Larval fish assemblages off central Chile upwelling ecosystem

Asociaciones ictioplanctónicas del ecosistema de surgencias de Chile central

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Resumen.- Se detectaron diferencias espaciales (a escala vertical y horizontal) y estacionales en las asociaciones de larvas de peces recolectadas en estaciones fijas sobre el talud y plataforma continental frente a Chile central muestreadas por 24 h durante octubre de 1998 y julio de 1999. Durante octubre, la columna de agua en las estaciones de la plataforma y talud estuvo caracterizada por aguas frías y salinas, indicativa de un reciente evento de surgencia; durante este periodo las asociaciones de larvas de peces estuvieron estructuradas por la hora del día en la estación de la plataforma. Esta asociación larval estuvo dominada por el pez mesopelágico *Maurolicus parvipinnis* y anchoveta *Engraulis ringens*. Por otra parte, sobre el talud continental, el ictioplancton estuvo estructurado verticalmente, con diferentes asociaciones en función de la profundidad. La asociación estuvo dominada por *M. parvipinnis* y el mictófido *Hygophum bruuni*. Durante julio de 1999, las condiciones oceanográficas se caracterizaron por una mayor temperatura superficial, inversión térmica y una capa superficial de baja salinidad (33,6-33,8). Las asociaciones ictioplanctónicas de la plataforma y el talud estuvieron estratificadas verticalmente, y se agregaron bajo la haloclina. Las larvas de *E. ringens* y *H. bruuni* fueron altamente abundantes en ambas estaciones, y varias especies de hábitat submareal/intermareal (*Hypsoblennius sordidus, Sebastes capensis*) fueron recolectadas sobre la plataforma. La importancia de las características oceanográficas en la estructura de las asociaciones de larvas de peces frente a Chile central cambió entre ambos periodos de muestreo, siendo más notable durante julio (efectos de la capa de baja salinidad) que en octubre (presencia de aguas de surgencia).

Palabras clave: Ictioplancton, Pacífico suroriental, surgencia, haloclina

Abstract.- Spatial (both vertical and horizontal) and seasonal differences were detected in larval fish assemblages from samples collected off central Chile. Vertically-stratified sampling was carried out over the slope and continental shelf off Talcahuano in central Chile, during October 1998 and July 1999 to examine differences in larval fish assemblages. During October, the entire water column in the shelf and slope stations was characterized by cold and saltier waters, indicative of a recent upwelling event; during this period the larval fish assemblage was structured by time of the day in the shelf station. This assemblage was dominated by larvae of the mesopelagic lightfish *Maurolicus parvipinnis* and anchoveta *Engraulis ringens*. By contrast, ichthyoplankton was vertically structured in the slope station, showing different taxa associations in function of the depth (largely dominated by *M. parvipinnis* and the myctophid *Hygophum bruuni*). During July 1999, oceanographic conditions were characterized by higher surface temperatures, thermal inversion and a low salinity surface layer (33.6-33.8). Larval fish assemblages from slope and shelf were vertically stratified, and were aggregated below the halocline. Larval *E. ringens* and *H. bruuni* were highly abundant in both stations, and larvae of several taxa of subtidal/intertidal habitat (*Hypsoblennius sordidus, Sebastes capensis*) were collected over the shelf. During both periods the oceanographic features affecting the structure of larval fish assemblages off central Chile changed, wich was more noticeable during July (effects of the low salinity layer) than October (presence of recently upwelled waters).

Key words: Ichthyoplankton, southeast Pacific, upwelling, halocline

Introduction

In eastern boundary systems worldwide, wind-driven coastal upwelling injects nutrients to the photic layer producing high levels of primary production and, as such, constitutes one of the most important mesoscale oceanic physical processes (Daneri *et al.* 2000, Montero *et al.* 2007). Along the southeast Pacific Ocean, the Humboldt Current System supports one of the largest epipelagic fisheries in the world (Bakun 1996). An important upwelling area is located off Talcahuano in central Chile (36°S, 73°W), which is characterized by the seasonal

occurrence of 3-10 d southerly and southwesterly wind events during spring-summer, producing alternating upwelling and relaxation conditions (Strub *et al.* 1998, Figueroa & Moffat 2000, Sobarzo *et al.* 2007). The wind forcing generates upwelling of cold, nutrient-rich Equatorial SubSurface Waters (ESSW) leading to subsequent increases in primary and secondary production rates (Daneri *et al.* 2000) and therefore, favourable feeding conditions for larval fishes among other plankton organisms (*i.e.* high concentrations of copepod eggs and nauplii; Grunewald *et al.* 2002). However, if southerly wind events are frequent and/or persistent, the probability of offshore larval transport through the Ekman surface layer increases. Conversely, the prevailing northerly winds during late autumn and winter induce a net coastward flux of the Ekman layer, enabling the maintenance of less cold Surface SubAntarctic Waters (SSAW) which favours the retention of fish eggs and larvae along the coast, although productivity is substantially lower than during the upwelling season (Castro *et al.* 2000, Cubillos *et al.* 2007, Montero *et al.* 2007). Also, others processes at seasonal scale may influence the vertical structure of the water column, such as the mixed layer's heat balance which is dominated by solar radiation during summer, and the freshwater balance, which is dominated by river discharge and precipitation with maxima in June and July (Sobarzo *et al.* 2007). Under this scenario, marine fish populations living in the area must adjust their reproductive tactics to deal with environmental heterogeneity and thereby maximize larval survival (Castro *et al.* 2000, Landaeta & Castro 2002, Sponaugle *et al.* 2002, Landaeta *et al.* 2006, Lett *et al.* 2007).

Life histories of fish species may evolve to synchronize their reproductive activities to the frequency of certain oceanographic events (Bakun 1996, Sponaugle *et al.* 2002) which implies spawning at selected areas and times. The co-occurrence of individual species in a larval fish assemblage not only results from a similar spawning behaviour of several species, but it also suggests that they share common requirements during their early life history (Nonaka *et al.* 2000). An approach for understanding the sympatric occurrence of eggs and larvae of marine fishes and the influence of physical and biological processes on these associations is to study the structure and dynamic of larval fish assemblages. (Smith *et al.* 1999, Berasategui *et al.* 2004, Espinosa-Fuentes & Flores-Coto 2004, Vélez *et al.* 2005, Peguero-Icaza *et al.* 2008). For example, Sánchez-Velasco *et al.* (2006) described that cyclonic circulation inside a shallow bay was linked to the spatial distribution of a coastal assemblage that spread out in the same area of circulation. Presence of more stable water column, wind induced mixing and the depth and the strength of the thermocline may also influence the

abundance and vertical distribution of larval fish assemblages (Gray & Kingsford 2003, Sabatés 2004, Sánchez-Velasco *et al.* 2007). Also, even in very nearshore areas, larval fish assemblages seem to be vertically structured at a small scale (a few meters) (Borges *et al.* 2007a).

Despite the importance of the coasts of southeast Pacific, particularly central-south Chile, as some of the most productive fishing areas in the world, larval fish assemblage studies are scarce. These studies have considered interannual (Loeb & Rojas 1988) and seasonal variability (Balbontín & Bravo 1999, Hernández-Miranda *et al.* 2003, Vélez *et al.* 2005) and the effects of El Niño events (Rodriguez-Graña & Castro 2003), but all of them off northern and central Chile. However, there are several aspects about spatial and temporal variability of larval fishes off central-south Chile which are still unknown, and to date there is no information on the vertical structure of larval fish assemblages in this zone. Since this area is affected by environmental variability in a seasonal frequency as upwelling events during spring-summer, and drastic increases of the freshwater input in the coastal area during winter, we should also expect seasonal differences of the fish larval assemblages structure due to physical forcing (advection, vertical structure of the water column) during upwelling favourable (October) and non favourable (July) months over the continental shelf and slope. Therefore, our hypothesis is that spatial (shelf and slope) and temporal (October-July) variability of larval fish assemblages off central Chile is related with seasonal occurring mesoscale physical processes (e.g. upwelling).

