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Research Article

Fish larvae retention linked to abrupt bathymetry at Mejillones Bay (northern Chile) during coastal upwelling events

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ABSTRACT. The influence of oceanic circulation and bathymetry on the fish larvae retention inside Mejillones Bay, northern Chile, was examined. Fish larvae were collected during two coastal upwelling events in November 1999 and January 2000. An elevated fish larvae accumulation was found near an oceanic front and a zone of low-speed currents. Three groups of fish larvae were identified: the coastal species (*Engraulis ringens* and *Sardinops sagax*), associated with high chlorophyll-*a* levels; larvae from the families Phosichthyidae (*Vinciguerria lucetia*) and Myctophidae (*Diogenichthys laternatus* and *Triphoturus oculeus*), associated with the thermocline (12°C), and finally, larvae of the families Myctophidae (*Diogenichthys atlanticus*) and Bathylagidae (*Bathylagus nigrigenys*), associated with high values of temperature and salinity. The presence of a seamount and submarine canyon inside Mejillones Bay appears to play an important role in the circulation during seasonal upwelling events. We propose a conceptual model of circulation and particles retention into Mejillones Bay. The assumption is that during strong upwelling conditions the flows that move along the canyon emerge in the centre of Mejillones Bay, producing a fish larvae retention zone. Understanding the biophysical interactions responsible to trap and/or concentrate particles is essential to protect these fragile upwelling ecosystems.

Keywords: bottom topography, fish larval assemblages, coastal circulation, northern Chile.

Retención de larvas de peces asociada a una batimetría abrupta en Bahía Mejillones (norte de Chile) durante eventos de surgencia costera

RESUMEN. Se analiza la influencia de la circulación oceánica y batimetría en la retención de larvas de peces en Bahía Mejillones. Las larvas de peces fueron recolectadas durante dos eventos de surgencia costera, en Noviembre 1999 y Enero 2000. Se encontró una alta acumulación de larvas de peces cerca de un frente oceánico y una zona de baja velocidad de corrientes. Se identificaron tres grupos de larvas de peces: las especies costeras (*Engraulis ringens* y *Sardinops sagax*), asociadas con valores altos de clorofila-*a*; larvas de las familias Phosichthyidae (*Vinciguerria lucetia*) y Myctophidae (*Diogenichthys laternatus* y *Triphoturus oculeus*), asociados con la termoclina (12°C); y larvas de las familias Myctophidae (*Diogenichthys atlanticus*) y Bathylagidae (*Bathylagus nigrigenys*), asociadas con altos valores de temperatura y salinidad. La presencia de un monte y cañón submarino al interior de Bahía Mejillones parece jugar un rol importante en la circulación durante eventos de surgencia estacional. Se propone un modelo conceptual de circulación y retención de partículas para Bahía Mejillones. Éste asume que durante condiciones intensas de surgencia, los flujos que se mueven a lo largo del cañón emergen en el centro de Bahía Mejillones, produciendo una zona de retención larval. La comprensión de las interacciones biofísicas responsables de atrapar y/o concentrar partículas es esencial para proteger estos frágiles ecosistemas de surgencia.

Palabras clave: topografía de fondo, asociaciones de larvas de peces, circulación costera, norte de Chile.

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INTRODUCTION

The dynamics of the physical components play an important role to explain the spatial variability of pelagic fish in the environment (Bertrand *et al*., 2008; Lee *et al*., 2009). Oceanographic research have shown that several physical processes are key factors. For example, transport (Vikebø *et al*., 2005; Christensen *et al*., 2007), stability of the water column (Coyle *et al*., 2008), mesoscale eddies (Allen *et al*., 2001; Logerwell & Smith, 2001; León-Chavez *at al*., 2010), coastal upwelling (Mann & Lazier, 1991), internal waves (Pineda, 1999), tidal currents (Le Fevre, 1986) and the interaction between waves and bathymetric features (*e.g.*, submarine canyons) (Kunze *et al*., 2002). Canyons are abrupt, bounded depressions crossing wide continental slopes also are places where exchanges frequently occur between the shelf and open sea (Genin, 2004). Some fish larvae aggregations over abrupt topographies are associated with local upwelling (Sabatés *et al*., 2004), whereby enhanced phytoplankton growth propagates up the food web generating local patches of herbivorous zooplankton and possibly predators. This feature linked with coastal upwelling may have important implications for the structure and dynamics of planktonic communities and therefore in the spatial distribution of fish larval communities (Bosley *et al*., 2004).

The coastal upwelling is one of the major oceanographic processes generating filaments of cold water rich in nutrients in Ecosystems Currents Eastern Boundary (Strub *et al*., 1998). The spatial variability of this process is affected by the coastline geometry and bathymetry, producing highly heterogeneous environments (Strub *et al*., 1991). The upwelling ecosystems are able to sustain large populations of pelagic fish. These ecosystems show strong variability in fish population abundance, mainly explained by changes in recruitment (Hutchings *et al*., 1995; Rojas *et al*., 2002; Rojas, 2014). Of the many processes that affect the recruitment, the loss of eggs and larvae by advection seems to be one of the main oceanographic processes which explain the spatial distribution of adult fish (Hutchings, 1992; Bakun, 1996). Thus, upwelling events in the coastal environment may have potential consequences on the ecology of fish larvae, particularly coastal retention and larval feeding success (Dower *et al.*, 1997; MacKenzie, 2000; Porter *et al.*, 2005).

Several mechanisms that minimize the effects of offshore transport (*e.g.*, diel vertical migration and/or ontogenetic migration) have been described for zooplankton living in coastal upwelling zones (Wing *et al*., 1998; Pringle, 2007). However, this vertical movement of zooplankton is affected, among other factors, by displacement of the oxygen minimum zone (OMZ, <0.5 mL L^{-1}) within the euphotic zone establishing a strict physiological limit of vertical movement (Morales *et al*., 1996; González & Quiñones, 2002) forcing the aggregation of planktonic organisms above 50 m depth (Escribano & Hidalgo, 2000). An alternative mechanism for retention would be the result of the spatial and temporal variability on the nearshore circulation. For example, the flow-structures known as "upwelling shadows" have been proposed as an important flow-dependent retention mechanism (Graham & Largier, 1997; Wing *et al*., 1998; Marín *et al*., 2003). Mathematical simulation studies have investigated the dispersion/retention particles in the oceans. From hydrodynamic models have been simulating the processes that control larval transport toward coastal area (Parada *et al*., 2003; Vaz *et al*., 2007; Brochier *et al*., 2008).

Península de Mejillones (Chile) is an upwelling center located in the northern Humboldt Current System (HCS) (Marín *et al*., 1993). The mesoscale studies, especially the processes and coastal circulation patterns are scarce at northern Chile. This ecosystem is dominated by small pelagic fishes such as sardine (*Sardinops sagax*) and anchovy (*Engraulis ringens*), which spawn at nearshore areas (Loeb & Rojas, 1988; Rojas *et al*., 2002; Rodriguez-Graña & Castro, 2003). Off northern Chilean coast presence of dense abundances of phyto- and zooplankton near surface and nearshore during the spawning period (austral winter) could facilitate a successful larval feeding (Escribano, 1998; Escribano & Hidalgo, 2000; Herrera & Escribano, 2006). However, the cross-shelf currents derived from the upwelling process may cause significant offshore transport of fish eggs and larvae as well as mortality due starvation in fish larvae advected to oceanic waters (Pizarro *et al*., 1998).

At mesoscale, changes in bathymetry and coastal geometry may play an important role in the creation of recirculation zones, which will have a significant effect on the meroplankton distribution and retention (Palma *et al*., 2006). The concentrating around shallow topographies of planktonic organisms in coastal upwelling are related to biophysical coupling (Dower & Brodeur, 2004) that compensated the loss of organisms due to horizontal offshore transport (*i.e.*, by the Ekman layer; Sinclair, 1988; Pringle, 2007), that ensures the recruitment/settlement of individuals inside a nursery area (Landaeta & Castro, 2006; Palma *et al*., 2006). In upwelling areas, diel vertical migration (DVM) of fish larvae may increase coastal retention over the onshore nursery areas (Landaeta & Castro, 2002; Parada *et al*., 2008). Off the Peninsula de Mejillones, DVM partially explain a nearshore larval retention of myctophids during a coastal upwelling event (Rojas *et al*., 2002; Rojas, 2014). However, little is known about the mechanisms that favour the nearshore fish larvae retention during upwelling events off northern Chile. Our hypothesis suggests that mesoscale physical structures (*e.g.*, eddies, fronts and upwelling shadows) occurring during upwelling events and the presence of two bathymetric structures (*e.g.*, seamount and submarine canyon) may favour larval fish retention into Mejillones Bay. The aim of this study is to investigate the interaction of the circulation with bathymetry and its potential role in the ichthyoplankton retention and assemblages structure inside Mejillones Bay, northern Chile.

MATERIALS AND METHODS

Study area

The area of Mejillones Bay (23°29'S, 70º59'W), northern Chile (coastal zone of the Atacama Desert), is an upwelling centre situated in a transition zone between southward flowing equatorial waters and northward flowing subantarctic waters, (Strub *et al*., 1998; Rojas *et al*., 2011). Has a relatively homogenous topography with a length of 37 km and a 15 km wide continental shelf. The seamount (7 km wide, 150 m deep) is located on the northern side of the bay, while the submarine canyon with a maximum depth of ~1000 m, rises to a depth of ~150 m oriented in NW-SE direction towards Mejillones Bay (Fig. 1).

Sampling design and collection of samples

Oceanographic data and plankton samples were collected inside Mejillones Bay during two surveys, November (7-8) 1999 (austral spring) and January (15-16) 2000 (austral summer), on board the R/V "Purihaalar" from the Universidad de Antofagasta. In both cruises, we used a grid of 27 stations, covered over 26 h (Fig. 2). At each station, vertical temperature profiles (ºC), salinity (S_A) and dissolved oxygen (mL L^{-1}) were made from surface to ~150-200 m depth with a SeaBird SBE-19 conductivity temperature depth (CTD) device, equipped with a calibrated YSI Beckman oxygen sensor. In addition, fluorescence profiles were obtained from 100 m to surface, using a Wetstar fluorometer attached to an Ocean Sensor CTD. Current profiles were measured with the vessel anchored at each station using a Doppler sensor current meter (Aanderaa RCM-9). Fluorescence units were converted to Chl-*a* concentration through a linear algorithm derived from an *in situ* calibration (Escribano & McLaren, 1999).

For plankton sampling, we used 27 fixed stations in the area of influence of upwelling filaments (Lutjeharms & Stockton, 1987), where six stations cover different mesoscale physical structures such as upwelling shadow, fronts (oceanic and coastal) and upwelling filament center (Fig. 2); in accordance with satellite NOAA images of sea surface temperature (SST) obtained on November 6 (1999) and January 14 (2000), respectively, one day before sampling begun. Detailed information on satellite-derived SST is described in Marín *et al*. (2001). The following two days after the oceanographic grid was finished, zooplankton samples were collected using a vertically towed Hensen net with 0.5 m opening, 200 µm mesh, equipped with a double opening-closing system, and a calibrated General Oceanic flowmeter during day and night-time along two days. All plankton samples were preserved in 4% buffered formalin.

This design considered the spatial variability introduced by the presence of physical structures derived from the upwelling process. Changes in the vertical distribution patterns were evaluated by sampling three depth strata each time: 200-80, 80-20 and 20-0 m. According with Escribano *et al*. (2001), during upwelling events the upper 20 m of the water column represent the Ekman layer, the 80-20 m stratum shows a reversal flow, and the 200-80 m stratum is a deep and more stable layer. To confirm the presence of cold upwelling filaments or plumes into the study area, regression analyses were applied using sea surface temperature and dissolved oxygen values.

