).

Distribution and abundance of zooplankton biomass

The zooplankton biomass showed high spatial variability during each cruise, being highly abundant (> 800 cc m^{-3}) in the coastal stations off Arica, Iquique and Río Loa during December 1997 (Fig. 2d). A similar spatial trend was observed during February and May 1998. However, zooplankton biomass did not differ among cruises nor between El Niño conditions (Table 3).

Spatial distribution of anchoveta eggs and larvae

Except for December 1997, abundance of anchoveta eggs was low (< 15,000 eggs 10 m^{-2}) throughout the sampled study area (Fig. 4). Two isolated clusters of anchoveta eggs were registered in nearshore zones off Arica and Antofagasta in December 1997 (Figs. 4). The abundance of anchoveta larvae was low during the December 1997 cruise. In February 1998 the highest egg density (58,937 eggs 10 m^{-2}) was collected at the nearshore stations off Antofagasta, where low larval abundance was found. During May 1998, results showing a low abundance of anchoveta larvae was obtained (mean ± SD, 94 ± 340 ind. 10 m^{-2}, Table 2), however restricted only to some nearshore stations off Arica, Rio Loa and Tocopilla. During this period the vertical distribution of anchoveta larvae was influenced by the increase of surface temperature, limiting aggregations near the coast above the 15°C isotherm and at mid-depths (20-100 m depth) (Fig. 6).

Relationship of biological variables with the different El Niño conditions

There were significant differences in the abundance of larval anchoveta among cruises (K-W test, $F_{(1, 201)} = 26.32$; $P < 0.001$), as well as among stations ($F_{(1, 201)} = 9.36$; $P < 0.05$). The egg abundance showed important seasonal differences ($F_{(1, 201)} = 5.40$; $P < 0.05$) and significant differences ($F_{(1, 201)} = 5.79$; $P < 0.05$) in egg abundance were observed between inshore and offshore stations (Table 3).

Table 2. Average values of zooplankton biomass and anchoveta eggs-larvae registered for the different time periods / Valores promedio para la biomasa de zooplancton, huevos y larvas de anchoveta en los diferentes periodos

Biomass	Before El Niño			During El Niño		
	Sep.96	May.97	Aug.97	Dec.97	Feb.98	May.98
Zooplankton (cc m^{-3})						
Range (min-max)	79-484	33-416	61-534	63-1331	54-758	35-888
Median	218	176	192	399	252	109
Mean	240	192	197	450	307	164
SD	103	107	95	284	190	177
Eggs (N°10 m^{-2})						
Range (min-max)	0-29,539	0-6,751	0-71,908	0-66,293	0-58,937	0-16,871
Median	1,265	621	829	1,726	4,038	8795
Mean	1,356	269	3,239	3,730	2,233	517
SD	5,198	1,167	12,529	14,779	10,180	2,892
Larvae (N°10 m^{-2})						
Range (min-max)	0-19,916	0-1,510	55-17,614	0-3,933	0-2,243	0-1,937
Median	371	93	550	256	113	169
Mean	1,526	109	1,780	315	134	94
SD	4,126	305	3,369	784	396	340

Table 3. Results of Kruskal-Wallis test for anchoveta eggs-larvae abundance and zooplankton biomass with El Niño conditions (before El Niño/during El Niño) and station locations (nearshore/offshore) / Resultados del test Kruskal-Wallis para la abundancia de huevos y larvas de anchoveta, biomasa de zooplancton con las distintas condiciones El Niño (antes El Niño/durante El Niño) y con la ubicación de las estaciones (cerca de la costa/mar adentro)

Source	SS	df	MS	*F*-ratio	*P*-level
Eggs					
El Niño	11.17	1	11.17	5.40	0.021*
Stations	11.98	1	11.98	5.79	0.017*
Interaction	0.71	1	0.71	0.34	0.560
Error	416.09	201	2.07		
Larvae					
El Niño	83.66	1	83.66	26.32	0.000**
Stations	29.74	1	29.74	9.36	0.003*
Interaction	9.32	1	9.32	2.93	0.088
Error	638.84	201	3.18		
Zooplankton					
El Niño	0.16	1	0.16	0.03	0.862
Stations	17.76	1	17.76	3.32	0.070
Interaction	0.09	1	0.09	0.02	0.894
Error	1076.02	201	5.35		