Material and methods

Study area

The study area (36-37ºS, Fig. 1) is located at the coastal edge of the northward-flowing Humboldt Current system off central Chile, and is bounded by the Itata Canyon to the north and the Biobio Canyon to the south. The continental shelf narrows from 60 km in the north to 25 km in the south over an alongshore expanse of 70 km (Sobarzo & Djurfeldt 2004). On this shelf, there are several embayments utilized as spawning and nursery zone by several marine fishes (Castillo *et al.* 1991, Landaeta & Castro 2006a), two important rivers (Biobio and Itata), and one prominent point (Punta Lavapié) that is an important coastal upwelling site in central Chile.

Sampling design and collection of samples

Oceanographic cruises were carried out during 18-23 October 1998 (MIRC I, spring) and 9-14 July 1999 (MIRC II, winter) onboard RV Abate Molina, as part of a
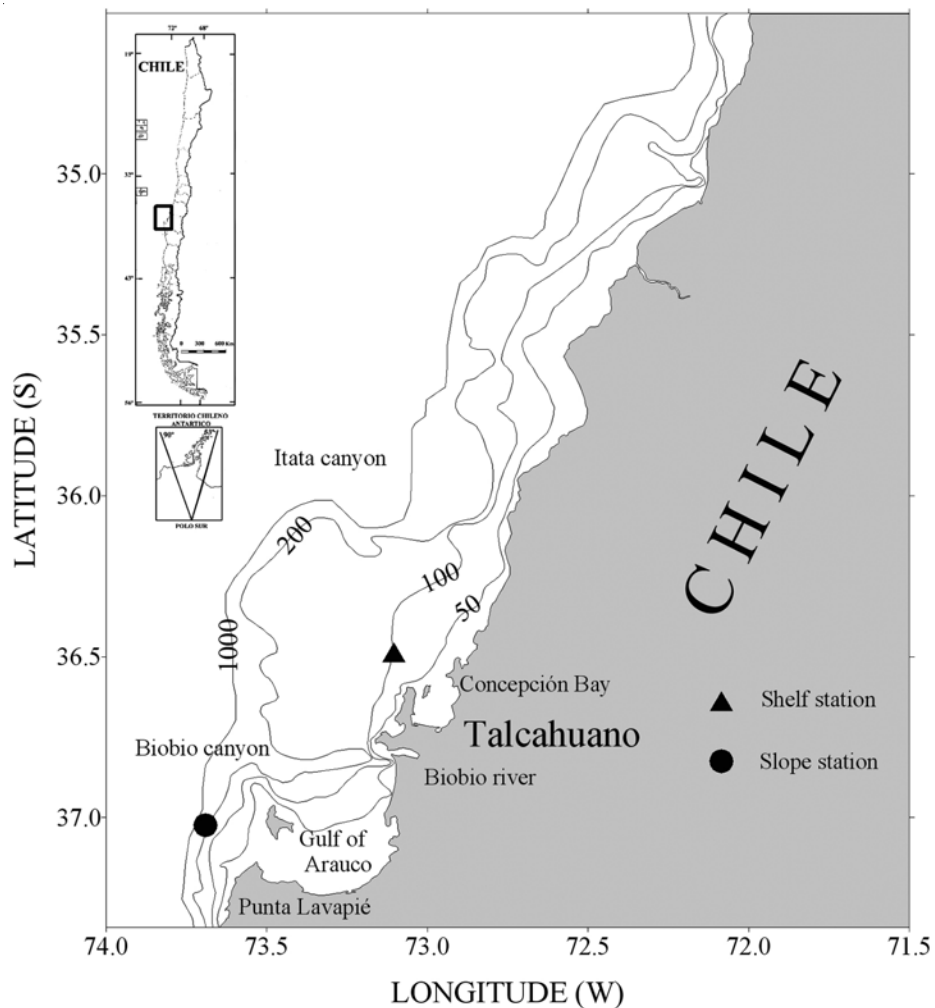
Figure 1

Map showing the location of stations where 24-h sampling was carried out over the continental shelf (black triangle) and slope (black circle) in central Chile during October 1998 and July 1999

Mapa que muestra la ubicación de las estaciones de 24 h llevadas a cabo durante octubre de 1998 (primavera austral) y julio de 1999 (invierno austral), sobre la plataforma continental (triángulo negro) y talud (círculo negro) en Chile central

project designed to determine carbon flux rates in the Humboldt Current System (FONDAP-Humboldt) (Morales *et al*. 2007). During both cruises, two stations were sampled over a period of 24 h, one over the continental shelf off Talcahuano and another on the slope off Punta Lavapié, Chile (Fig. 1). At these stations hydrographic casts were performed to 200 m or 10 m above the seafloor with a Seabird SB-19 CTD (Conductivity–Temperature–Depth) profiler. Other physical data obtained for the study period included selected satellite wind, sea surface temperatures (SST) and altimetry data. Wind stress data from the close to shore pixel (73.5°W-36.5°S) was extracted from ERS 2

gridded images (spatial resolution of 111 km) between 1998 and 2000. Images of Sea Surface Temperature (spatial resolution of 1.1 km) were produced by the AVHRR sensor onboard NOAA satellite series and they correspond for 20 October 1998 and 13 July 1999. The geostrophic velocity field (spatial resolution of 27.75 km) was obtained from the AVISO program (www.jason.oceanobs.com), as 10 days composite. Alongshore wind stress component estimates were computed from ERS wind reports according to the following bulk aerodynamics equation:

$$\tau = \rho\, C_d\, |V|\, V$$

Table 1

Summary of the main characteristics of the surveys carried out

Resumen de las principales características de los cruceros realizados

Cruise	Survey dates	Station	Sampling strata (m)	Number of samples (day/night)
MIRC I	18 - 23 October 1998	Shelf	0-25; 25-50	12 (6/6)
		Slope	0-50; 50-100; 100-150	18 (9/9)
MIRC II	9 - 14 July 1999	Shelf	0-10; 10-25; 25-50; 50-75	24 (12/12)
		Slope	0-25; 25-50; 50-100; 100-150	20 (12/8)

where τ is the stress vector, ρ is the density of air, V is the wind velocity, $|V|$ is the wind speed and C_d is a dimensionless drag coefficient (Okubo 1980).

Five to six oblique plankton tows (three during daytime and two or three at night) were carried out every 4 to 6 h during a period of 24 h at each station with an opening-closing 1-m² mouth Tucker trawl, equipped with three 250-μm mesh nets and a General Oceanic flowmeter mounted on the frame. The net was obliquely deployed to a maximum depth of 150 m or near the seabed in depths <150 m, and two to four strata were sampled (Table 1) depending on bottom depth. Towing speed was c. 2-3 knots. Volume filtered in each tow (October 1998: range = 61–1306 m³ tow⁻¹, mean = 423 m³ tow⁻¹, July 1999: range = 64-536 m³ tow⁻¹, mean = 313 m³ tow⁻¹) was calculated from flowmeter counts. After recovery, the nets were rinsed and ichthyoplankton samples preserved in 4% buffered formaldehyde.