In the laboratory, all fish larvae were removed for counting and identified to the lowest taxonomic level using descriptions by Fisher (1958, 1959), Moser & Ahlstrom (1970, 1974, 1996), Balbontín & Garretón (1977), Brownell (1979), and Orellana & Balbontín (1983). Larvae were separated into three ontogenetic groups according to the notochord flexion state (preflexion, flexion and postflexion) and classified as coastal or oceanic (coastal, epipelagic, mesopelagic, epi-mesopelagic and demersal) according to the adult fish habitat following the classification given by Moser & Ahlstrom (1996). The number of individuals collected in the different sampling strata was standardized to a number per unit of filtered water volume (densities): 1000 m^3 for fish larvae (densities) for comparisons in the vertical axis (mean depth). 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 mesoscale physical structures into Mejillones Bay irrespective of the sampled strata.

Data analysis

The weighted mean depth (WMD) of the vertical distributions of fish larvae at each station was calculated as the centre of density (centroid):

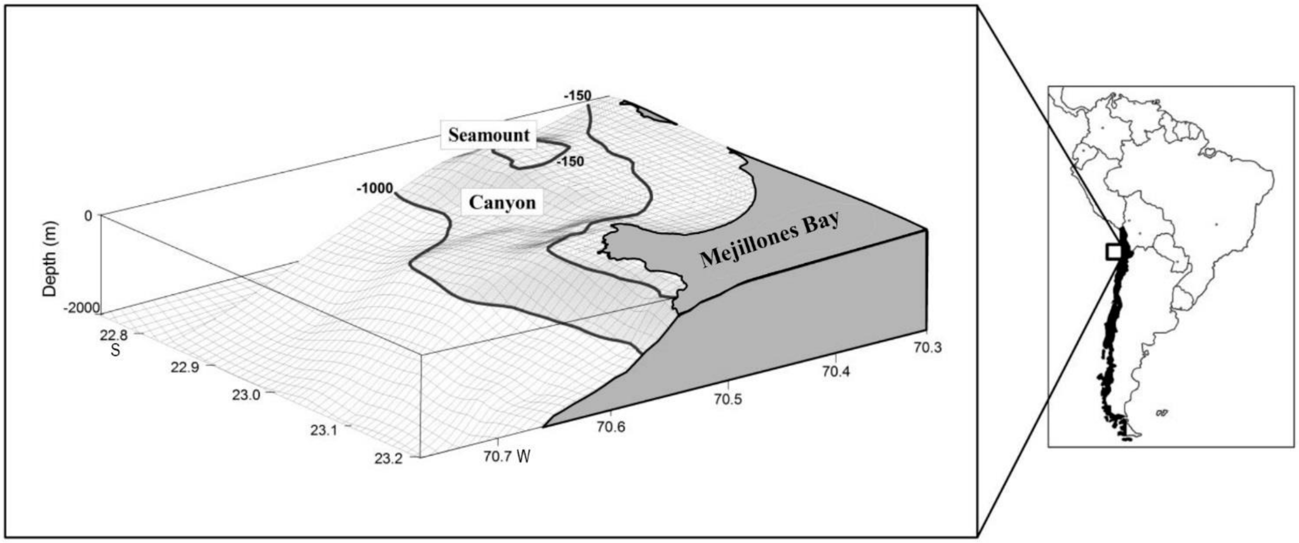

Figure 1. Three-dimensional view of bathymetry into Mejillones Bay. Data: Bathymetric chart SHOA 2005; Datum: WGS84; Scale: 1:50.000.

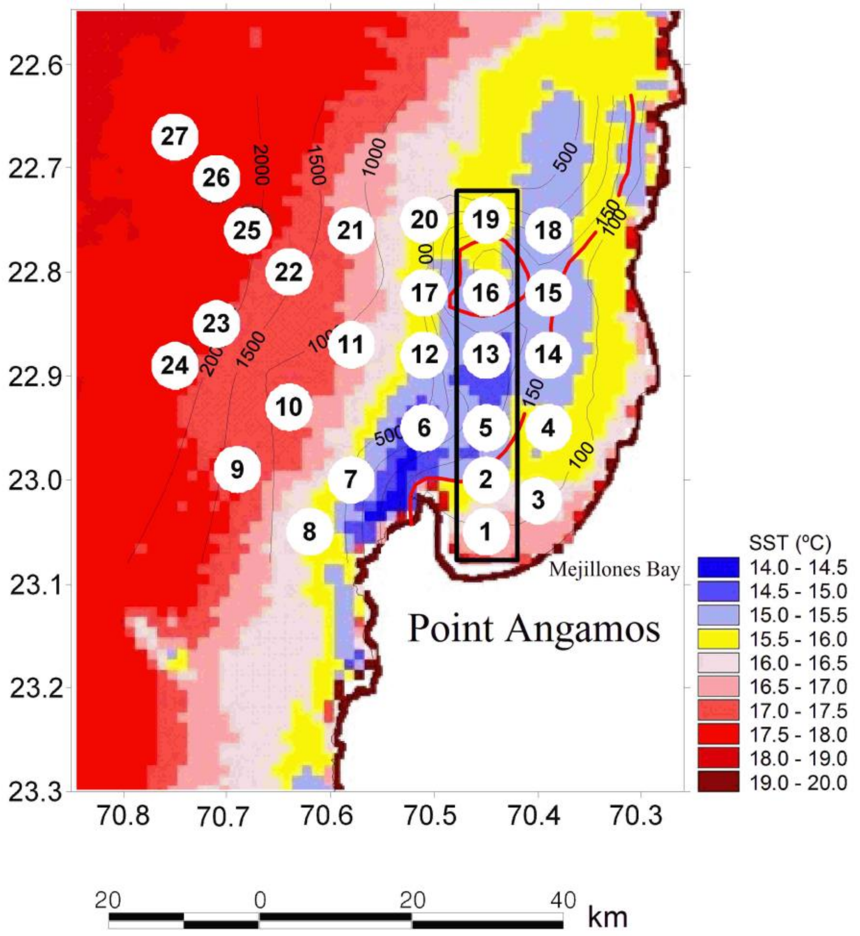

Figure 2. Satellite NOAA image of SST of Peninsula de Mejillones at northern Chile illustrating the cold upwelling filament on 14 January 2000, also location oceanography stations (physical/biological) and depth contours into Mejillones Bay. The box indicates six stations covering mesoscale physical structures, where station 1: Upwelling shadow, station 2: Coastal front, stations 5, 13 and 16: Upwelling filament centre, station 19: Oceanic front.

$$WMD = \sum_{i-1}^{n} p_i Z_i = \frac{\sum_{i=1}^{n} C_i Z_i}{\sum_{i=1}^{n} C_i}$$

where p_i and C_i are, respectively, the proportion and the concentration of fish larvae (number 1000 m^{-3}) in the ith stratum, and Z_i is the mid-depth of the ith stratum (*e.g.*, Gronkjaer & Wieland, 1997).

The effect of physical mesoscale structures, generated by a complex bathymetry during upwelling events, on fish larval abundance was analyzed by means of an one-way ANOVA and Tukey test multiple, over [$\log_{10}(x+1)$] transformed data to homogenize variances, level of significance $\alpha = 0.05$.

To investigate the relationship between fish larvae distribution and oceanographic variables (*i.e.*, Chl-*a* max., Sea Surface Temperature (SST), Tº thermocline, salinity and superficial oxygen) a non-metric multidimensional scaling (*n*MDS) ordination from statistical package PRIMER was used (Cox & Cox 2000). Goodness of fit was determined by a stress coefficient. Only species with a relative abundance of more than 5% in each cruise were considered for the analysis (*n*MDS). The Spearman´s R correlation test (Hays, 1981) was used to investigate the relationship between the mean depth of the different species of fish larvae with the depth of maximum fluorescence (Chl-*a* max.), thermocline and minimum oxygen zone. All statistical analyses were carried out using software package STATISTICA 7.0 and contour maps were constructed with the software SURFER 8.0.

RESULTS

Oceanographic conditions

Sea-surface temperature maps showed well-developed upwelling filaments during both surveys, and the upwelling focus occurred off Punta Angamos (Fig. 3), as consequence of seasonal variations in the intensity (~3-5 m s^{-1}) of southwest wind components (Marín *et al.*, 2003). The area of low temperature (<18°C) inside Mejillones Bay for both periods was consistent with current measurements indicating presence of upwelling filaments and agrees with the hypothesis that the upwelling was related with bathymetry along the major axis of the submarine canyon. The upwelling filaments defined two frontal zones, a coastal front and an oceanic front both associated with upwelled cold-waters (Fig. 3b). High concentrations of chlorophyll (6.0-8.5 mg L^{-1}) were found only nearshore during both periods (Fig. 3). Patches of Chl-*a* were found (Figs. 3c-3d), two of them located inside Mejillones Bay, the other patch was located northeast of the bay. Low dissolved oxygen concentrations were found in one nearshore location during both cruises (Fig. 3); significant relationships ($r = 0.97$, $P < 0.05$) were detected between the distribution of dissolved oxygen and temperature of the upwelling filaments.

Coastal circulation in Mejillones Bay

The current vector diagrams during November 1999 and January 2000 showed the area was dominated by a poleward flow (~0.2-0.3 m s^{-1}; Fig. 4). The combined effect of the coastline geometry and bathymetry on the upwelling circulation was observed above (Fig. 4a) and below 20 m depth (Figs. 4b-4c) in both cruises. Currents over the canyon showed a divergence associated with upwelling waters that moved through the canyon. Indeed, although the main flow was poleward, the flow within the bay was mostly coastward. At surface, lowest speeds were found over the canyon (<0.1 m s^{-1}, Fig. 4a), while the highest speeds (>0.3 m s^{-1}, Fig. 4a) were seen in the northern sector of the seamount, gradually decreasing towards the bottom. In general, the values of the circulation fields at different depths in both periods showed low-speed areas (~0.03-0.1 m s^{-1}) influenced by the presence of a seamount and a submarine canyon (Figs. 4a, 4b, 4c).

Vertical and horizontal distribution of fish larvae

During the oceanographic surveys, 150 positive samples of fish larvae were collected with a frequency of occurrence of 92.6%. A total of 885 larvae were separated, 14 taxa identified, representing 88.9% of total larvae (Table 1). The most abundant species (six) were well represented throughout sampled water column; however, these taxa were dominated in the mid-depth stratum (20-80 m) (Table 2). The small pelagic larvae (*E. ringens* and *S. sagax*) showed mean depth distribution (~30-40 m) restricted to well-oxygenated waters (5-6 mL L^{-1}) above the thermocline in both periods. Some meso-bathypelagic fish larvae (*B. nigrigenys* and *V. lucetia*, respectively) and epi-mesopelagic (*D. laternatus* and *T. oculeus*) habits were associated with intermediate oxygen values (3-4 mL L^{-1}) below the thermocline (~30-50 m; Fig. 5).

Larvae exhibited an heterogeneous distribution, forced mainly by the presence of a low-speed zone (*i.e.*, retention area) in the surface (~6 m), as well as by frontal zones formed during upwelling active phase near Mejillones Bay (Fig. 6); no significant relationships were detected between larval abundance and current velocity during November ($r = 0.27$, $P > 0.05$) or January ($r = 0.11$, $P > 0.05$). The distribution of the six most abundant species was as follows (Fig. 6).