* $P < 0.05$; ** $P < 0.001$

The Principal Component Analysis (PCA) between biological variables (*e.g.*, anchoveta eggs-larvae and zooplankton biomass) and oceanographic variables before El Niño showed that the two first components explained 70.19% of the variance. In this period two types of associations were observed: the first group was composed of biological variables associated with high levels of dissolved oxygen (4.5-6.7 ml L^{-1}), and the second group was composed only of oceanographic variables (*e.g.*, SST; Salinity) (Fig. 7a). During the El Niño, the two first components explained 63.91% of the variance. Moreover, similarly to the previous period, two other associations were detected: the first group the zooplankton to high values of sea-surface temperature and salinity. The second group was composed of anchoveta eggs and larvae associated with dissolved oxygen (Fig. 7b).

Relationship between physical and biological variables

Before El Niño conditions, anchoveta larvae showed a significant positive relationship with thermal anomalies, and a negative relationship with salinity (Table 4). Anchoveta eggs showed significant negative relationships with SST and salinity. Zooplankton showed

Table 4. Spearman correlation coefficient between different biological variables during the El Niño conditions and sea-surface temperature (SST), thermal anomaly, salinity and dissolved oxygen. Zoo= zooplankton biomass / Coeficientes de correlación R Spearman entre las diferentes variables biológicas durante las diferentes condiciones El Niño con la temperatura superficial del mar (SST), anomalías térmicas, salinidad y oxigeno disuelto. Zoo= biomasa de zooplancton

Condition	Variables	SST	Anomaly	Salinity	Oxygen
Before El Niño	Larvae	-0.15	0.43*	-0.48*	-0.29
	Eggs	-0.57*	0.26	-0.53*	-0.53*
	Zoo	-0.09	0.36*	-0.15	0.55*
During El Niño	Larvae	-0.52*	0.45*	-0.30	0.12
	Eggs	-0.36*	0.64*	-0.17	0.20
	Zoo	0.64*	-0.07	0.69*	0.14

*$P < 0.05$

positive and significant changes with thermal anomalies and dissolved oxygen concentrations. In general, during this period low correlation coefficients (r ~0.4-0.5) were estimated between biological and physical variables (Table 4).

During El Niño conditions, anchoveta eggs and larvae showed significant relationships with changes in thermal anomalies and SST, with low correlation coefficients (r ~0.5; Table 4). Anchoveta larvae showed a negative and significant relationship with salinity values. It is remarkable the strong positive relationship detected between zooplankton biomass and SST and salinity; however, only with salinity did the zooplankton biomass show a high correlation coefficient (r ~ 0.7).

Discussion

In this study, the abundance of anchoveta eggs and larvae showed variations in their distribution patterns during El Niño 1997-98 conditions, while the traditional spawning sites for anchoveta (Loeb & Rojas 1988) were gradually moved southward as the El Niño intensified. This disturbance is explained both by changes in the positive thermal anomalies that increased gradually (~3.5-4°C) with the arrival of El Niño conditions, as well as by high salinity, which is a typical feature of surface water bodies of subtropical origin. With the onset of the El Niño event, warm water (> 15°C) was moved southward due to a weakening of the upwelling. In the 1997-1998 period, the 15°C isotherm remained at 70 m depth and was located 50 nautical miles offshore while on the surface the physical effects to El Niño reached central-southern Chile (Arcos *et al*. 2001).