All larval fishes were removed from samples, counted and identified to the lowest possible taxonomic level using descriptions by Fahay (1983), Moser (1996), and Neira *et al.* (1998). Larvae were classified according to the adult habitat as mesopelagic, epipelagic, demersal or subtidal/ intertidal, and the concentration of each taxon (larvae 1000 m⁻³) estimated at each stratum for comparisons in the vertical axis. The integrated abundance of larvae in the water column (larvae 10 m⁻²) was also estimated for each sampling station to compare the ichthyoplankton composition between shelf and slope irrespective of the sampled strata.

Data analyses

Multivariate analyses were performed to determine the seasonal and vertical variability of larval fish assemblages utilizing the software package Primer 5. Standardized ichthyoplankton abundance integrated in sampled the water column (larvae 10 m⁻²) was fourth root transformed to enhance the contribution of less abundant taxa and a Bray-Curtis similarity matrix was generated from these data. Similarities between assemblages were graphically represented by non-metric multidimensional scaling (MDS, Cox & Cox 2000) ordination. Goodness of fit was determined by a stress coefficient. Classification and MDS ordination were performed using abundance of larval fishes by strata (larvae 1000 m⁻³) instead of integrated values to determine vertical structure of ichthyoplankton assemblages by sampling month (October and July) and location (shelf and slope).

Results

Oceanographic conditions

Persistent alongshore south winds during October 1998 favoured upwelling events and produced negative (offshore) Ekman transport (mean ± 1 SD, -4.40 ± 0.34 m² s⁻¹) (Fig. 2). Sea surface temperature (SST) showed horizontal heterogeneity, with areas of colder, recently upwelled waters (<10ºC) in nearshore waters off Punta Lavapié and Concepción Bay (Fig. 3a). The larger upwelling plume of cold water (12.5-13ºC) originated off Punta Lavapié was advected offshore and extended westward to 75ºW as an anticyclone filament. The latter structure coincides spatially with an anticyclone vortex observed through geostrophic current vectors (Fig 3). Altimetry derived speeds were higher (>30 cm s⁻¹) than surrounding waters, particularly between the coastal zone and the filament. The CTD-derived data over the slope and continental shelf showed almost identical surface (<5 m) temperatures ranging between 11.29 ± 0.37ºC and 11.30 ± 0.22ºC, respectively (Fig. 4). However, mean surface salinity at the slope station was lower (34.05 ± 0.05) than that at the shelf station (34.32 ± 0.04). In deeper waters, there was a weak thermocline at both stations, varying between 25 and 49 m depth over the shelf, and between 40 and 60 m in the slope. In the slope station a surface thermocline was observed between 5 and 15 m deep. With the increase of temperature there was also a decrease in salinity. A pycnocline was observed at both stations, but was more intense over the shelf.
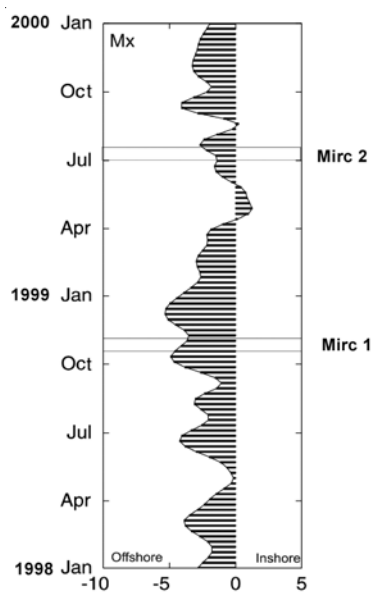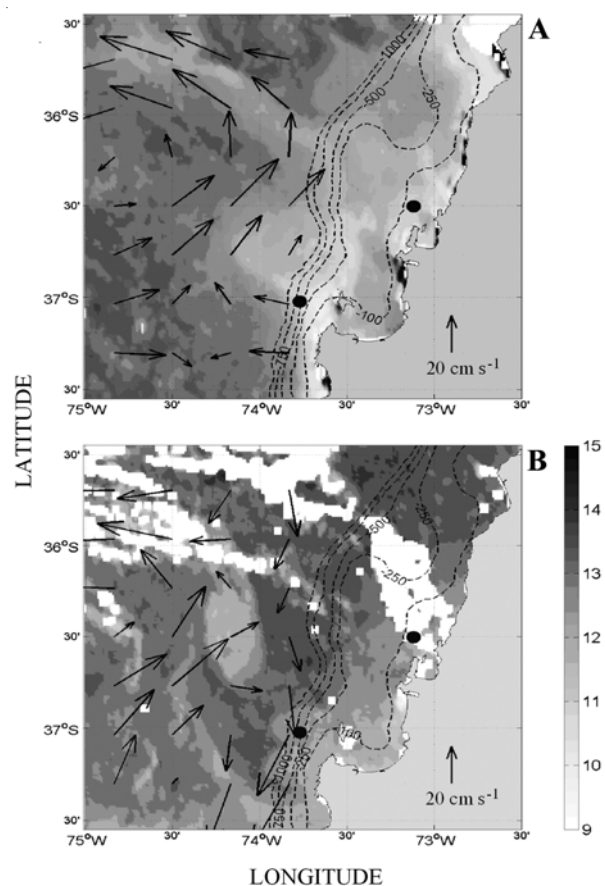
Figure 2

Time series of Ekman transport (m² s⁻¹) off Talcahuano area during 1998 and 1999. Mirc 1 and Mirc 2 correspond to sampling dates

Serie de tiempo de transporte de Ekman (m² s⁻¹) frente a Talcahuano durante 1998 y 1999. Mir 1 y Mirc 2 corresponden a las fechas de muestreo

Figure 3

Sea surface temperature (ºC) image and geostrophic flows (cm s⁻¹) off central Chile during October 20 1998 (a) and July 13 1999 (b). Image taken from AVHRR sensor

Temperatura Superficial del Mar (ºC) y flujos geostróficos (cm s⁻¹) frente a Chile central durante el 20 de octubre de 1998 (a) y el 13 de julio de 1999 (b). Imagen tomada por el sensor AVHRR

The wind pattern during July 1999 was dominated by weaker, highly variable equatorward wind stress, and lower offshore Ekman transport (-1.84 ± 0.49 m² s⁻¹) than during spring (Fig. 2). The SST images showed an irregular spatial pattern, and areas of cold waters and filaments were absent (Fig. 3b). In the coastal zone, especially in the Gulf of Arauco zone (37ºS), the predominant SST was around 12ºC. An irregular pattern of geostrophic velocity field resulted from altimetry data. However, a poleward flow following the bathymetry of the slope was evident (Fig. 3b), with increasing speeds (~ 20 cm s⁻¹) off Punta Lavapié. There was a clear thermal inversion along the mixed layer at the slope station, with a subsurface maximum temperature of 13.05 ± 0.22ºC at a depth of 35 m (Fig. 4). This thermal inversion was associated with a surface low salinity layer at 35 m which ranged from 33.71 ± 0.05 to 34.12 ± 0.04. Below the low-salinity layer, temperature values decreased and salinity increased steeply. At the shelf station, the mixed layer was deeper than that in the slope (~ 50 m) and uniform in temperature, but the salinity increased with depth from 33.85 ± 0.07 to 34.09 ± 0.09. Density profiles indicated a stable water column in the first 30 m depth with a pycnocline at 50 m (Fig. 4).

Larval fish assemblages

A total of 10,961 larval fishes were captured during both cruises. These comprised 34 taxa representing 25 families (Table 2). The MDS ordination plots of similarities for integrated data defined four assemblages according to sampling month (October and July) and location (shelf and slope): an October Shelf Assemblage (OSH), October Slope Assemblage (OSL), July Shelf Assemblage (JSH), and a July Slope Assemblage (JSL) (Fig. 5).