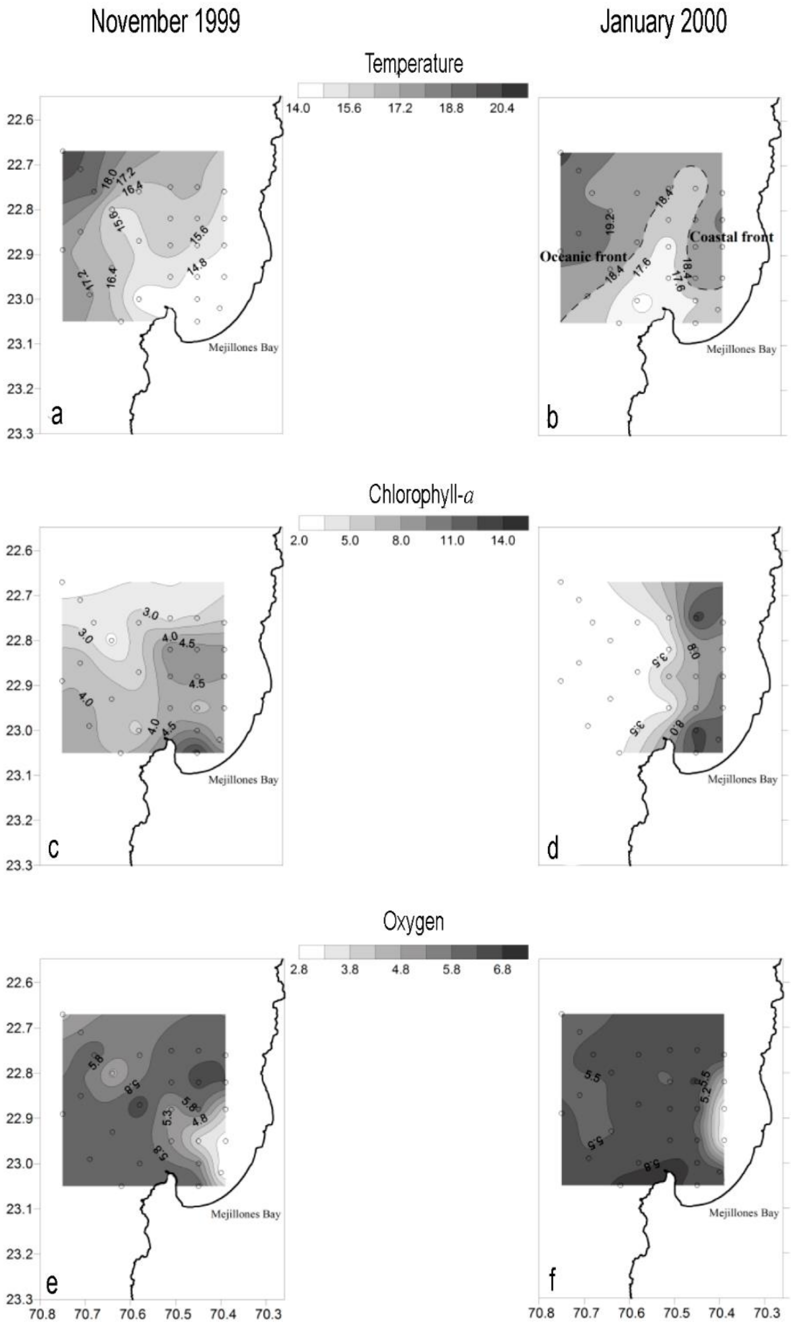

Figure 3. Spatial distribution of sea-surface temperature (ºC), Chlorophyll-*a* (mg L^{-1}) and dissolved oxygen (mL L^{-1}) into Mejillones Bay in November 1999 and January 2000. Circles indicate location of Hensen net and CTD stations.

Vinciguerria lucetia larvae (41.1%) showed a wide distribution in November 1999 and limited by oceanic fronts derived from the upwelling process in January 2000. The *Diogenichthys laternatus* larvae (18.2%) showed a heterogeneous distribution covering continental shelf, associated with upwelled cold-waters, and with high levels of Chl-*a* (>9.5 mg L^{-1}). Anchovy larvae (*E. ringens*) (14.4%) aggregated near coastal and oceanic fronts formed inside Mejillones Bay. *Bathylagus nigrigenys* larvae (7.6%) were associated mainly with warmer waters outside bay, while *Sardinops sagax* larvae (5.0%) showed a distribution mainly associated with the intrusion of upwelled cold-water inside Mejillones Bay. Finally, the

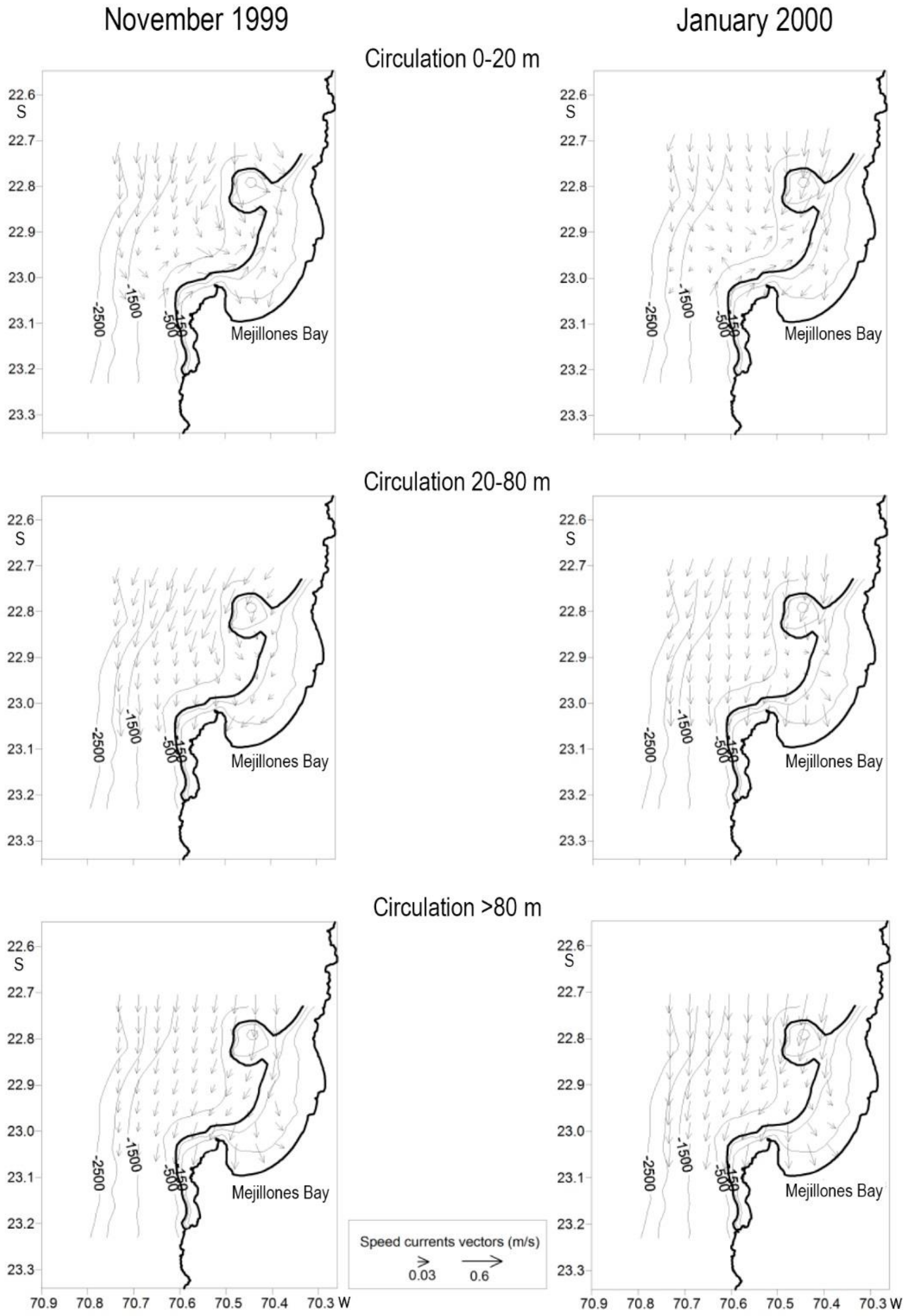

Figure 4. Two-dimensional current vectors at different depths into Mejillones Bay during November 1999 and January 2000. Average velocity field for the 0-20 m, 20-80 m and beyond 80 m water column, respectively. Current profiles were measured using a Doppler sensor current meter (Aanderaa RCM-9).

myctophid *Triphoturus oculeus* (4.8%) showed a spatial distribution restricted by oceanic fronts. Mesoscale structures (*i.e.*, upwelling shadow (US), coastal front (CF), retention area (RA), cceanic front (OF)) explained a significant part of the spatial distribution of all ichthyoplankton (r = 0.4, $F_{[3,20]} = 3.70$, $P < 0.05$) collected during both surveys in Mejillones Bay (Fig. 7). However, in November 1999 and January 2000 the mesoscale structures do not significantly explained the patterns seen for each taxon (Table 3).

Influence of mesoscale structures on circulation and vertical location of larval fish assemblages

Changes in the vertical location of fish larvae were detected in Mejillones Bay during austral spring and

Table 1. Total fish larvae collected inside Mejillones Bay in November 1999 and January 2000. The number corresponds to larvae per 10 m^2. Occurrence corresponds to the proportion of samples where the species were found. Habitats, C: coastal, B: bathypelagic, D: demersal, BD: bathydemersal, EM: epi-mesopelagic, MB: meso-bathypelagic.

		November 1999					January 2000				
Family	Species	Habitat	Maximum abundance	Relative abundance (%)	Occurrence frequency (n = 81)	Mean abundance (ind 10 m^{-2})	Habitat	Maximum abundance	Relative abundance (%)	Occurrence frequency (n = 81)	Mean abundance (ind 10 m^{-2})
Myctophidae	*Diogenichthys atlanticus*	EM	111	18.5	35.4	32	EM	194	2.2	25.9	27
	Diogenichthys laternatus	EM	79	17.2	43.8	30	EM	771	18.2	70.3	218
	Triphoturus oculeus	EM	52	4.4	16.7	27	EM	363	4.8	44.4	57
	Diaphus theta	EM	33	3.1	12.5	26	EM	83	1.0	18.5	12
	Lampanyctus sp.	EM	26	1.5	4.2	24	EM	287	4.6	44.4	55
	Diogenichthys sp.	EM	33	1.2	4.2	29	-	-	-	-	-
	Protomyctophum crockeri	EM	23	0.5	2.1	23	-	-	-	-	-
	Hygophum bruuni	EM	20	0.4	2.1	20	-	-	-	-	-
	Myctophum nitidulum	EM	18	0.4	2.1	18	EM	73	0.9	18.5	11
	Gonichthys tenuiculus	-	-	-	-	-	EM	55	0.2	3.7	2
	Unidentified sp.	-	59	11.1	29.2	36	-	-	-	-	-
Engraulidae	*Engraulis ringens*	C	233	16.8	29.2	52	C	926	14.4	70.3	172
Clupeidae	*Sardinops sagax*	C	310	10.8	14.6	76	C	257	5.0	55.5	59
Phosichthyidae	*Vinciguerria lucetia*	B	78	8.4	18.8	42	B	2045	41.1	55.5	492
Bathylagidae	*Bathylagus nigrigenys*	-	-	-	-	-	MB	259	7.6	77.7	91
Normanichthyidae	*Normanichthys crockeri*	D	66	2.4	6.3	39	-	-	-	-	-
Sebastidae	*Sebastes oculatus*	D	29	0.6	2.1	29	-	-	-	-	-
Macrouridae	Unidentified sp.	-	26	0.9	4.2	23	-	-	-	-	-
Ophidiidae	*Genypterus* sp.	BD	22	0.7	4.2	17	-	-	-	-	-

Table 2. Location of dominant fish larvae groups per strata depth (m) in November 1999 and January 2000. The abundance corresponds to abundance (N) expressed as ind 1000 m^3 and occurrence (%) represents the number of cases (samples = 81) in which the species was present.