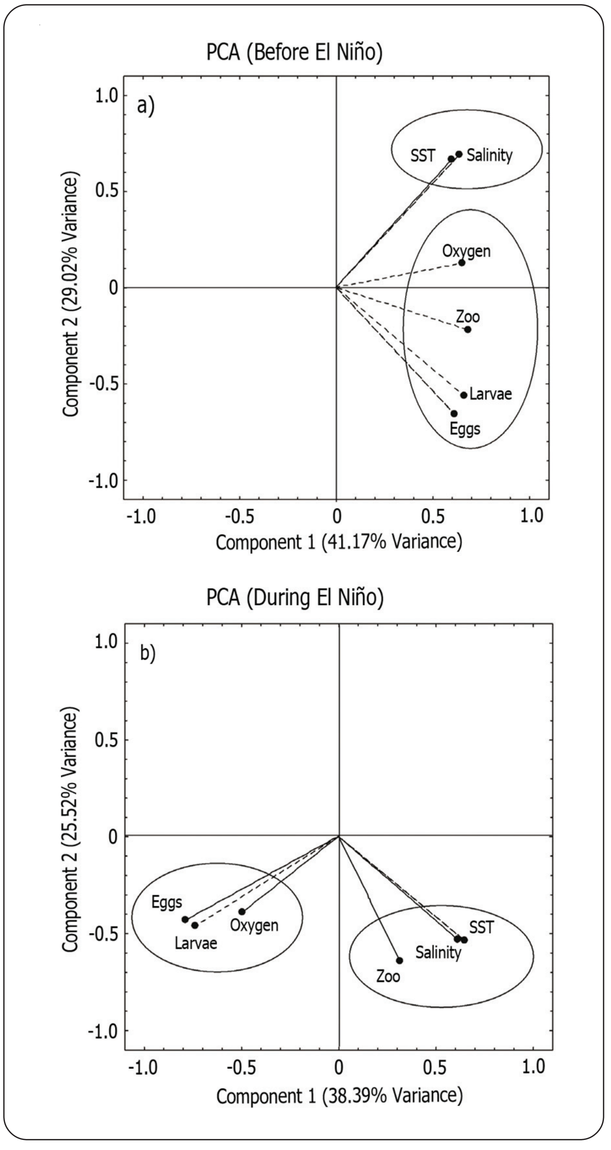

Figure 7. Projection of components 1 and 2 of the Principal Component Analysis (PCA), for the physical and biological variables in different El Niño conditions. SST= sea-surface temperature; Zoo= zooplankton biomass / Proyección de los componentes 1 y 2 del Análisis de Componentes Principales (ACP), para las variables físicas y biológicas, en diferentes condiciones El Niño. SST= temperatura superficial del mar; Zoo= biomasa del zooplancton

During the warm phase of El Niño 1997-1998, surface waters were warmer (> 20°C), the fronts weakened or disappeared (Blanco *et al*. 2002), and the photic layer deepened below 100 m (Gonzalez *et al*. 1998). Along with the changes in the water bodies associated with the coastal zone, the thermocline, oxycline and minimum oxygen layer (MOL) also deepened, causing oxygenation of the subsurface waters near the shelf and shelf break (Blanco *et al*. 2002). The coastal upwelling persisted during the warm phase (Carr *et al*. 2002) but the nutricline deepened, thus limiting the input of new nutrients to the photic area and favouring regenerated production (Carr 2003).

The measurements made during these cruises correspond to a transition summer of an El Niño event (or Pre-El Niño, January 1997) and an El Niño Winter (July 1997). The effects of El Niño 1997-1998 began to register as a positive thermal anomaly since March 1997, however, January 1997 can be considered as a transition between La Niña and El Niño conditions, which was marked by very clear days and a relaxation of the upwelling favourable winds (Rutllant 1993[2]). As a result, an anomalous decrease in the frequency and magnitude of upwelling events at the study area also occurred. Based on satellite images of sea surface temperature (IGOSS, NOAA image), it was found that during December 1997 the positive thermal anomaly was approximately 3-4°C (González *et al*. 1998).

An immediate consequence to the organisms that face a physical environment with the oceanographic features mentioned above, involves acquiring the ability to continually adjust to the components of low-frequency variation, or to face the risk of being unable to adapt to local conditions (Bakun 2001). We have observed that in response to the arrival of warm waters during the active phase of the El Niño event, anchoveta larvae gradually deepen its vertical distribution at the same time that the thermocline was deepened below 50 m, in response to the entrance of Kelvin waves in nearshore areas (Escribano *et al*. 2004). However, it is known that the Humboldt Current System presents an extensive minimum oxygen layer near the surface (< 100 m depth; Morales *et al*. 1996) with low concentration values (approx. 1.0 ml O_2 L^{-1}) in its higher limit, associated to the intrusion of water masses of equatorial subsurface origin, as well as to cold waters from coastal upwelling. Thus, the depth attained by the anchoveta larvae through vertical migration could not exceed the upper limit of the minimum oxygen layer.