The OSH assemblage was dominated by larval anchoveta *Engraulis ringens* (mean = 23 larvae 10 m⁻²), common sardine *Strangomera bentincki* (21 larvae 10 m⁻²) and mesopelagic lightfish *Maurolicus parvipinnis* (24 larvae 10 m⁻²) (Table 2). Other species such as hake
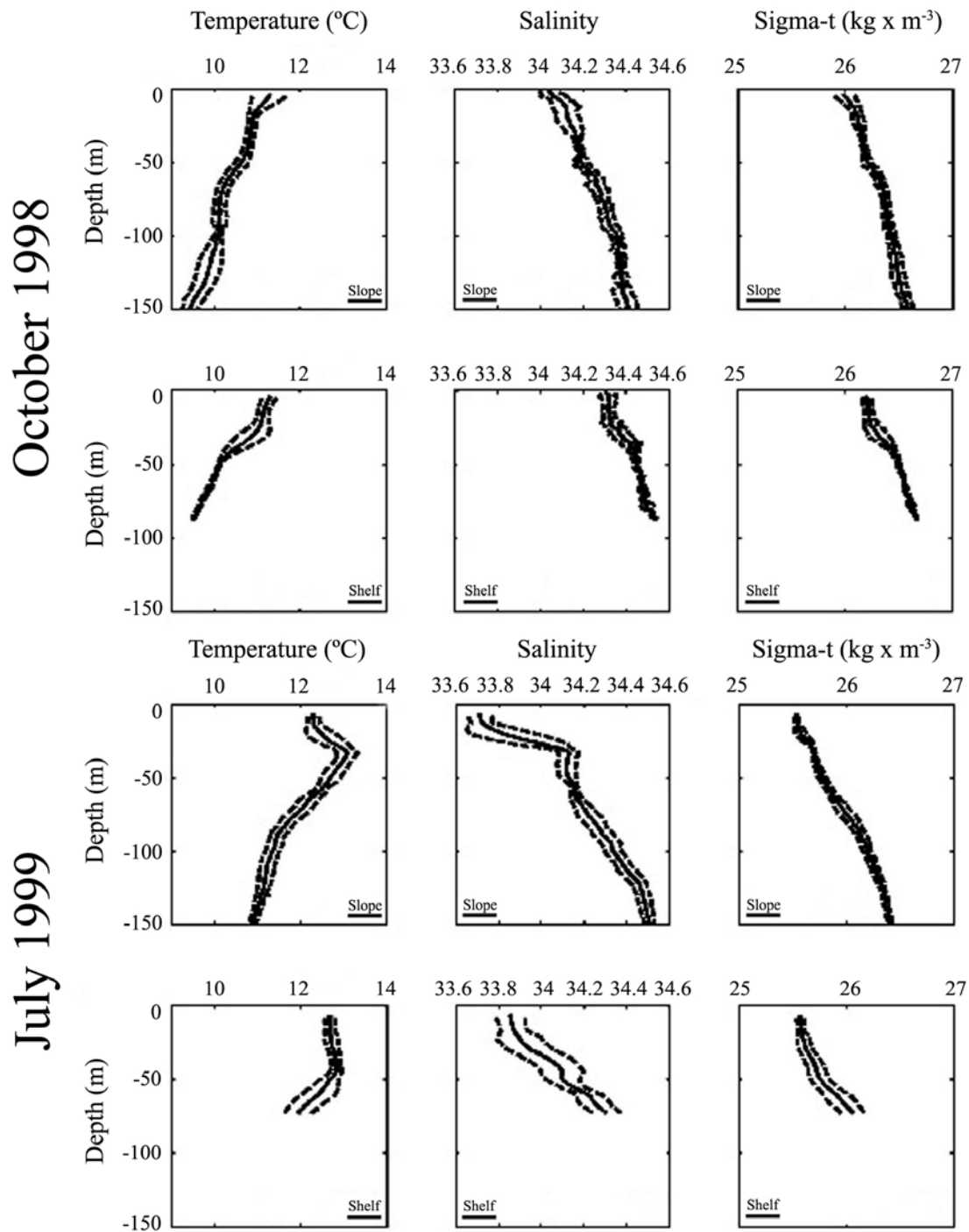
Figure 4

CTD derived water temperature (°C), salinity and sigma-t (kg x m⁻³) during Mirc 1 (October 1998) and Mirc 2 (July 1999) surveys over continental slope and shelf

Perfiles verticales de temperatura (°C), salinidad y sigma-t (kg x m⁻³) derivados del CTD durante los cruceros Mirc 1 (octubre de 1998) y Mirc2 (julio de 1999) sobre la plataforma y talud continental

Table 2

Composition of larval fishes collected during MIRC 1 (October 1998) and MIRC 2 (July 1999) cruises off Talcahuano area, central Chile. Larval abundances are expressed as individuals 10 m^{-2}; SD = standard deviation, %F = frequency of occurrence

Composición de larvas de peces recolectadas durante los cruceros MIRC 1 (octubre 1998) y MIRC 2 (julio 1999) frente al área de Talcahuano, Chile central. Las abundancias larvales están expresadas como individuos 10 m^{-2}; SD = desviación estándar, %F = frecuencia de ocurrencia