		November 1999		January 2000	
Strata (m)	Species	n	%	n	%
0-20	*Engraulis ringens*	136	4.0	248	5.3
	Sardinops sagax	45	2.6	85	5.3
	Diogenichthys laternatus	201	4.0	225	3.3
	Triphoturus oculeus	34	6.0	-	
	Vinciguerria lucetia	773	4.0	239	1.3
	Bathylagus nigrigenys	-		66	5.3
20-80	*Engraulis ringens*	257	4.7	297	4.7
	Sardinops sagax	134	5.3	156	3.3
	Diogenichthys laternatus	290	5.3	330	3.3
	Triphoturus oculeus	40	2.7	175	2.7
	Vinciguerria lucetia	269	2.0	1539	6.0
	Bathylagus nigrigenys	200	5.3	144	4.7
80-200	*Engraulis ringens*	121	4.0	141	2.7
	Sardinops sagax	-		72	1.3
	Diogenichthys laternatus	163	3.3	345	6.0
	Triphoturus oculeus	147	6.0	157	4.7
	Vinciguerria lucetia	432	4.0	-	
	Bathylagus nigrigenys	73	4.0	153	4.0

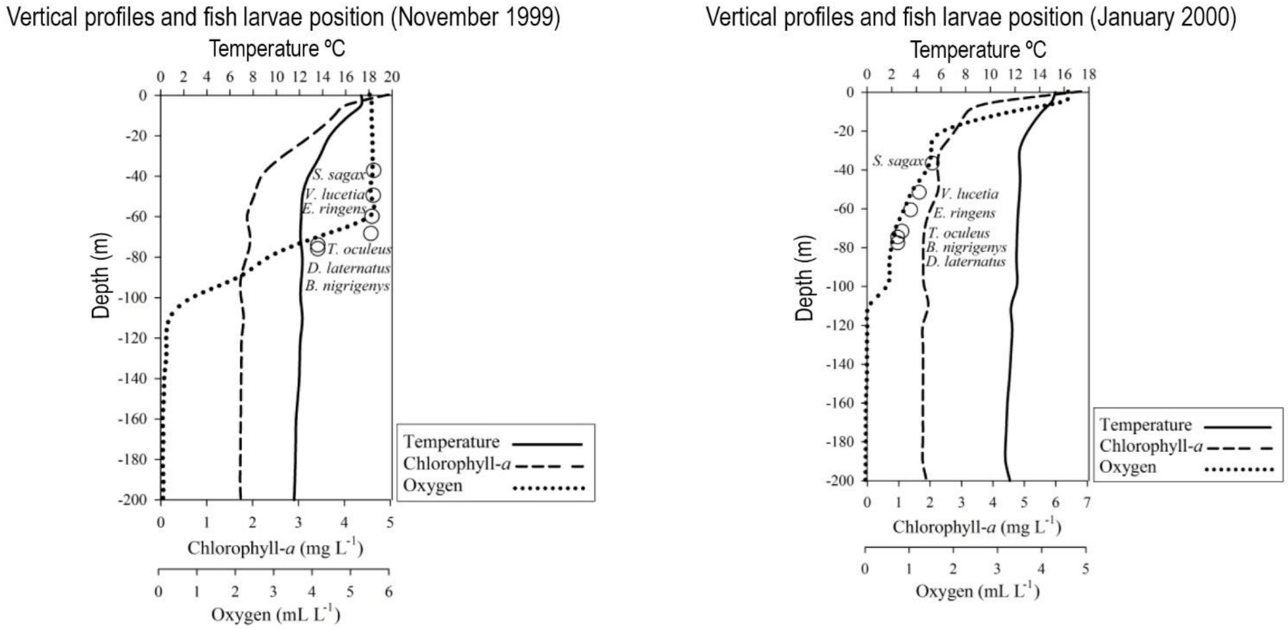

Figure 5. Mean position of fish larvae associated with hydrographic condition of water column during November 1999 and January 2000. The open circles indicate the location of the depth centroid of dominant taxa associated with dissolved oxygen values.

summer (Fig. 8). Fish larvae collected in stations into Mejillones Bay (Fig. 2) were captured near surface associated to northward currents in both periods (Fig. 8). In November 1999 and January 2000 the vertical current speed section in the surface (~4-9 m) showed average values fluctuating between ~0.2-0.3 m s^{-1} north-

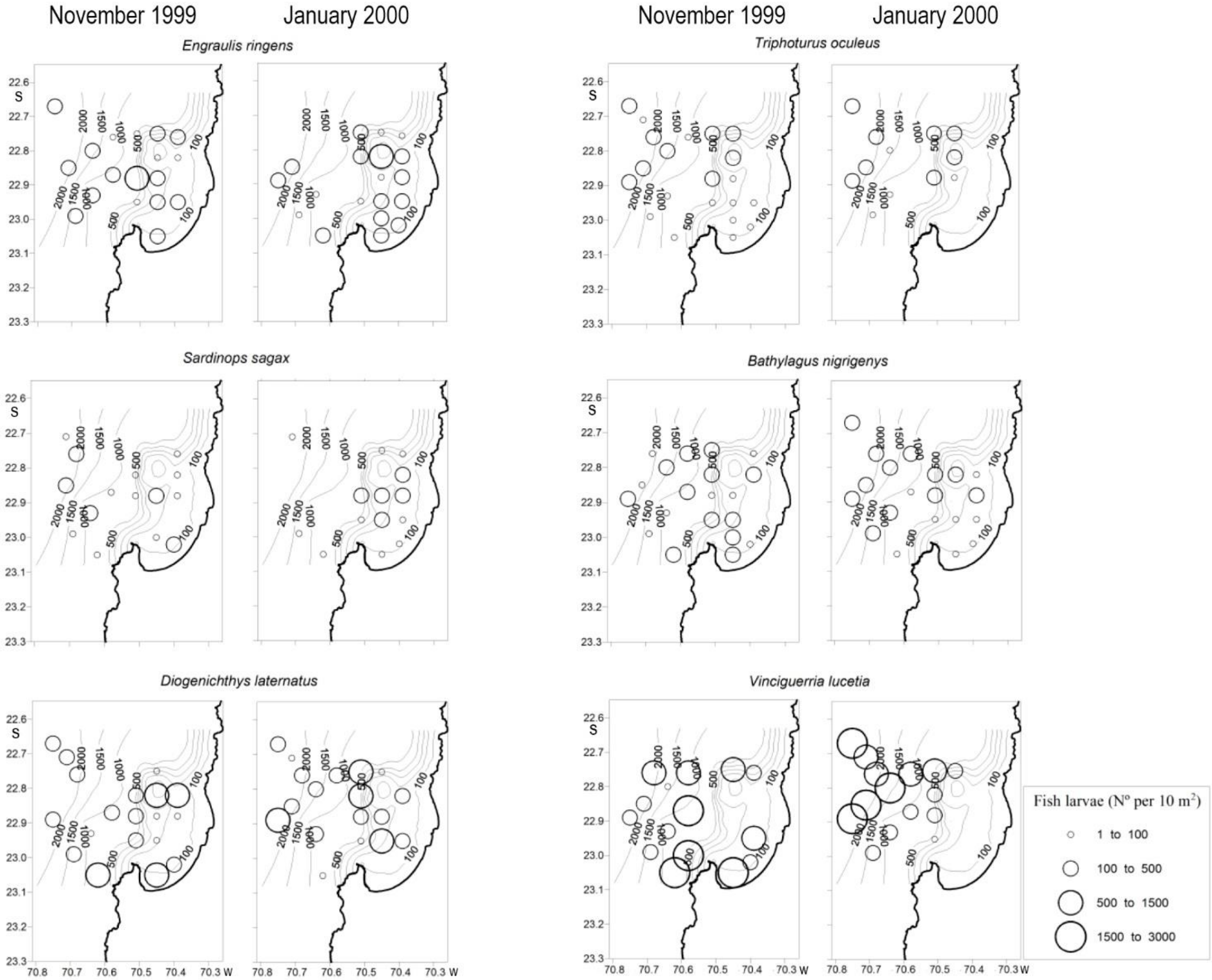

Figure 6. Spatial distributions of dominant fish larvae into Mejillones Bay in November 1999 and January 2000. The lines indicate depth contours.

ward, while southward currents fluctuated between ~0.4-0.6 m s^{-1}. On the coast, the first four stations, were influenced by northward surface coastal currents, while the other two stations influenced by the dominant southward flow (Fig. 8).

Early stages of fish related to mesoscale physical structures

Early life stages of fish showed a distribution forced by the physical structure in both periods. Mesoscale structures explained a significant ($F_{[3,123]} = 4.08$, $P < 0.05$) fraction of the preflexion larval abundance in November 1999 (Fig. 9a). Higher abundance of fish larvae found at upwelling shadow ($P = 0.005$; Tukey *post-hoc*) explained the difference. On the contrary, neither flexion ($F_{[3,49]} = 1.74$, $P > 0.05$) nor postflexion ($F_{[3,54]} = 0.93$, $P > 0.05$) larval abundance were affected by mesoscale structures. However, presence of upwelling shadow and oceanic front explained partially the pattern (Figs. 9b, 9c). In January 2000, mesoscale structures showed significant effect ($F_{[3,109]} = 4.66$, $P < 0.05$) over preflexion larval abundance (Fig. 9d). The pattern may be explained by differences in current speeds (*i.e.*, retention area, $P = 0.005$, Tukey *post-hoc*). As well as the previous cruise, upwelling mesoscale structures did not show significant effects on flexion ($F_{[3,35]} = 1.62$, $P > 0.05$) and postflexion ($F_{[3,24]} = 1.84$, $P > 0.05$) larval abundance. However, for both cases highest abundances were found at retention area (Figs. 9e, 9f).

Fish larvae related with oceanographic variables

In November 1999, the *n*MDS ordination plots of similarities between fish larvae distribution and oceano-

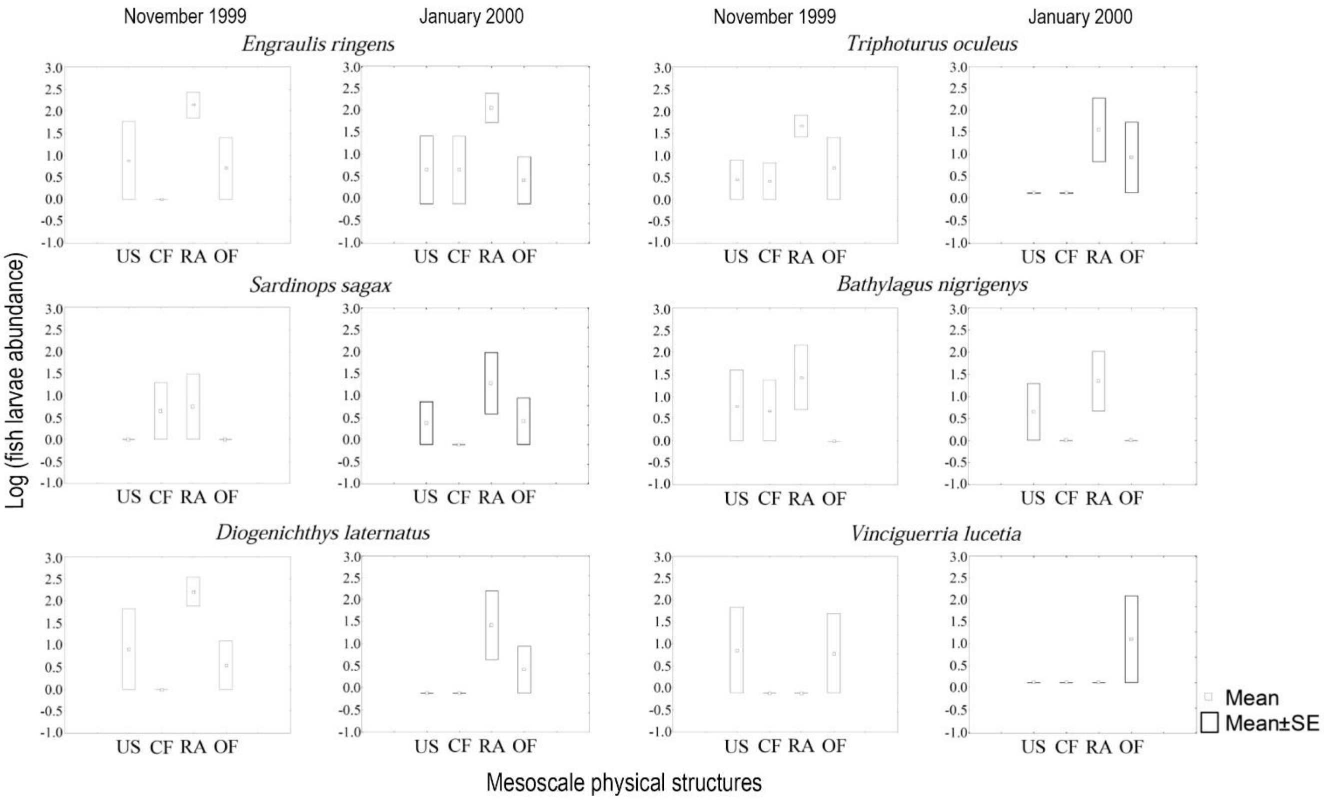

Figure 7. Fish larvae of six species dominant associated with different physical structures inside Mejillones Bay during November 1999 and January 2000. US: Upwelling shadow, CF: coastal front, RA: retention area, OF: oceanic front.