From an evolutionary perspective, the anchoveta has adapted to the coastal upwelling ecosystems of northern

[2]Rutllant J. 1993. Coastal lows and associated southerly winds events in north-central Chile. Preprints of the IV International Conference on Southern Hemisphere Meteorology and Oceanography, pp. 268-269. American Meteorological Society, Hobart, Australia, 29 March - 2 April 1993.

Chile, taking advantage of high levels of chlorophyll as well as favourable oceanographic and topographic characteristics present at some sites during the active upwelling phase to spawn in a highly favourable habitat providing food, protection and growth for the larvae and post-larvae of pelagic species (Rojas 2003). However, a period of environmental stress caused by the El Niño event has an immediate effect on the anchoveta population which are moving their usual spawning sites southwardly (Espino 1999). The immediate impact on the anchoveta populations is highlighted through the differences in the distribution patterns observed for its early life stages over the different campaigns. Alterations in the aggregation patterns caused by strong environmental changes adversely affect the ecological relationships, among others: the feeding behaviour, the susceptibility of the species to natural predation (*e.g.*, predator-prey relationships), distribution of spawning areas and therefore, the future abundance of the population (Perry *et al*. 2002). For example, in regards to the cod from the northwest Atlantic, the changes in the aggregation patterns of its larvae had a strong impact on the population dynamics, altering the susceptibility of this species to fishing pressures (Rose & Kulka 1999).

With the arrival of warm surface water during El Niño conditions, high levels of zooplankton biomass on the northern coast of Chile have been recorded. The presence of warm water masses would produce an ecological replacement of plankton (Lluch-Belda *et al*. 2005) and a change in the size structure of the zooplankton, from large to a smaller size (Ulloa *et al*. 2001). This replacement in the phyto- and zooplankton composition could be due mostly to exotic species that differ in shape and size to the actual ones found during cold non-El Niño conditions (González *et al*. 2000, Hidalgo & Escribano 2001). Anchoveta larvae are able to directly feed on phytoplankton; however, this small pelagic fish might not have a diet mainly based on filtering phytoplankton, due to its ability for capturing prey (Konchina 1991, Van der Lingen 2002) which is composed mainly of dinoflagellates, microzooplankton, small copepods and crustacean larvae (Llanos *et al*. 1996, Llanos-Rivera *et al*. 2004). Thus, anchoveta are incapable of sustaining growth based exclusively on a diet composed of phytoplankton (Espinoza *et al*. 2000). Consequently, high mortality rates may result because of a low availability of trophic resources in some coastal areas of northern Chile, forcing the species to use energy storage (Cubillos *et al*. 2001) that involves changing its reproductive tactics while waiting for favourable environmental conditions (*i.e.,* skipping spawning).

The multivariate analysis showed changes in the relationships between the physical and biological variables during different El Niño conditions. Before the El Niño event, anchoveta larvae and eggs were concentrated mainly in coastal stations with intermediate values of dissolved oxygen (~5.5 mg L^{-1}) and a low abundance (~300 cc m^{-3}) of zooplankton biomass. This suggests that during this period the associations among different variables would not be so strong. During the El Niño event both anchoveta larvae and eggs show a marked segregation only with oxygen values close to 5 mg L^{-1}, not so with other hydrographic variables. Thus, it is reasonable to assume that the different distribution patterns of anchoveta eggs and larvae found off the northern Chilean coast would be the result of an ongoing search of favorable environmental conditions that apparently are influenced by oxygen.

Changes in the typical reproductive seasonality (Cubillos *et al*. 2001) of the anchoveta probably represent variability in the distribution of eggs and larvae in relation to environmental alterations in the short, medium and long term. The thermal conditions in northern Chile during periods before and after El Niño and its relation to the anchoveta distribution patterns partially explain the displacement of anchoveta spawning areas. The effect of the progressive increase in temperature would leave a strip where the spawning is virtually non-existent, except for a few nearshore stations located in Arica and Antofagasta, it was possible to find anchoveta egg cores. Consequently, the distribution patterns of anchoveta larvae in northern Chile were altered as part of a strategy to cope with strong environmental changes. In agreement with Bertrand *et al*. (2004a), the anchoveta behaviour seems to be forced by bio-physical requirements as a result of adaptation to highly variable environmental conditions. We believe that events of this magnitude partially explain anchoveta population dynamics because of strong climate changes that occur at different time scales in the HCS, significantly altering the successive recruitment processes in northern Chile after a strong El Niño event.

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