| | October 1998 | | | | | | July 1999 | | | | | |
| | Continental Shelf | | | Slope | | | Continental Shelf | | | Slope | | |
	Mean abundance (ind per 10 m^2)	SD	%F	Mean abundance (ind per 10 m^2)	SD	%F	Mean abundance (ind per 10 m^2)	SD	%F	Mean abundance (ind per 10 m^2)	SD	%F
Mesopelagic taxa												
Bathylagus sp.	-	-	-	1,65	0,91	0,07	-	-	-	0,94	-	0,11
Diogenichthys atlanticus	-	-	-	6,26	-	0,13	-	-	-	-	-	-
Diogenichthys laternatus	-	-	-	-	-	-	0,90	0,07	0,07	1,61	0,86	0,77
Hygophum bruuni	1,16	0,35	0,98	30,28	23,58	3,89	102,36	53,53	15,61	148,36	183,97	88,77
Lampanyctodes hectoris	2,11	1,52	1,78	30,00	14,51	3,85	-	-	-	-	-	-
Lampanyctus iselinoides	-	-	-	3,33	0,47	0,14	1,61	1,26	0,12	4,51	6,12	2,16
Maurolicus parvipinnis	24,28	20,44	25,62	546,79	397,46	70,24	-	-	-	-	-	-
Melamphaidae	-	-	-	0,77	-	0,02	-	-	-	-	-	-
Protomyctophum chilensis	-	-	-	14,01	18,44	1,80	0,64	0,25	0,03	1,02	-	0,12
Protomyctophum crockeri	-	-	-	12,28	-	0,26	-	-	-	1,42	0,57	0,34
Epipelagic taxa												
Engraulis ringens	22,99	9,36	29,12	65,06	50,66	8,36	451,32	115,56	68,85	5,11	2,98	1,22
Ethmidium maculatum	-	-	-	5,17	3,33	0,33	1,32	-	0,03	-	-	-
Normanichthys crockeri	2,13	2,17	1,35	3,00	-	0,13	18,97	7,12	2,89	-	-	-
Sardinops sagax	-	-	-	1,50	-	0,03	-	-	-	-	-	-
Strangomera bentincki	20,52	22,24	25,99	41,40	19,76	4,43	5,75	3,47	0,88	-	-	-
Stromateus stellatus	-	-	-	-	-	-	0,40	-	0,01	-	-	-
Demersal taxa												
Coelorhynchus sp.	-	-	-	2,44	1,42	0,21	-	-	-	-	-	-
Genypterus sp.	-	-	-	1,42	0,39	0,09	1,38	-	0,04	1,46	0,55	0,35
Hippoglossina macrops	0,47	-	0,10	-	-	-	7,37	5,92	1,12	2,49	1,48	1,19
Merluccius gayi	7,29	5,43	6,15	32,69	16,95	4,20	34,29	22,54	5,23	14,12	17,89	3,38
Moridae	-	-	-	4,50	-	0,10	-	-	-	-	-	-
Ophichthyid sp.	2,27	-	0,48	1,50	-	0,03	-	-	-	-	-	-
Subtidal and Intertidal taxa												
Bovictus chilensis	-	-	-	-	-	-	0,84	0,45	0,06	-	-	-
Congiopodus peruvianus	0,47	-	0,10	-	-	-	-	-	-	-	-	-
Helcogrammoides chilensis	-	-	-	1,83	1,04	0,12	0,72	0,57	0,06	-	-	-
Hypsoblennius sordidus	3,60	3,44	3,04	5,00	1,73	0,32	4,49	2,08	0,68	2,14	-	0,26
Kyphosidae	-	-	-	-	-	-	0,71	0,37	0,04	-	-	-
Labrisomidae	-	-	-	-	-	-	0,46	-	0,01	-	-	-
Leptonotus blainvilleanus	-	-	-	-	-	-	2,34	1,59	0,24	-	-	-
Paralichthys microps	-	-	-	-	-	-	1,32	-	0,03	-	-	-
Prolatilus jugularis	0,92	-	0,19	-	-	-	3,38	1,54	0,52	-	-	-
Sciaenidae	-	-	-	-	-	-	0,97	-	0,02	-	-	-
Sebastes capensis	4,54	4,64	4,79	9,62	4,01	1,24	22,41	17,84	3,42	2,78	3,10	1,33
Syciases sanguineus	1,42	-	0,30	-	-	-	0,77	-	0,02	-	-	-
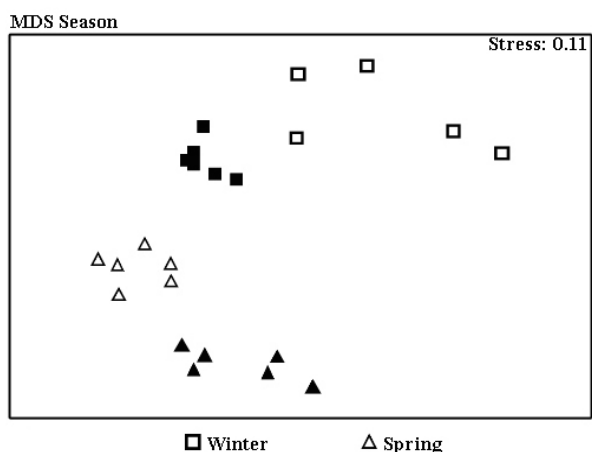
Figure 5

**MDS plot showing larval fish assemblages for both
surveys and locations. Black and white geometric
figures correspond to samples collected in the
slope and shelf stations, respectively**

Gráfico de MDS mostrando las asociaciones de larvas
de peces de ambos cruceros y localidades. Las figuras
geométricas negra y blanca corresponden a muestras
recolectadas en las estaciones del talud
y plataforma, respectivamente

Merluccius gayi, rockfish *Sebastes capensis,* goby *Hypsoblennius sordidus* and mote sculpin *Normanichthys crockeri* also occurred frequently. Epipelagic species accounted for 57% of total catch while mesopelagic larvae represented 28%. Subtidal/intertidal and demersal larval fishes captured comprised approximately 8% and 7%, respectively. The MDS plot by strata showed a diel aggregation, however, the vertical structure was not evident (Fig. 6a). The larval fish assemblage from shelf (OSH) was composed of a highly abundant night-time group in the shallower stratum (0-25 m) which included *S. bentincki, M. parvipinnis, E. ringens* and *M. gayi* (Fig. 7a, Table 3), and a group found mainly during day which comprised mostly *S. capensis* and *H. sordidus.* In addition, myctophids were found almost exclusively in the shallower strata during night (Table 3). This result may be more associated with the water column mixing than to day/night effects.

The more frequent and abundant taxa in the OSL were of mesopelagic origin, with dominant species including *M. parvipinnis* (70%; 547 larvae 10 m^{-2}), and the myctophids *Hygophum bruuni, Lampanyctodes hectoris, Lampanyctus iselinoides* and *Protomyctophum chilensis.* Larvae of demersal taxa such as *M. gayi, Genypterus* sp. and *Coelorhinchus* sp., were also more abundant and
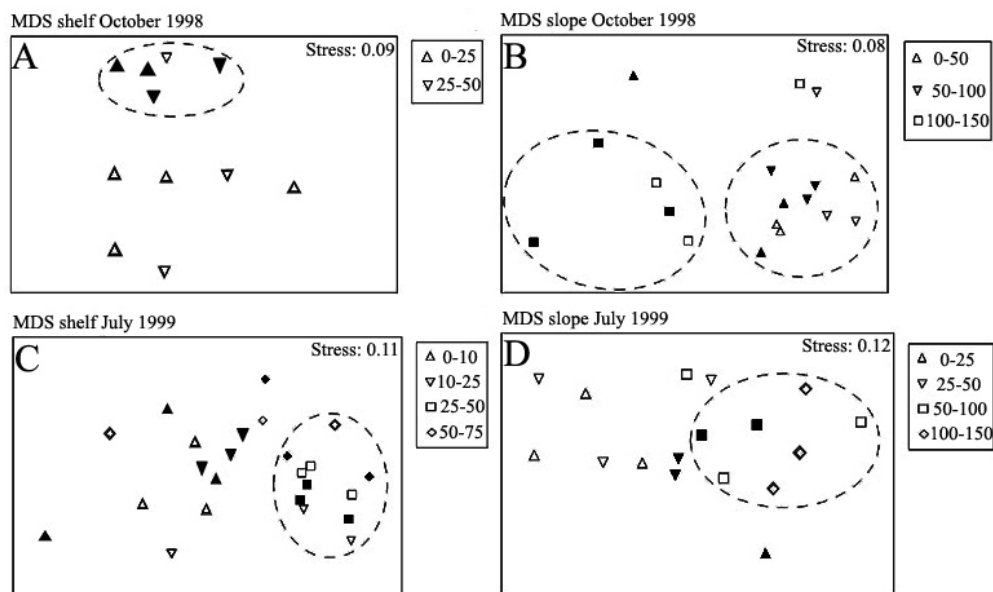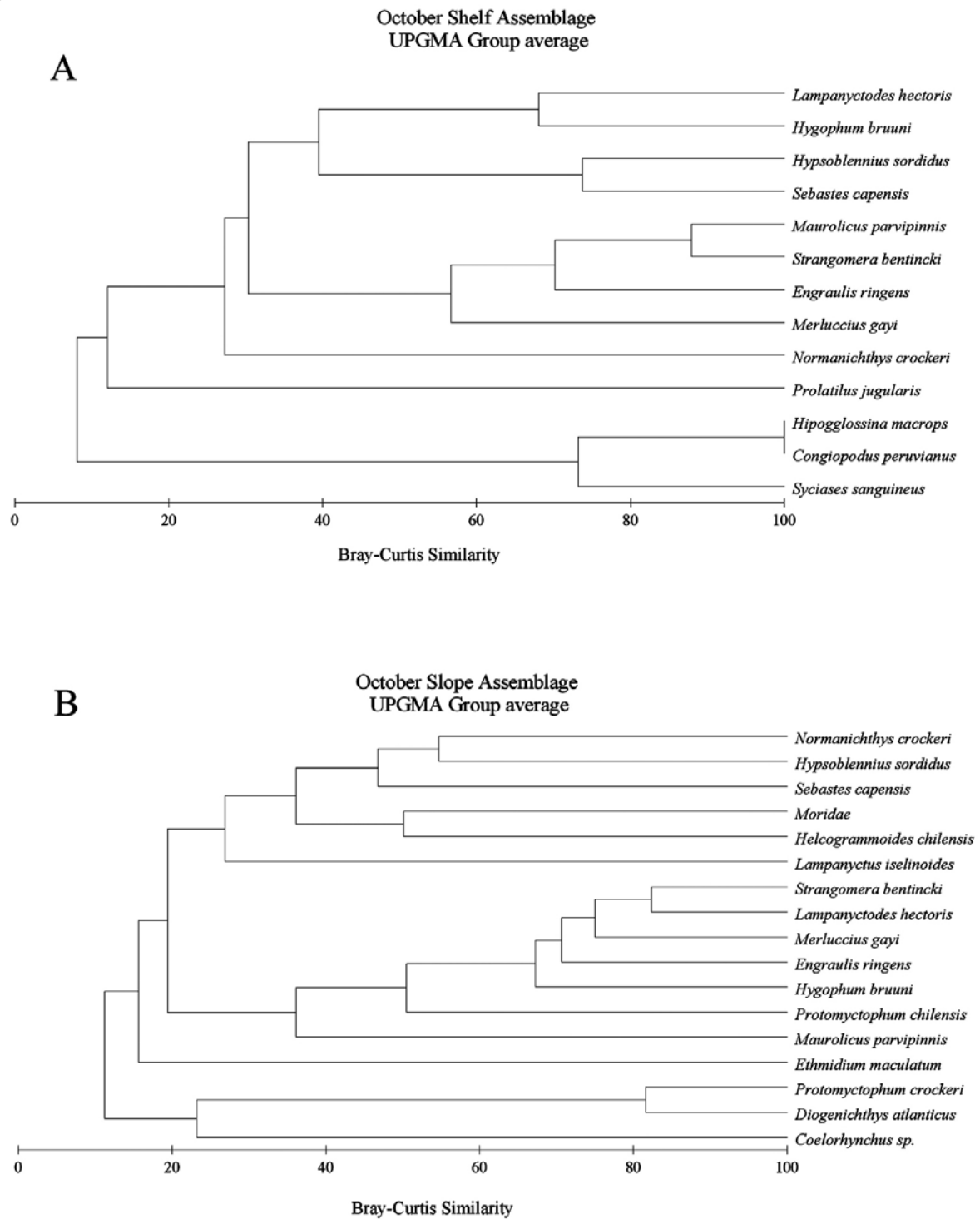