Tabla 3. One-way ANOVA test results between different taxa and physical structures in November 1999 and January 2000. * Not significant.

	November 1999					January 2000				
Source/Taxa	SS	df	MS	*F*-ratio	*P*-level	SS	df	MS	*F*-ratio	*P*-level
E. ringens										
Physical structures	7.14	3	2.38	1.16	>0.05*	6.39	3	2.13	0.66	>0.05*
Error	18.38	9	2.04			29.07	9	3.23		
S. sagax										
Physical structures	1.46	3	0.49	0.60	>0.05*	3.85	3	1.28	0.87	>0.05*
Error	7.25	9	0.81			13.27	9	1.47		
T. oculeus										
Physical structures	3.05	3	1.02	0.69	>0.05*	3.30	3	1.10	1.21	>0.05*
Error	13.16	9	1.46			8.19	9	0.91		
D. laternatus										
Physical structures	7.99	3	2.66	1.36	>0.05*	6.00	3	2.00	1.65	>0.05*
Error	17.60	9	1.96			10.91	9	1.21		
B. nigrigenys										
Physical structures	3.08	3	1.03	0.57	>0.05*	3.70	3	1.23	1.34	>0.05*
Error	16.21	9	1.80			8.29	9	0.92		
V. lucetia										
Physical structures	3.37	3	1.12	0.60	> 0.05*	1.66	3	0.55	1.00	>0.05*
Error	16.81	9	1.87			4.97	9	0.55		

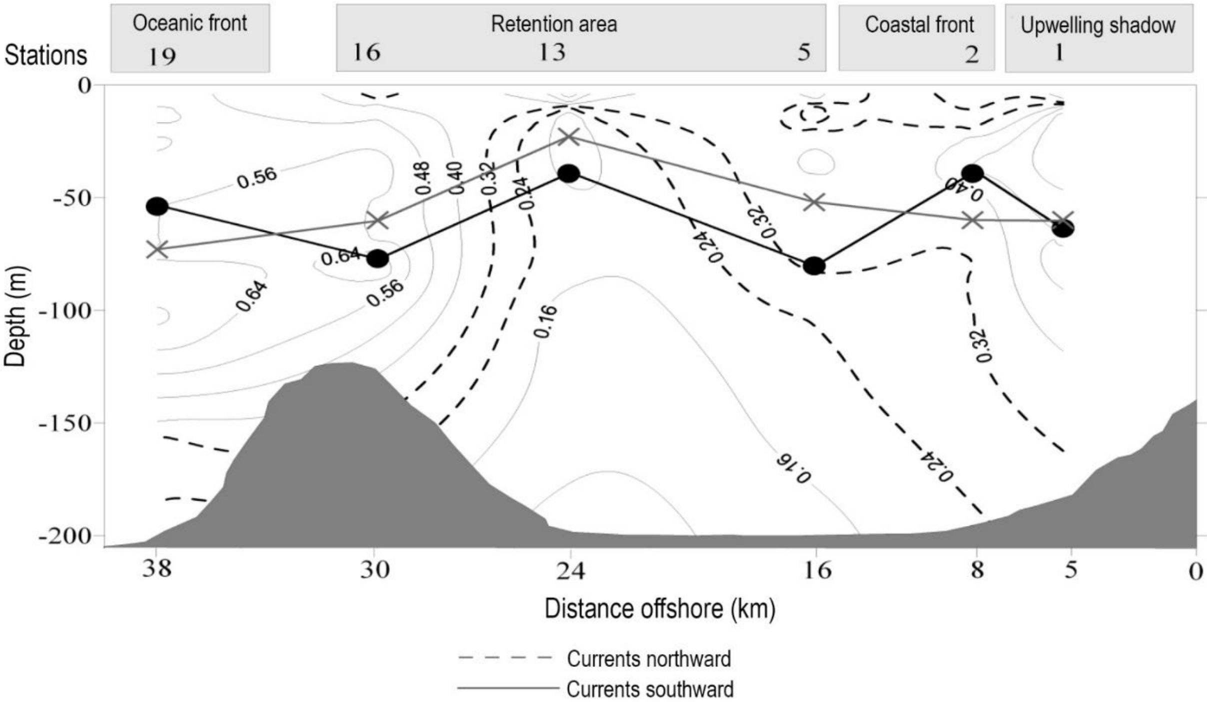

Figure 8. Vertical section with average values of current velocity (both cruises) affected by mesoscale physical structures and bathymetry within Mejillones Bay. Black circles and crosses, respectively, indicate the location of the depth centroid of fish larval assemblages on November 1999 and January 2000. The transect direction is northward (from station 1 to station 19). Data: Bathymetric chart SHOA 2005, Datum: WGS84, Scale: 1:50.000.

graphic variables defined two groups (Fig. 10). Larval of South American pilchard (*Sardinops sagax*, coastal epipelagic) was associated with four oceanographic variables (*i.e.*, SST, Chl-*a* max, T° thermocline and superficial oxygen). The second group was composed by larval Myctophidae (*i.e.*, *D. laternatus*, *D. atlanticus*, *T. oculeus*) and fish larvae from Engraulidae and Phosichthyidae (*i.e.*, *E. ringens* and *V. lucetia*) were associated with values of superficial salinity.

In January 2000, the *n*MDS plots showed two groups between oceanographic variables and larval fish assemblages (Fig. 10). Fish larvae from Clupeidae and Myctophidae (*i.e.*, *S. sagax* and *D. atlanticus*) were associated with temperature values of the thermocline. The second group was formed by larval Myctophidae (*i.e.*, *D. laternatus* and *T. oculeus*) and fish larvae from Engraulidae and Phosichthyidae (*i.e.*, *E. ringens* and *V. lucetia*) were associated with values the sea surface temperature (SST), salinity and superficial oxygen.

The Spearman´s R correlation analysis revealed a significant and positive relationship between mean depth from assemblages with the depth of the oxygen minimum zone (OMZ; Table 4). Mean depth for *V. lucetia* showed a positive and significant correlation with depth values of three physical variables (*i.e.*, Chl-*a* max; thermocline and OMZ), however, only the relationship with the latter two variables showed a high correlation coefficient (r = ~0.7). These statistically significant relationships involve 41% of total fish larvae from assemblage. The anchovy larvae (*E. ringens*) showed a significant and negative correlation with depth values of the three physical variables (*i.e.*, Chl-*a* max.; thermocline and OMZ); *S. sagax* larvae showed negative associations (r = ~-0.4) and significant relationships only with thermocline depth and OMZ. Mean depth for myctophid *T. oculeus* showed a significant and positive relationship with the thermocline depth values and oxygen minimum zone, however this relationship should be considered with caution since only 4.8% of the total larvae was represented by this analysis. This consideration should be also applied to the correlation found between the mean depth for *S. sagax* with the thermocline depth values and oxygen minimum zone.

DISCUSSION

Community structure and distribution of fish larvae assemblages

The persistent aggregation of plankton inside Mejillones Bay, suggest the presence of physical processes favoring retention of planktonic organisms. Previous

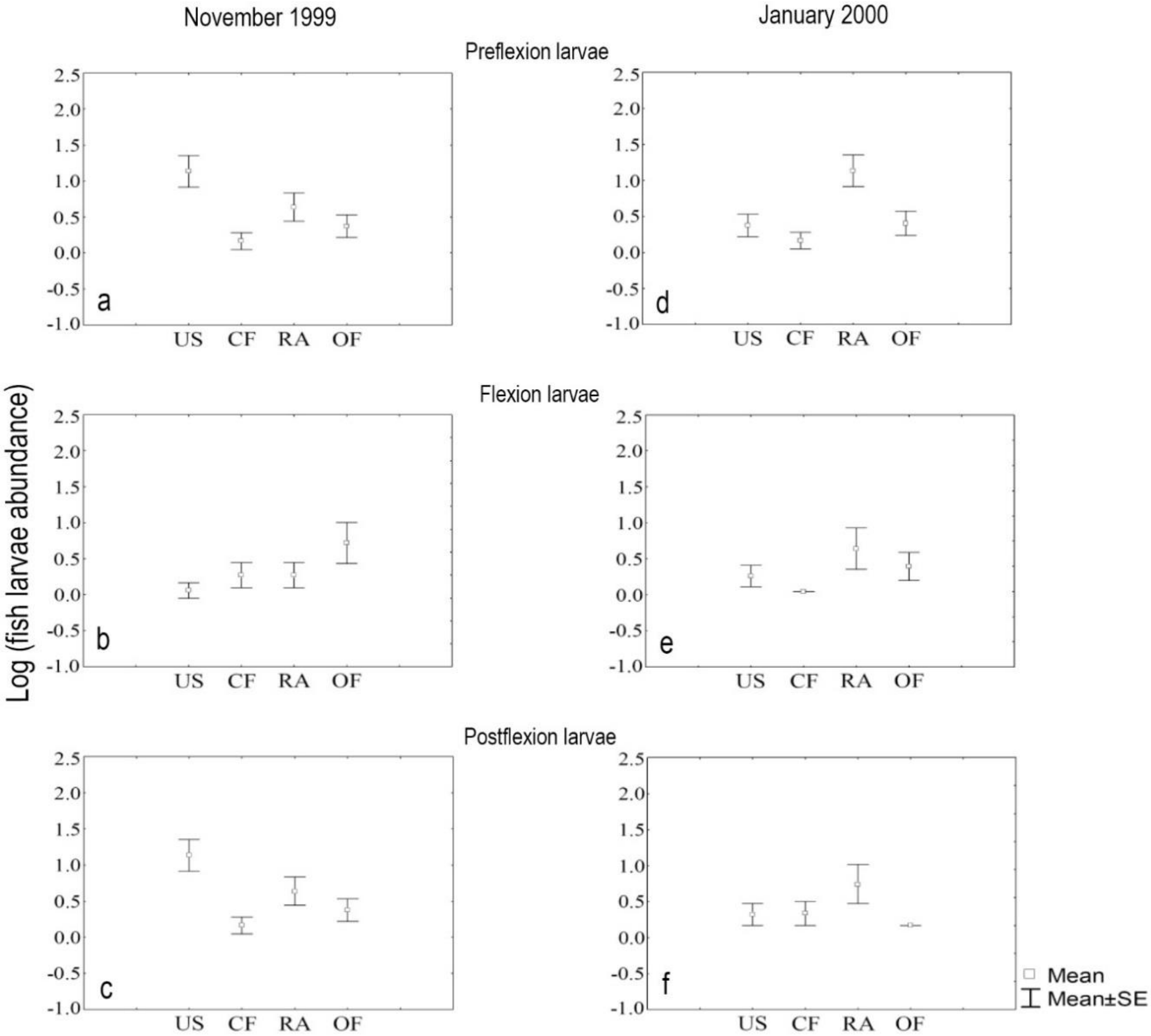

Figure 9. Early life stages of fish in relation to physical structures inside Mejillones Bay during November 1999 and January 2000. US: upwelling shadow, CF: coastal front, RA: retention area, OF: oceanic front.

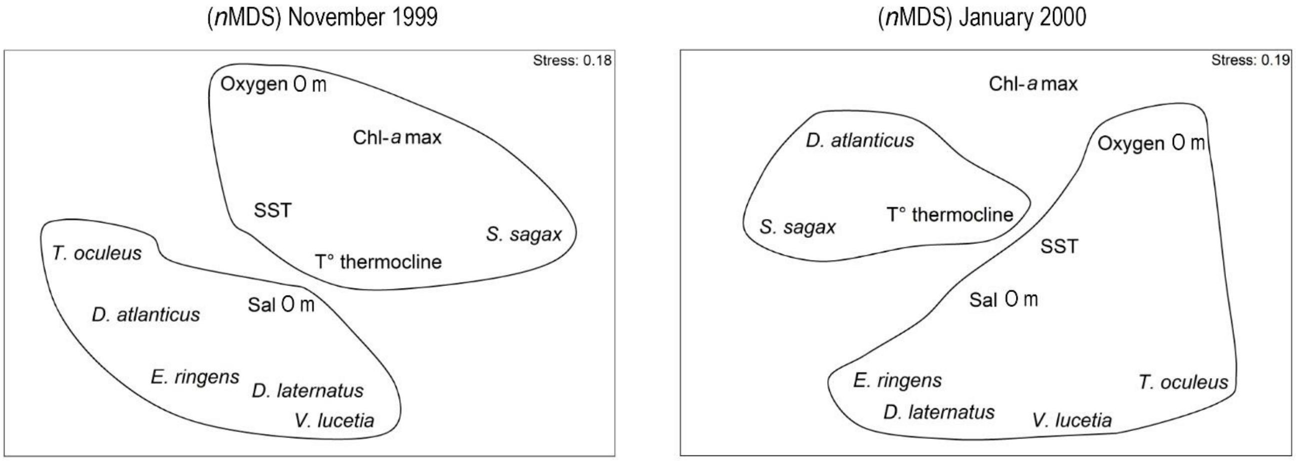

Figure 10. Projection of the physical variables with different taxas through the non-metric multidimensional scaling (*n*MDS) between fish larvae distribution and oceanographic variables during November 1999 and January 2000. SST = sea surface temperature, Chl-*a* max: maximum fluorescence, Sal 0 m: superficial salinity, Oxygen 0 m: superficial oxygen.

Table 4. Correlation coefficients R Spearman between weighted mean depths (WMDs) of single fish larval species and fish larval assemblages with the maximum fluorescence (Chl-*a* max) depth, thermocline depth and oxygen minimum zone (OMZ) depth. **P* < 0.05.

WMD	Chl-*a* max. depth	Thermocline depth	OMZ depth
E. ringens	-0.57*	-0.69*	-0.61*
S. sagax	-0.06	-0.44*	-0.43*
D. laternatus	0.31	0.26	0.32
D. atlanticus	-0.06	0.12	0.07
V. lucetia	0.46*	0.77*	0.79*
T. oculeus	0.05	0.55*	0.60*
B. nigrigenys	0.16	0.14	0.18
Lampanyctus sp.	0.27	0.04	-0.01
D. theta	0.24	0.08	0.13
M. nitidulum	-0.05	0.22	0.25
G. tenuiculus	0.03	0.10	0.06
Fish larval assemblages	0.24	0.36	0.50*

studies in other upwelling areas show the presence of thermal fronts that retain water masses near coast (Graham & Largier, 1997), double layer circulation allowing compensatory flows in the vertical plane (Wroblewski, 1982; Peterson, 1998), and eddies induced by the coastal morphology (Hutchings *et al*., 1995; Wing *et al*., 1998). Only one of these processes has been studied in Mejillones Bay (Marín *et al*., 2003), even so, our data suggests that the continuing influence of an active upwelling center into the bay might be key in the formation of a retention zone of holo- and meroplanktonic populations. Thus, the community structure and fish larvae distribution found within Mejillones Bay may be explained as the result of specific interactions between reproductive tactics and environmental conditions. For example, dominant species in adult stage shown different reproductive tactics; nearshore (*E. ringens* and *S. sagax*) and offshore spawning (*D. laternatus*, *T. oculeus*, *V. lucetia* and *B. nigrigenys*) were the more usual (Loeb & Rojas, 1988; Rodríguez-Graña & Castro, 2003).

The combined effects of coastline and bathymetry on the upwelling circulation may generate a spatially structured coastal habitat where three types (coastal, mesopelagic and bathypelagic) of fish larval assemblages can coexist. The hypothesis of feeding at rest suggests that planktivorous fish (juveniles and adults) may benefit from strong currents in locations with broad refuges during resting periods or when they are feeding passively (McFarland & Levin, 2002). This mechanism would be capable of generating "trophic focus" through a process where different preys accumulate or are trapped in big water volumes in a relatively small area. Thus, an increase in the suspended particulates concentration inside Mejillones Bay due to the entrance of deep-flows through the submarine canyon (Allen & Durrieu de Madron, 2009) as well as a marked increase in food availability during upwelling events might provide a favourable habitat for food and/or refuge not only to adult fish but also to ichthyoplanktonic communities present.

The many fish larvae with bathy-mesopelagic and epi-mesopelagic habits associated with warm waters formed a particular pattern whose limit was the frontal zone of the upwelling filament. For the same area, Rojas *et al*. (2002) found that myctophids larvae were associated with non-upwelling waters. The fish larvae distribution patterns would be the result of ecological preferences favoured by the formation of physical structures generated by upwelling circulation. Despite the high environmental heterogeneity linked to the upwelling circulation within Mejillones Bay, the distribution patterns of the coastal pelagic fish larvae in northern Chile usually show a direct relationship with high chlorophyll concentrations, since it shows high concentration (5 mg m^{-3}) from coast to 20 km offshore (Yuras *et al*., 2005), in the same areas where spawning of clupeiform fishes occur (Morales *et al*., 1996). This spatial pattern may explain the reduced starvation mortality estimated for anchovy larvae detected by Pizarro *et al*. (1998).

The distribution of early life stages inside Mejillones Bay was forced by the formation of physical structures resulting from upwelling circulation, facilitating the aggregation of preflexion fish larvae because of their lesser swimming ability. The fish larvae permanence in more advanced stages (*i.e.*, flexion and postflexion) is likely to be the result of ontogenetic migrations and/or advection processes.

However, the energetic cost to maintain its position implies the use of several food resources found in the shelf and shelf-break (Landaeta & Castro, 2002). For example, Vikebø *et al*. (2007) documented that survival of cod larvae would be directly related to the physical structures formation derived from oceanic circulation, as well as from changes during its ontogenetic development.

Effect of physical variables in the fish larvae vertical distribution

Larval fish have behavioural mechanisms that allow them to alter their position at the water column to address environmental gradients, selecting the most favourable (*i.e.*, turbulence avoidance, vertical migration; Olla & Davis, 1990). The vertical distribution of fish larvae has often been linked to the thermal stratification of the water column (Roepke *et al*., 1993; Boehlert & Mundy, 1994; Moser & Pommeranz, 1999). The thermocline is considered important as a barrier (Smith & Suthers, 1999) or as an indirect measurement of the offshore Ekman layer, that acts above or below in the vertical distribution of some fish larvae (Coombs *et al*., 1981; Davis *et al*., 1990; Olla & Davis, 1990; Rojas, 2014). The significant correlations found between the depth values of physical variables with the vertical position of some fish larvae having bathy-mesopelagic (*V. lucetia*) and epi-mesopelagic (*T. oculeus*) habits, suggest that location of the thermocline and oxygen minimum zone may have a large influence on the vertical distribution of these species. In contrast, the coefficients found for coastal pelagic larvae (*E. ringens* and *S. sagax*) suggest that the depth of the different physical variables may have a lesser effect on the vertical distribution, being forced mainly by the oceanographic conditions in the area. It should be noted that into Mejillones Bay potential investment flows due to variability of the upwelling focus, is more relevant in the upper layer (>40 m), affecting the vertical distribution of small pelagic that spawn nearshore (*E. ringens* and *S. sagax*) unlike to those species that spawn offshore where vertical distribution is influenced by strongly stratified water column.

Short, shelf-break canyons are shown to have a substantial influence on local water properties and zooplankton distribution. The observed aggregation of these planktonic organisms in November 1999 and January 2000 appears to be linked to their ability to remain at specific depths combined with advection by horizontally convergent flows in the eddy (Allen *et al*., 2001). However, changes in tidal mixing could play an important role in the vertical distribution of fish larvae inside Mejillones Bay in both periods.

Bathymetry influences fish larvae retention

The spawning of many fish species generally occurs near eddies, upwelling areas, or other directional circulations that are frequently associated with higher currents systems (Allain *et al*., 2001; Hutchings *et al*., 2002; Avendaño-Ibarra *et al*., 2013). This is an important feature because these species fix the direction of larval drift and the nursery area. Thus, the directions of larval drift as well as the nursery zone are determined by regular current systems. In the Humboldt Current System of northern Chile, the spawning of several groups of epipelagic fish is carried out in zones where the coastal geometry and topographic features could reduce the offshore transport, facilitating the nearshore retention of eggs and larvae. Moreover, the reduced wind stress and eddy kinetic energy between 20° and 30°S reduce the offshore transport along northern Chile, increasing coastal retention (Hormazábal *et al*., 2004).

Similarly, for the coastal area of Senegal, Roy (1998) suggested, using a double-cell circulation model, that retention of particles in coastal areas is the result of the interaction between upwelling circulation and bottom topography. According to this approach we generated a three dimensional conceptual model of circulation and particles retention during the upwelling season at Mejillones Bay (Fig. 11). This model assumes that circulation in the area is dominated by a southward flow, which reverses in the presence of strong upwelling conditions (Marín *et al*., 2001; Escribano *et al*., 2004). Flows 1 and 2 represent currents that move along the canyon (*i.e.*, flow 1) and due to the coastal boundary, emerge in the centre of the bay. The variation in the location of focus and upwelling fronts can, according to the topographic effect (Wolanski & Hammer, 1988), induce changes in the interaction flow/reflux water and its properties within Mejillones Bay as shown in the current velocity vectors, producing a low-speed zone (*i.e.*, retention zone).

This retention area inside Mejillones Bay is protected from the prevailing equatorial ward winds and is also the site where the filaments of coastal upwelling generated at Punta Angamos (Flow 3) are presented. The upwelling of cold-water due to flows 1 and 3 generated a thermal front, which separated the coastal upwelling water from the oceanic warm-water. This upwelling front represents an obstacle to the larvae from Phosichthyidae and Myctophidae, whereas the adjacent coastal area to the upwelling front may be dominated by coastal pelagic species, particularly *Engraulis ringens*, as well as by epi-mesopelagic fish larvae retained in a low-speed currents zone in Mejillones Bay.