Figure 6

**MDS plots showing vertical structure of larval fish assemblages for a) shelf October station, b) slope October station, c) shelf
July station and d) slope July station. Black and white geometric figures correspond to night and day samples, respectively**

Gráficos de MDS mostrando la estructura de las asociaciones de larvas de peces para a) estación de plataforma durante octubre, b)
estación del talud durante Octubre, c) estación de plataforma durante julio, d) estación del talud durante julio. Las figuras
geométricas negra y blanca corresponden a muestras de noche y día, respectivamente

October Shelf Assemblage
UPGMA Group average

A

Lampanyctodes hectoris
Hygophum bruuni
Hypsoblennius sordidus
Sebastes capensis
Maurolicus parvipinnis
Strangomera bentincki
Engraulis ringens
Merluccius gayi
Normanichthys crockeri
Prolatilus jugularis
Hipogglossina macrops
Congiopodus peruvianus
Syciases sanguineus

Bray-Curtis Similarity

October Slope Assemblage
UPGMA Group average

B

Normanichthys crockeri
Hypsoblennius sordidus
Sebastes capensis
Moridae
Helcogrammoides chilensis
Lampanyctus iselinoides
Strangomera bentincki
Lampanyctodes hectoris
Merluccius gayi
Engraulis ringens
Hygophum bruuni
Protomyctophum chilensis
Maurolicus parvipinnis
Ethmidium maculatum
Protomyctophum crockeri
Diogenichthys atlanticus
Coelorhynchus sp.

Bray-Curtis Similarity

Figure 7

Cluster analysis showing relationship among larval fishes during October 1998 for the a) shelf station and b) slope station

Análisis de dendogramas mostrando la relación entre larvas de peces durante octubre de 1998 para la estación de
a) plataforma y b) talud continental

diverse over the slope (Table 2). Also, epipelagic larvae (13%), and particularly larval clupeiforms (e.g. *Engraulis, Strangomera*) were more abundant in the slope than on the shelf during austral spring. The MDS plot showed that SSL was stratified according to depth, i.e. > and < 100 m (Fig. 6b). The first group was formed by *N. crockeri*, *H. sordidus*, *S. capensis*, morids and *Helcogrammoides chilensis* (Fig. 7b) which were found exclusively >100 m, whereas the other taxa were collected throughout the water column (down to 150 m), although

in the deeper stratum (100-150 m) the larval abundances were considerably reduced (Table 3).

Larvae of epipelagic taxa dominated the JSH assemblage, with five taxa accounting for 73% of the total catch at the shelf station (Table 2). Most abundant species were anchoveta (69%; 450 larvae 10 m^{-2}) and *N. crockeri* (19 larvae 10 m^{-2}). Among the oceanic taxa, larval *H. bruuni* were the most abundant (16%; 106 larvae 10 m^{-2}). Demersal fishes were represented by three species (7% of total catch), whereas subtidal/intertidal fishes by 11

Table 3

Abundance at different depth strata of selected larval fishes captured during October 1998 off Talcahuano area, central Chile. Mean values of larval abundance (ind. 1000 m^{-3}) ± 1 standard deviation

Abundancia a diferentes estratos de profundidad de algunas larvas de peces seleccionadas durante Octubre de 1998 frente al área de Talcahuano, Chile central. Valores promedios de abundancia larval (ind. 1000 m^{-3}) ± 1 desviación estándar

Taxa	October Shelf Station				October Slope Station				
	Day		Night		Day			Night	
	0-25	25-50	0-25	25-50	0-50	50-100	100-150	0-50	50-100
Engraulis ringens	65.7 ± 63.7	37.1 ± 21.4	62.4 ± 10.3	26.5 ± 27.1	101.0 ± 12.7	83.5 ± 113.8	4,6	31.5 ± 18.1	69.5 ± 85.3
Strangomera bentincki	12.7 ± 7.4	26.6 ± 32.1	124.6 ± 36.5	69.1 ± 25.2	26.5 ± 3.5	22.0 ± 26.9	7,6	25.3 ± 7.1	58.2 ± 38.4
Hygophum bruuni	3,7	3,7	3.7 ± 0.1	-	17.6 ± 15.1	7.5 ± 4.9	13,6	43.6 ± 33.6	29.1 ± 19.4
Merluccius gayi	5,9	17.9 ± 19.7	31.3 ± 33.5	6.1 ± 3.4	19.0 ± 2.8	42.0 ± 18.4	32.1 ± 23.9	16.2 ± 16.1	29.8 ± 12.7
Sebastes capensis	16.4 ± 1.5	32,8	7,3	1,4	7.3 ± 6.0	21.0 ± 9.9	-	14.5 ± 12.0	3,0
Hypsoblennius sordidus	14.7 ± 10.2	6.1 ± 2.9	-	1,4	12,0	-	-	-	9.0 ± 4.2
Maurolicus parvipinnis	17.6 ± 8.4	42.9 ± 55.1	111.0 ± 76.4	62.4 ± 10.5	513.0 ± 428.5	751.5 ± 352.8	498.1 ± 522.8	211.0 ± 141.2	495.3 ± 95.5
Lampanyctodes hectoris	-	-	-	-	21.2 ± 13.7	34,4	3,1	24.5 ± 6.2	47.4 ± 12.7
Protomyctophum chilensis	-	-	-	-	26.4 ± 27.6	14.4 ± 16.2	15.2 ± 19.3	5,3	16.3 ± 7.1

Table 4

Abundance at different depth strata of selected larval fishes captured during July 1999 off Talcahuano area, central Chile. Mean values of larval abundance (ind. 1000 m^{-3}) ± 1 standard deviation

Abundancia a diferentes estratos de profundidad de algunas larvas de peces seleccionadas durante Julio de 1999 frente al área de Talcahuano, Chile central. Valores promedios de abundancia larval (ind. 1000 m^{-3}) ± 1 desviación estándar

Taxa	July Shelf Station							
	Day				Night			
	0-10	10-25	25-50	50-75	0-10	10-25	25-50	50-75
Engraulis ringens	91.9 ± 49.4	1004.0 ± 1111.4	784.8 ± 307.9	323.2 ± 260.2	143.6 ± 121.6	280.1 ± 87.4	1044.7 ± 634.8	593.1 ± 420.9
Hygophum bruuni	32.8 ± 30.9	67.7 ± 46.7	240.5 ± 222.9	26.6 ± 17.9	19.1 ± 14.7	25.2 ± 11.2	247.5 ± 83.8	227.7 ± 266.5
Merluccius gayi	14.1 ± 16.8	4.6 ± 2.2	71.8 ± 19.9	102.6 ± 121.4	31,3	5.4 ± 0.9	25.9 ± 5.3	68.8 ± 31.0
Normanichthys crockeri	17.1 ± 14.4	49.1 ± 34.9	34.9 ± 16.9	17.5 ± 7.4	29,3	28.4 ± 16.3	39.7 ± 39.2	8.2 ± 3.9
Hippoglossina macrops	2,7	5.9 ± 0.5	14.2 ± 2.2	3,8	-	-	9.2 ± 11.2	45.7 ± 27.3
Sebastes capensis	17.8 ± 6.4	48.8 ± 32.1	27.2 ± 14.2	45.9 ± 65.5	7.5 ± 6.0	4,8	18.2 ± 8.7	152,8

Taxa	July Slope Station							
	Day				Night			
	0-25	25-50	50-100	100-150	0-25	25-50	50-100	100-150
Hygophum bruuni	329.4 ± 195.4	538.5 ± 643.5	25.9 ± 17.3	10.5 ± 2.6	6,1	69.2 ± 19.5	29.8 ± 18.3	-
Merluccius gayi	20,4	6,7	30,6	6.2 ± 4.6	-	-	-	-
Engraulis ringens	25,5	7.7 ± 6.1	-	-	-	-	-	-
Diogenichthys laternatus	5,1	3.7 ± 0.5	5,1	-	-	-	3,1	-
Sebastes capensis	15.4 ± 14.5	3.8 ± 0.3	-	-	6,1	-	-	-

taxa (5%). The most abundant species in both groups were *M. gayi* (34 larvae 10 m^{-2}) and *S. capensis* (22 larvae 10 m^{-2}), respectively. Multivariate analysis of the vertical structure of JSH revealed dispersion of larval fishes collected in the shallower depths (>25 m) and aggregation of ichthyoplankton in middle and deep strata, i.e. between 25 and 75 m (Fig. 6c, Table 4), regardless of their adult habitat (i.e. *S. capensis, N. crockeri* and *M. gayi*, Fig. 8a). No diel structuring of larval fishes was observed during this survey, although some species showed a deepening during night-time (*E. ringens*, *H. macrops* and *S. capensis*) while others like larval hake *M. gayi* were

located in the deepest stratum (50-75 m) during day and night hours (Table 4).

The JSL assemblage showed a reduction in number of taxa captured (26 vs 12), and the overall abundance of all individual taxa except larvae of mesopelagic taxa (Table 2). This group comprised >90% of total larvae and was dominated by *H. bruuni* (88%; 148 larvae 10 m^{-2}). Larvae of demersal species (*M. gayi*, *H. macrops* and *Genypterus* sp.) were the second-most abundant group, contributing 5% to the total catch. Epipelagic and subtidal/ intertidal taxa were reduced to ~1% each. Larval fish
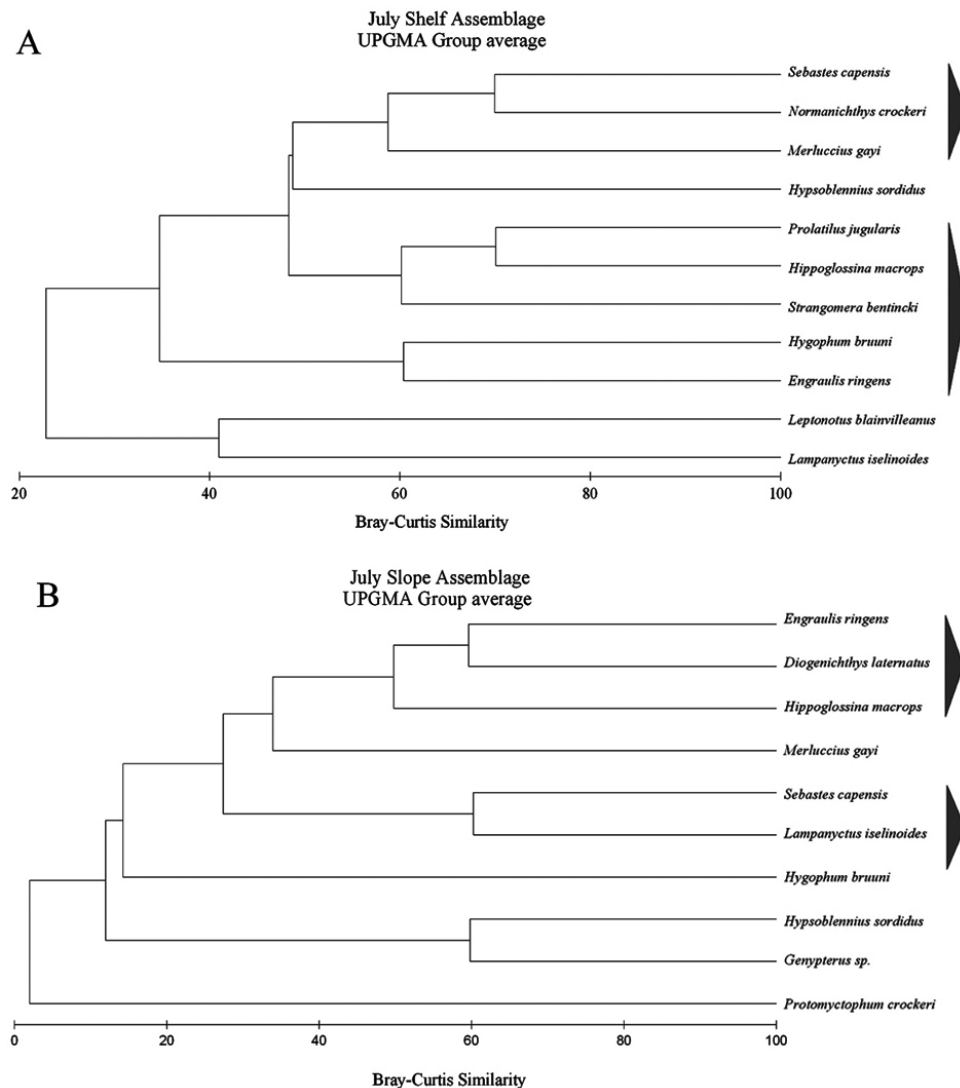
Figure 8

Cluster analysis showing relationship among larval fishes during July 1999 for the a) shelf station and b) slope station

Análisis de dendogramas mostrando la relación entre larvas de peces durante julio de 1999 para la estación de
a) plataforma y b) talud continental

assemblages in the slope stations also exhibited a depth-related distribution trend at shallow (<50 m) and deep (>50 m) sites (Fig 6d). Most larval fishes were collected in the top 50 m depth during the day (Table 4). The highly abundant larval stages of *H. bruuni* were collected in higher abundance between 25 and 50 m of the water column (Table 4). *P. crockeri* was found only at 50-100 m depth, and *Diogenichthys atlanticus* were collected throughout the water column (Fig. 8b).