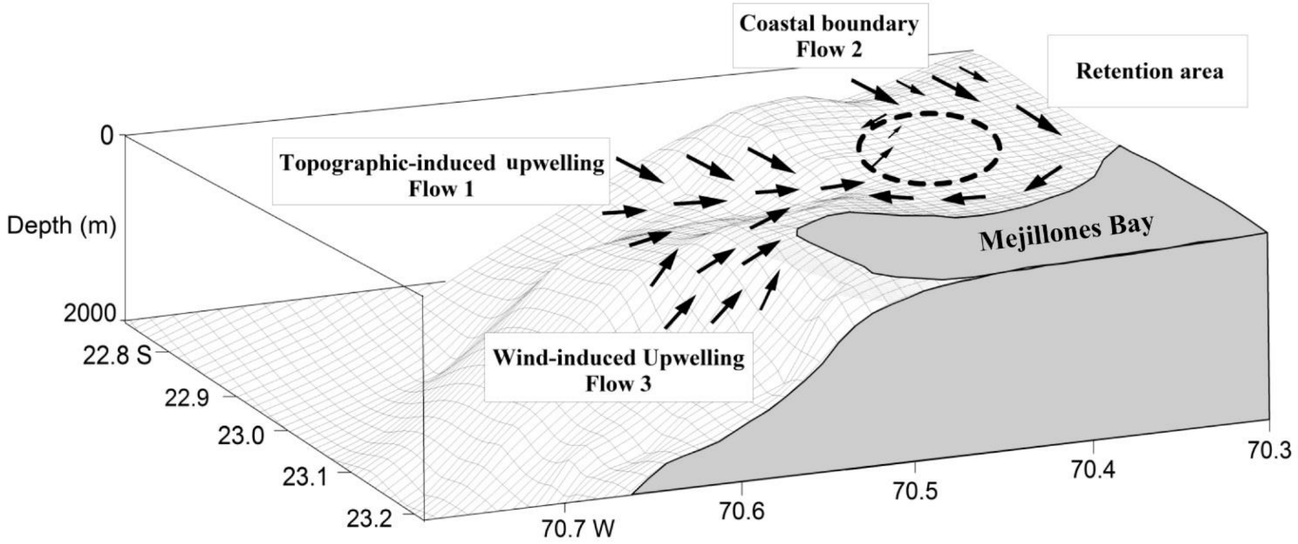

Figure 11. Conceptual model three-dimensional of coastal circulation and fish larvae retention into Mejillones Bay during November 1999 and January 2000.

The different physical structures in Mejillones Bay showed a high accumulation of fish larvae particularly near an oceanic front and a low-speed currents area, possibly as a result of the encounter between flows derived from the upwelling circulation and flows entering through the submarine canyon, affected by the presence of a seamount (Figueroa & Moffatt, 2000; Sobarzo & Djurfeldt, 2004; Morales *et al*., 2007; Sobarzo *et al*., 2007). The fish larvae associated with upwelling shadows inside Mejillones Bay confirms the important role of these structures in the accumulation of the planktonic organisms during upwelling events in *spin-up* phase off Punta Angamos (Marín *et al*., 2003).

The interaction between the current regime during upwelling events and the bathymetry, as well as the high primary productivity inside Mejillones Bay, may be responsible for the creation of a habitat that potentially increases the survival of several planktonic groups (Marín *et al*., 2001; Escribano *et al*., 2004). For example, Uda & Ishino (1958) suggest that bathymetry effect induces upwelling of deep water that favours the increase of primary production and biomass consumption on seamounts. The theory predicts that the encounter of flows with a seamount produces currents around the mountains which induce upwelling water. This reduction of flows and the change in potential vorticity, favours the formation of an anticyclonic semi-stationary eddy (*e.g.*, Taylor column) able to trap and retain particles above the seamount for some time (Huppert, 1975; Huppert & Bryan, 1976). Therefore, the occurrence of seasonal blooms and long residence time of upwelling waters are theoretically possible conditions to form a highly structured habitat.

From an ecological perspective, the different spatial patterns observed at early life stages of fish larvae would be explained by fluctuations in the oceanographic conditions, and its interaction with reproductive tactics, behavioural adaptations, and differences in the survival of different developmental stages (Palma & Silva, 2004; Landaeta *et al*., 2006; Yannicelli *et al*., 2006). Our data suggest that the pattern of distribution observed can be partially explained as the result of "specific groups" due to the interaction between the bathymetry and strong upwelling conditions, forming a complex system that including transport, retention and accumulation of fish larvae as a meso-scale. By understanding the biophysical interactions that regulate production and/or particle retention and its consequences in fish larval assemblages in these fragile upwelling ecosystems from northern Chile, we can learn to protect them from adverse antrophic effects in the future.

CONCLUSIONS

The analysis of the distribution and ichthyoplankton communities composition in Mejillones Bay (northern Chile) showed that the relationship between bathymetry and mesoscale structures during strong upwelling conditions in November 1999 and January 2000 affect the spatial distribution of the fish larvae assemblages. The fish larvae taxa showed different aggregation pattern into Mejillones Bay as a consequence of the coupling between a complex bathymetry and the coastal circulation during upwelling condition. In

January 2000, the influence of an upwelling filament into Mejillones Bay revealed a pattern of distribution more clearly unlike November 1999. This heterogeneous distribution may be explained due to the unique characteristics for refuge and feeding that provides Mejillones Bay to populations of adult fish and their early stages. The main conclusions derived from this research are as follows:

1) The conceptual model proposed provides important evidence about the influence of bathymetry and its role in the creation of areas of recirculation into Mejillones Bay during strong upwelling condition.
2) The spatial distribution of ichthyoplankton in both periods was strongly related to the mesoscale physical structure into Mejillones Bay.
3) The presence of mesoscale physical structures in November 1999 and January 2000, favours the fish larvae retention inside Mejillones Bay during upwelling conditions.
4) The small coastal species *E. ringens* and *S. sagax* is found more disperse in November 1999, while in January 2000 fish larvae were concentrated mainly in a zone of low-speed currents (retention area) within Mejillones Bay.
5) The presence of frontal zones limited of horizontal distribution of mesopelagic species *D. laternatus* and *T. oculeus* during both study period, while the presence of a marked thermocline has a significant effect on the vertical position of the larval myctophid fishes.

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REFERENCES

Allain, G., P. Petitgas & P. Lazure. 2001. The influence of mesoscale ocean processes on anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay estimated with a three-dimensional hydrodynamic mode. Fish. Oceanogr., 10(2): 151-163.

Allen, S.E & X. Durrieu de Madron. 2009. A review of the role of submarine canyons in deep-ocean exchange with the shelf. Oceanogr. Sci., 5: 607-620.

Allen, S.E., C. Vindeirinho, R.E. Thomson, M.G.G. Foreman & D.L. Mackas. 2001. Physical and biological processes over a submarine canyon during an upwelling event. Can. J. Fish. Aquat. Sci., 58: 671-684.

Avendaño-Ibarra, R., E. Godínez-Domínguez, G. Aceves-Medina, E. González-Rodríguez & A. Trasviña. 2013. Fish larvae response to biophysical changes in the Gulf of California, Mexico (Winter-Summer). J. Mar. Biol., 213: 1-17.

Balbontín, F. & M. Garretón. 1977. Desove y primeras fases de desarrollo de la sardina española, *Sardinops sagax* musica, en Valparaíso. Rev. Biol. Mar., 16(2): 171-181.

Bakun, A. 1996. Patterns in the ocean. Ocean processes and marine population dynamics. California Sea Grant Colllege System, USA, in cooperation with Centro de Investigaciones Biológicas del Norte, La Paz, Baja California Sur, 323 pp.

Bertrand, A., F. Gerlotto, S. Bertrand, M. Gutiérrez, L. Alza, A. Chipollini, E. Díaz, P. Espinoza, L. Ledesma, R. Quesquén, S. Peraltilla & F. Chavez. 2008. Schooling behaviour and environmental forcing in relation to anchoveta distribution: an analysis across multiple spatial scales. Prog. Oceanogr., 79: 264-277.

Boehlert, G.W. & B.C. Mundy. 1994. Vertical and onshore-offshore distributional patterns of tuna larvae in relation to physical habitat features. Mar. Ecol. Prog. Ser., 107: 1-13.

Bosley, K.L., J.W. Lavelle & R.D. Brodeur. 2004. Biological and physical processes in and around Astoria submarine canyon, Oregon, USA. J. Mar. Syst., 50: 21-37.

Brochier, T., C. Lett, J. Tam, P. Freon, F. Colas & P. Ayón. 2008. Anchovy early life in the northern Humboldt Current system: an individual-based model study. Prog. Oceanogr., 79: 313-325.

Brownell, C.L. 1979. Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology Rhodes University, Grahamstown, 40: 84 pp.

Coyle, K.O., A.I. Pinchuk, L.B. Eisner & J.M. Napp. 2008. Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: the potential role of water column stability and nutrients in structuring the zooplankton community. Deep-Sea Res., 55: 1755-1791.

Coombs, S.H., R.K. Pipe & C.E. Mitchell. 1981. The vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) in the eastern North Atlantic and North Sea. Rapp. P-v. Réun. Cons. Int. Explor. Mer, 178: 188-195.

Cox, T.F & M.A.A Cox. 2000. Multidimensional scaling. Monographs on statistics and applied probability. Chapman & Hall/ CRC, Boca Raton, 328 pp.

Christensen, A., U. Daewel & H. Jensen. 2007. Hydrodynamic backtracking of fish larvae by individual-based modelling. Mar. Ecol. Prog. Ser., 347: 221-232.

Davis, T.L.O., G.P. Jenkins & J.W. Young. 1990. Diel patterns of vertical distribution in larvae of southern bluefin *Thunnus maccoyii*, and other tuna in the East Indian Ocean. Mar. Ecol. Prog. Ser., 59: 63-74.

Dower, J.F. & R.D. Brodeur. 2004. The role of biophysical coupling in concentrating marine organisms around shallow topographies. J. Mar. Syst., 50: 1-2.

Dower, J.F., T.J. Miller & W.C. Leggett. 1997. The role of microscale turbulence in the feeding ecology of fish larval. Adv. Mar. Biol., 31: 169-220.

Escribano, R. 1998. Population dynamics of *Calanus chilensis* in the Chilean eastern boundary Humboldt Current. Fish. Oceanogr**.** 7(3/4): 245-251.

Escribano, R. & I.A. McLaren. 1999. Production of *Calanus chilensis* in the upwelling area of Antofagasta, northern Chile. Mar. Ecol. Prog. Ser., 177: 147-156.

Escribano, R. & P. Hidalgo. 2000. Spatial distribution of copepods during coastal upwelling in a northern area of the eastern Boundary Humboldt Current. J. Mar. Biol. Assoc. UK, 80: 283-290.

Escribano, R., V. Marín & P. Hidalgo. 2001. The influence of coastal upwelling on the distribution of *Calanus chilensis* in the Mejillones Peninsula (northern Chile): implications for its population dynamics. Hydrobiologia, 453(454): 143-151.

Escribano, R., S. Rosales & J.L. Blanco. 2004. Understanding upwelling circulation off Antofagasta (northern Chile): a three-dimensional numerical-modelling approach. Cont. Shelf. Res., 24: 37-53.

Figueroa, D. & C. Moffat. 2000. On the influence of topography in the induction of coastal upwelling along the Chilean coast. Geophys. Res. Lett., 27: 3905-3908.

Fischer, W. 1958. Huevos, crías y primeras pre-larvas de la “anchoveta” (*Engraulis ringens*) Jenyns. Rev. Biol. Mar., 8(1-3): 111-124.

Fischer, W. 1959. Huevos, crías y prelarvas de la merluza (*Merluccius gayi*). Rev. Biol. Mar., 8: 224-249.

Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst., 50: 3-20.

González, R.R. & R.A. Quiñones. 2002. LDH activity in *Euphausia mucronata* and *Calanus chilensis*: implications for vertical migration behaviour. J. Plankton Res., 24(12): 1349-1356.

Graham, W.M. & J.L. Largier. 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Cont. Shelf Res., 17: 509-532.

Gronkjaer, P. & K. Wieland. 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Mar. Ecol. Prog. Ser., 154: 91-105.

Hays, W.L. 1981. Statistics. Holt, Rinehart & Winston, New York, pp. 108-141.

Herrera, L. & R. Escribano. 2006. Factors structuring the phytoplankton community in the upwelling site off El Loa River in northern Chile. J. Mar. Syst., 61: 13-38.

Hormazábal, S., G. Shaffer & O. Leth. 2004. Coastal transition zone off Chile. J. Geophys. Res., 109: C01021: 1-13.

Huppert, H.E. 1975. Some remarks on the initiation of inertial Taylor columns. J. Fluid Mech., 67: 397- 412.

Huppert, H.E. & K. Bryan. 1976. Topographically generated eddies. Deep-Sea Res., 23: 655-679.