Discussion

The interaction between mesoscale physical processes such as upwelling and larval fish assemblages has been well established in several ecosystems of the ocean world. The deep and cold waters upwelled by wind forcing in coastal areas may affect the diversity of larval fishes, by reducing the number of fish species (Olivar *et al.* 1993, Franco-Gordo *et al.* 2002), increasing it (Sanchez-Velasco & Flores-Coto 1994) or displacing larval fishes from slope to shelf areas (Smith & Suthers 1999).

Plankton and larval fish assemblage spatial variability are influenced by the interaction of topography and currents (Wing *et al.* 1998, Palma *et al.* 2006, Muhling & Beckley 2007). For example, in less than 30 km cross-shelf Smith *et al.* (1999) described six ichthyoplankton groups associated to coastal, shelf and shelf-break areas of East Australia. Additionally, Marancik *et al.* (2005) also found distinctive assemblages related to inner, mid and outer continental shelf off the Atlantic coast of United States across a transect of 100 km. Despite neither of both observations correspond to an upwelling system, they are consistent with our results of distinct assemblages for shelf and slope areas. Franco-Gordo *et al.* (2002) described a spatially homogeneous larval fish assemblage when advective processes dominated the system off the Pacific coast of Mexico. In our case, the studied area has a considerable variability in its topography, with a continental shelf limited by two submarine canyons which directly affect the coastal circulation (Figueroa & Moffatt 2000, Sobarzo & Djurfeldt 2004, Sobarzo *et al.* 2007, Morales *et al.* 2007) and indirectly may influence the spatial structure of larval fish assemblages off Talcahuano area (see Castillo *et al.* 1991). In this sense, over the Oregon shelf it has been described that during upwelling season the Astoria Canyon causes currents to flow landward (Hickey 1997), carrying and concentrating normally offshore organisms closer to shore (Bosley *et al.* 2004, Parnell *et al.* 2008). In our study, the occurrence of demersal and oceanic larval fishes such as lightfish *Maurolicus parvipinnis*, hake *M. gayi*, bigeye flounder *H. macrops* and rockfish *S. capensis* over shelf during October may be the result of advective processes

associated to upwelling events occurring at shelf break and/or through submarine canyons of Itata and Biobio rivers (transport from shelf break to coastal waters through the subsurface flow that compensates the offshore surface Ekman layer, Smith & Suthers 1999, Vargas & Castro 2001, Landaeta & Castro 2002, Landaeta *et al.* 2006) and/or by retention near headlands in upwelling shadows during the upwelling relaxation (Wing *et al.* 1998) or in proximity of frontal areas (Bjorkstedt *et al.* 2002), rather than spawning events near the coast (Landaeta & Castro 2006a).

Larval epipelagic fishes were dominated by clupeiform such as anchoveta *Engraulis ringens* and common sardine *Strangomera bentincki*. Both species spawns nearshore and associated to rivers during austral winter in the Humboldt ecosystem (Castro *et al.* 2000, Vargas *et al.* 2003, Lett *et al.* 2007, Cubillos *et al.* 2007) where gelatinous predator levels are low and food items (eggs and nauplii of copepods) are high (Castro *et al.* 2000). On the other hand, as suggested by Figs. 2 and 3a, offshore advection of surface Ekman layer (~20 m depth in the area according to Sobarzo & Djurfeldt 2004) may partially explain the higher abundance of larval clupeiform fishes in the slope station during October 1998 (austral spring).

Larval fish assemblages were mostly vertically structured irrespective of the time of the day. In northern Chile, Rojas *et al.* (2002) suggested that larval myctophids (*Diogenichthys atlanticus* and *D. laternatus*) and anchoveta *E. ringens* avoided the highly advective upper layer keeping below 80 m depth. The exception occurred for the OSH, which was structured according to the time of the day. Temporal changes of larval fish assemblages in the shelf station may be triggered by vertical migrations of larval fishes as a way to avoid the offshore surface Ekman layer during the upwelling season (Landaeta & Castro 2002), and/or by net avoidance of larger larvae.

We found higher abundance and diversity of myctophids larval fishes over shelf and slope stations during July, in association to warmer surface waters moving onshore. This ocurrency pattern is typical throughout the world ocean (Loeb & Rojas 1988, Nonaka *et al.* 2000, Sassa *et al.* 2004). Instead, during October larval myctophids were mostly collected over the shelf break. Although the reproductive cycles of many mesopelagic fishes are weakly seasonal or non-seasonal (Moku *et al.* 2003), some species (like *Lampanyctodes hectoris* and *Maurolicus* spp.) spawns during late winter/spring at the shelf break (Prosch 1991, Landaeta & Castro 2002). Along Chile, great abundance of larval *Hygophum bruuni*, *D. atlanticus* and *Lampanyctus iselinoides* are frequently collected in coastal waters during winter time associated to subantarctic waters (Castro *et al.* 2000,

Acuña & Cabrera 2007) and in shallow waters as close to shore as 30 m (Hernández-Miranda *et al*. 2003). A potential explanation is that higher diversity of mesopelagic larvae over shelf during July may be consequence of onshore transport of oceanic water parcels, in a similar way to the intrusion of oceanic larval fishes onto the shelf observed by Olivar *et al*. (1998) in the Agulhas Current.

A similar pattern of abundance and diversity was also evident for intertidal and subtidal larval fishes, being higher during July (austral winter). Intertidal fishes generally have benthic or demersal eggs (Balbontín & Pérez 1979, Pérez 1981) and its larvae are highly abundant in very nearshore areas (Hernández-Miranda *et al.* 2003, Miranda Azeiteiro *et al.* 2006, Borges *et al*. 2007b). During winter off central Chile there is an increase of the freshwater input and rainfall in the coast (Faundez-Baez *et al.* 2001), reducing the surface salinity and increasing the extension of river plumes over the shelf (Piñones *et al.* 2005); by this mechanism intertidal larval fishes may be advected through the inner shelf and may explain the presence of larval blennies (*Hypsoblennius sordidus*), kyphosids, labrisomids and sciaenids in the shelf station.

Finally, results from this work indicate that the structure of ichthyoplankton assemblages over the shelf and slope in central Chile is influenced by a series of processes acting at different spatial and temporal scales, e.g. an interaction of the spawning behaviour of marine fishes that inhabit the southern part of the Humboldt Current and the frequency of occurrence of mesoscale physical processes such as upwelling events and river runoff. The importance of the oceanographic features in the structure of larval fish assemblages may change seasonally and differs from October (presence of recently upwelled waters) to July (effects of the low salinity layer).

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