Hutching, L. 1992. Fish harvesting in a variable, productive environmental-searching for rules or searching for excepcion? In: A.I.L. Payne, K.H. Brink, K. Mann & R. Hilborn (eds.). Benguela trophic functioning. S. Afr. J. Mar. Sci., 12: 279-318.

Hutching, L., G.C. Pitcher, T.A. Probin & G.W. Bailey. 1995. The chemical and biological consequences of coastal upwelling. Upwelling in the ocean: modern processes and ancient records. In: C.P. Summerhayes, K.-C. Emeis, M.V. Angel, R.L. Smith & B. Zeitzchel (eds.). Dhalem Workshop Reports. John Wiley & Sons, New York, pp. 65-82.

Hutchings, L., L.E. Beckley, M.H. Griffiths, M.J. Roberts, S. Sundby & C. Van der Lingen. 2002. Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. Mar. Fresh. Res., 53: 307-318.

Kunze, E., L.K. Rosenfeld., G.S. Carter & M.C. Gregg. 2002. Internal waves in Monterey submarine canyon. J. Phys. Oceanogr., 32(6): 1890-1913.

Landaeta, M.F. & L.R. Castro. 2002. Spring spawning and early nursery zone of the mesopelagic fish *Maurolicus parvipinnis* at the coastal upwelling zone off Talcahuano, central Chile. Mar. Ecol. Prog. Ser., 226: 179-191.

Landaeta, M.F. & L.R. Castro. 2006. Spawning and larval survival of the Chilean hake *Merluccius gayi* under later summer conditions in the Gulf of Arauco, central Chile. Fish. Res., 77: 115-121.

Landaeta, M.F., G.A. Herrera, M. Pedraza, C.A. Bustos & L.R. Castro. 2006. Reproductive tactics and larval development of bigeye flounder, *Hippoglossina* *macrops* off central Chile. J. Mar. Biol. Assoc. UK, 86: 1253-1264.

Lee, J-Y., K. Dong-Jin, K. Il-Nam, R. Taekeun, L. Tongsup, K. Chang-Keun & K. Kyung-Ryul. 2009. Spatial and temporal variability in the pelagic ecosystem of the East Sea (Sea of Japan): a review. J. Mar. Syst., 78: 288-300.

Le Fevre, J. 1986. Aspects of the biology of frontal systems. Adv. Mar. Biol., 23: 163-299.

León-Chávez, C.A., L. Sánchez-Velasco, E. Beier, M.F. Lavín, V.M. Godínez & J. Färber-Lorda. 2010. Larval fish assemblages and circulation in the Eastern Tropical Pacific in autumn and Winter. J. Plankton Res., 32: 397-410.

Loeb, V. & O. Rojas. 1988. Interanual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964-83. Fish. Bull., 86(1): 1-24.

Logerwell, E. & P. Smith. 2001. Mesoescale eddies of late stage Pacific sardine (*Sardinops sagax*) larvae. Fish. Oceanogr., 10(1): 13-25.

Lutjeharms, J.R.E. & P.L. Stockton. 1987. Kinematics of the upwelling front off southern Africa. S. Afr. J. Mar. Sci., 5: 35-49.

MacKenzie, B.R. 2000. Turbulence, larval fish ecology and fisheries recruitment: a review of field studies. Acta Oceanol., 23: 357-375.

McFarland, W. & S.A. Levin. 2002. Modelling the effects of current on prey acquisition in planktivorous fishes. Mar. Fresh. Behav. Phys., 35: 69-85.

Mann, K.H. & J.R.N. Lazier. 1991. Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Scientific Publications, Boston, 466 pp.

Marín, V., L.E. Delgado & R. Escribano. 2003. Upwelling shadows at Mejillones Bay (northern Chilean coast): a remote sensing *in situ* analysis. Invest. Mar., Valparaíso, 31(2): 47-55.

Marín, V., L. Rodríguez, L. Vallejo, J. Fuenteseca & E. Oyarce. 1993. Efectos de la surgencia costera sobre la productividad primaria de Bahía Mejillones del sur (Antofagasta, Chile). Rev. Chil. Hist. Nat., 66: 479-491.

Marín, V., R. Escribano, L.E. Delgado, G. Olivares & P. Hidalgo. 2001. Nearshore circulation in a coastal upwelling site off the northern Humboldt Current System. Cont. Shelf Res., 21: 1317-1329.

Morales, C.E., H.E. González & S.E. Hormazabal. 2007. The distribution of chlorophyll-*a* and dominant planktonic components in the coastal transition zone off Concepción, central Chile, during different oceanographic conditions. Prog. Oceanogr., 75: 452-469.

Morales, C.E., M. Braun, H. Reyes, J.L. Blanco & A. Davies. 1996. Anchovy larval distribution in the coastal zone off northern Chile: the effect of low dissolved oxygen concentration and of a cold-warm sequence 1990-95. Invest. Mar., Valparaíso, 24: 77-96.

Moser, H.G & E.H. Ahlstrom. 1970. Development of lanternfishes (Family Myctophidae) in the California Current. Part. I. Species with narrow-eyed larvae. Bull. Los Angeles County Mus. Nat. Hist., Sci., 7: 145 pp.

Moser, H.G & E.H. Ahlstrom. 1974. Role of larval stages in systematic investigations of marine teleosts: the Myctophidae, case study. Fish. Bull., 72(2): 391-413.

Moser, H.G. & E.H. Ahlstrom. 1996. The early stages of fishes in the California Current Region. In: H.G. Moser (ed.). CalCOFI Atlas No. 33, National Marine Fisheries Service Southwest Fisheries Science Center, La Jolla, California, 1505 pp.

Moser, H.G. & T. Pommeranz. 1999. Vertical distribution of eggs and larvae of northern anchovy, *Engraulis mordax*, and of the larvae of associated fishes at two sites in the Southern California Bight. Fish. Bull., 97: 920-943.

Olla, B.L. & M.W. Davis. 1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser., 63: 105-112.

Orellana, M.C & F. Balbontín. 1983. Estudio comparativo de las larvas de clupeiformes de la costa de Chile. Rev. Biol. Mar., Valparaíso, 19(1): 1-46.

Palma, S. & N. Silva. 2004. Distribution of siphonophores, chaetognaths, euphausiids and oceanogra-phic conditions in the fjords and channels of southern Chile. Deep-Sea Res. II, 51: 513-535.

Palma, A.T., L.M. Pardo & R. Veas. 2006. Coastal brachyuran decapods: settlement and recruitment under contrasting coastal geometry conditions. Mar. Ecol. Prog. Ser., 316: 139-153.

Parada, C., C.D. Van der Lingen, C. Mullon & P. Penven. 2003. Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. Fish. Oceanogr., 12(3): 1-15.

Parada, C., C. Mullon, C. Roy, P. Fréon, L. Hutchings & C.D. Van der Lingen. 2008. Does vertical migratory behaviour retain fish larvae onshore in upwelling ecosystems? A modelling study of anchovy in the southern Benguela. Afr. J. Mar. Sci., 30(3): 437-452.

Peterson, W. 1998. Life cycle strategies of copepods in coastal upwelling zones. J. Mar. Sys., 15: 313-326.

Pineda, J. 1999. Circulation and larval distribution in internal tidal bore warm fronts. Limnol. Oceanogr., 44: 1400-1414.

Pizarro, J., W. Palma & C. Flores. 1998. Validación de la hipótesis de mortalidad por inanición en larvas de *Engraulis ringens* Jenyns, 1842 (Pisces: Engraulidae) utilizando el criterio histológico en un área de surgencia costera en el norte de Chile. Invest. Mar., Valparaíso, 26: 97-108.

Pringle, J.M. 2007. Turbulence avoidance and the wind-driven transport of plankton in the surface Ekman layer. Cont. Shelf Res., 27: 670-678.

Porter, SM., L. Ciannelli & N. Hillgruber. 2005. Environmental factors influencing larval walleye pollock *Theragra chalcogramma* feeding in Alaskan waters. Mar. Ecol. Prog. Ser., 302: 207-217.

Rodríguez-Graña, L. & L. Castro. 2003. Ichthyoplankton distribution off the Peninsula de Mejillones, Chile (23ºS, 71ºW), under variable hydrographic conditions during the austral summer and winter of the 1997 El Niño. Hydrobiologia, 501: 59-73.

Roepke, A., W. Nellen & U. Piatkowski. 1993. A comparative study on the influence of the pycnocline on the vertical distribution of fish larvae and cephalopod paralarvae in three ecologically different areas of the Arabian Sea. Deep-Sea Res. II, 40: 801-819.

Rojas, P. 2014. Diel variation in the vertical distribution of fish larvae forced by upwelling filaments off Punta Angamos (northern Chile). Lat. Am. J. Aquat. Res., 42(3): 401-417.

Rojas, P., R. Escribano & V. Marín. 2002. Fish larvae distribution off Mejillones Peninsula (northern Chile) during a coastal upwelling event in spring 1999: interactions with the cold upwelling plume. Fish. Oceanogr., 11(4): 233-244.

Rojas, P., M. Landaeta & R. Ulloa. 2011. Changes in the spatial distribution of eggs and larval anchoveta (*Engraulis ringens*) off northern Chile before and during the 1997-1998 El Niño Event. Rev. Biol. Mar. Oceanogr., 46(3): 405-419.

Roy, C. 1998. An upwelling-induced retention area off Senegal: a mechanism to link upwelling and retention processes. S. Afr. J. Mar. Sci., 19: 89-98.

Sabatés, A., J. Salat & M. Masó. 2004. Spatial heterogeneity of fish larvae across a meandering current in the northwestern Mediterranean. Deep-Sea Res. I., 51: 545-557.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, 252 pp.

Smith, K.A. & I.M. Suthers. 1999. Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf. Mar. Ecol. Prog. Ser., 176: 49-62.

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Sobarzo, M. & L. Djurfeldt. 2004. Coastal upwelling process on a continental shelf limited by submarine canyons, Concepción, central Chile. J. Geophys. Res., 109(C12): C12012.1-C12012.20.

Sobarzo, M., L. Bravo & D. Donoso. 2007. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Prog. Oceanogr., 75: 363-382.

Strub, P.T., J.M. Mesias & V. Montecino. 1998. Coastal ocean circulation off western South America. Coastal segment (6, E). In: A.R. Robinson & K.H. Brink (eds.). The Sea, 11: 273-308.

Strub, P.T., P.M. Kosro & A. Huyer. 1991. The nature of the cold filaments in the California Current System. J. Geophys. Res., 96: 14743-14768.

Uda, M. & M. Ishino. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo Univ. Fish., 1-2: 105-119.

Vaz, A.C., C.E. Parada, E.D. Palma, J.H. Muelbert & J.D. Campos. 2007. Modeling transport and retention of *Engraulis anchoita* Hubbs & Marini, 1935 (Clupeiformes, Engraulidae) early life stages along the Central Southwestern Atlantic continental shelf. Pan. Am. J. Aquat. Sci., 2(2): 179-190.

Vikebø, F., C. Jørgensen, T. Kristiansen & Ø. Fiksen. 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. Mar. Ecol. Prog. Ser., 347: 207-219.

Vikebø, F., S. Sundby, B. Ådlandsvik & Ø. Fiksen. 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. ICES J. Mar. Sci., 62: 1375-1386.

Wing, S.R., L.W. Bostford, S.L. Ralston & J.L. Largier. 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnol. Oceanogr., 43(7): 1710-1721.

Wolanski, E. & W. Hamner. 1988. Topographically controlled fronts in the ocean and their biological influence. Science, 241: 177-181.

Wroblewski, J.S. 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone -a simulation. Deep-Sea Res., 29: 665-686.

Yannicelli, B., L. Castro, W. Schneider & M. Sobarzo. 2006. Crustacean larvae distribution in the coastal upwelling zone off central Chile. Mar. Ecol. Prog. Ser., 319: 175-189.

Yuras, G., O. Ulloa & S. Hormazabal. 2005. On the annual cycle of coastal and open ocean satellite chlorophyll off Chile (18°-40°S). Geophys. Res. Lett., 32: 1029-1033.